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THE EFFECTS OF INBREEDING AND CROSSBREEDING UPON DEVELOPMENT

BY

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INTRODUCTION.

Among the higher seed plants certain groups are characterized by almost universal and continuous self-fertilization. On the other hand certain other groups are completely, or to a large extent, cross-fertilized in every generation. Between these two extremes every gradation in the degree of self- and cross-fertilization can be illustrated. The structure and function of the floral organs have become more or less clearly adapted to the customary mode of sexual reproduction characteristic of each species. In the thallophytes, bryophytes and pteridophytes much the same situation exists whereby the gametes which enter into a sexual fusion may arise either from the same or from different organisms.

In the lower animals the same variation in the mode of sexual reproduction exists as in plants. Among the higher animals, however, hermaphroditism is replaced entirely by bisexuality; and sexual reproduction, except when parthenogenesis takes place, results only from the union of gametes originating in different organisms.

This array of facts has naturally led to searching inquiries as to the purpose of sexual reproduction as compared to other methods of propagation as well as to the effects of artificial inbreeding in bisexual animals and in naturally cross-fertilized plants. Bound up with this latter problem is that which is concerned with the effects of cross-fertilization in all types of animals and plants of different degrees of relationship.

The development of the Mendelian theory of heredity, carrying with it the conception of definable, hereditary units which are sufficiently stable in their transmission from generation to generation to be recognized and their somatic expression to be described,

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has made possible an attack upon these problems which has opened a way towards their solution.

From the knowledge of alternate inheritance it is possible to ascribe, very definitely and surely, certain of the results of inbreeding to the segregation and isolation of hereditary factors which results were formerly thought to be due solely to inbreeding as a cause in itself. Certain pathological, abnormal or otherwise undesirable conditions occurring more frequently in animals and plants produced by matings between nearly related individuals were formerly attributed to inbreeding as the cause, and it was thought that inbreeding must always show such undesirable results. It is now known that many of these pathological and abnormal conditions resulting from inbreeding do not owe their origin to that process, but are due solely to the segregation, into a pure state of the hereditary factors causing the anomalies which factors were present in the organisms previous to their being inbred. Inbreeding, then, has nothing to do with the origin of the undesirable characters under consideration but merely brings them into visible expression, and whether or not they appear depends upon their presence originally in the stock before inbreeding takes place. There still remains a conviction, however, that all the manifestations attending inbreeding and the converse effects of cross breeding cannot be accounted for solely on the basis of the operation of definable, hereditary factors, but that there is a stimulating effect resulting from crossing, which is lost by inbreeding, and that this stimulation differs somewhat from the expression of hereditary factors which can be transferred and fixed in different organisms. This stimulation is supposed to be of a physiological nature appearing when dissimilar germ-plasms are united, and disappearing as the germinal heterogeneity disappears in subsequent recombinations.

Since this physiological stimulation has always been purely hypothetical, having never been definitely proven, and since it has been used to account for certain facts heretofore inexplicable in any other way, the existence of such a stimulation may fairly be questioned, in so far as the facts can be logically accounted for in other ways. Recent advances in the knowledge of the methods of inheritance have made it possible to meet certain objections previously held against the view that the effects of inbreeding and crossbreeding can be attributed solely to the

operation of hereditary factors without assuming an additional hypothetical stimulation.

Some of the previous work bearing upon the effects of inbreeding and crossbreeding is reviewed here and with this are given original data obtained from the naturally cross-fertilized corn plant, *Zea mays* L. The facts at hand co-ordinate with the existing knowledge of heredity in such a way that it seems to the writer unnecessary any longer to make the fundamental distinction between the effects of inbreeding and crossbreeding and of heredity in development.

No attempt is made to canvas the extensive literature on hybridization (a bibliography of which alone would fill a volume) in order to list all the cases in which crossing does or does not result in increased development and inbreeding in a reduction. It does not take one long in reading over the many published results of crossing in animals and plants to become convinced that an increase in development following a cross is a frequent occurrence. It is hoped that sufficient references are given to show something as to the universality and nature of the phenomenon and a review of the more important contributions is made in order to sketch briefly the development of the ideas concerning the cause of the stimulation and the part it has played in evolution and in breeding practice.

The experiments on inbreeding, which have resulted in the material from which the data given here have been gathered, were started by Professor E. M. East at the Connecticut Agricultural Experiment Station and carried on by him and subsequently by Professor H. K. Hayes and later by the writer. From time to time reports on these experiments have been made and conclusions drawn from the facts as observed. These include various publications under the titles "Inbreeding in Corn," "The Distinction between Development and Heredity in Inbreeding" published by Professor East in the Report of the Connecticut Experiment Station and in the American Naturalist and "Heterozygosis in Evolution and in Plant Breeding" by Professors East and Hayes in a Bureau of Plant Industry bulletin. Under the title of "Dominance of Linked Factors as a Means of Accounting for Heterosis" the writer had proposed a different view as to the cause of hybrid vigor. This was published in Genetics and its application is discussed here in more detail.

Further publications are planned which will discuss more adequately much of the data which are scantily treated here.

The significance which these investigations may have for the practical improvement of plants and animals has only been briefly alluded to here. This phase of the subject has been reserved for another time when the methods which have suggested themselves as the result of these investigations have been more thoroughly tested. Finally this collection of facts and theories should be viewed as a report of progress rather than a well rounded presentation of the subject of inbreeding and crossbreeding.

The writer is especially indebted to his predecessors whose work has made these experiments possible. Grateful acknowledgement is due Dr. E. M. East for his careful supervision of the work and for his kindly advice and helpful criticism as to the presentation of the results obtained. The writer alone, however, must assume the responsibility for the opinions expressed. Much credit is due Mr. C. D. Hubbell, Dr. Charles Drechsler and Mr. G. A. Adsit for their careful assistance in the collection and preparation of the data.

DEFINITIONS.

The knowledge of a stimulating effect resulting from a cross between different animals and between different plants which gives progeny which may excel their parents in general vigor, size or other visible characteristics has naturally led to the use of terms to describe this effect. This stimulation is variously spoken of as "vigor due to crossing" or "hybrid vigor." Since hybrid vigor occurs only in crosses of which the parents are dissimilar in hereditary constitution more exact and comprehensive terms were needed. The zygote resulting from a union of unlike gametes is spoken of as a heterozygote (following the usage of Bateson), hence the term heterozygosis (used by Spillman, '09) refers to that germinal heterogeneity which results from the union of unlike gametes, and the stimulation to development which accompanies such a condition is spoken of as a "stimulus of heterozygosis," or "heterozygotic stimulation," meaning the stimulating effects of hybridity or the stimulation due to differences in uniting gametes. The converse fact of a reduction in vigor accompanying a return to a homozygous condition is therefore said to be due to, or result from, homozygosis. Shull ('14) has proposed the term "heterosis" to designate this increase in development which may result from a heterozygous condition; hence, heterosis, as used here, will be considered synonymous with "hybrid vigor" or "stimulus accompanying heterozygosis," in whatever form this may be manifested or whatever cause or causes it may be due to. Shull proposed this term, as he says, ". . . . to avoid the implication that all the genotypic differences which stimulate cell-division, growth, and other physiological activities of an organism, are Mendelian in their inheritance and also to gain in brevity of expression. . . ." Hence the term heterosis is not meant as a mere contraction of heterozygosis and is not synonymous with it. The adjective "heterotic" has also been proposed and such an expression as "heterotic stimulation" is synonymous with heterosis.

EARLY INVESTIGATIONS WITH PLANTS.

Certain evidence remains from the carvings of the ancient Egyptians to show that they had some conception of a sexuality in plants. However, it was not until the last of the 17th century, when Camerarius first demonstrated such condition, that interest in the production of artificial hybrids began. It is significant that the first artificial hybrids to be systematically studied, those of Kölreuter (1776), furnished some of the best examples of heterosis. Kölreuter made many interspecific crosses in *Nicotiana, Dianthus, Verbascum, Mirabilis, Datura and others*, many of which astonished their producer by their greater size, increased number of flowers and general vegetative vigor, as compared to the parental species entering into the cross. Concerning one of the tobacco crosses he says: (pp. 57–58) "Hybrids obtained from the cross of *Nicotiana maj.* ♀ and *glut.* ♂ produced a far greater number of flowers and grew to an uncommonly greater height and a much greater circumference than the pure species under the same conditions; the height of the plants which were kept in the hot bed or were set out in the field after they had obtained full growth, amounted to eight feet and 1 to 10 inches; the whole circumference of the branches to 24 feet; the largest diameter of the stalks from 2 inches to 2 inches and 3 lines; and the largest leaves were 2 feet, 2 inches and 9 lines long and 1 foot and 4 inches wide. Never has anyone seen more magnificent tobacco plants than these were."

Thomas Andrew Knight (1799) was one among several at that time who experimented with hybrids with the view of producing more desirable varieties of vegetables, flowers and fruits. Knight observed many instances of high vigor resulting from crossing; among these we note the following remarks about a cross between two varieties of peas.

> (P. 200) "By introducing the farina of the largest and most luxuriant kinds into the blossoms of the most diminutive and by reversing this process, I found that the powers of the male and female in their effects on the offspring, are exactly equal. The vigor of the growth, the size of the seeds produced, and the season of maturity, were the same, though the one was a very early, and the other a very late variety. I had, in this experiment, a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet; whilst the height of the large and luxuriant kind was very little diminished."

It is evident that, in these crosses, Knight was dealing with dwarf and standard peas and the dominance of standardness is expected. A sufficient number of cases, however, were observed in which the crosses were more vigorous than an average of the parents to convince him that "nature intended that a sexual intercourse should take place between neighboring plants of the same species." It was this principle which Darwin elaborated 50 years later.

Sageret ('26) reports vigorous hybrids in *Nicotiana* and also between different types of the Cucurbitaceae. Among other things he notes that in human crosses between one individual which shows a hereditary pathological condition and a normal individual, that the disease disappeared in the first generation but reappeared in the second and following generations. Wiegmann ('28) gives instances of hybrids in the Cruciferae which showed distinct evidences of heterosis.

Probably the most extensive series of experiments on hybridization were those of Gärtner ('49) and of Focke ('81). According to Lindley ('52) Gärtner made 10,000 crosses between 700 different species and produced 250 different hybrids. Many of these hybrids showed distinct evidences of heterosis, and this phenomenon was manifested in many different ways. Gärtner speaks especially of their general vegetative luxuriance, increase in root development, in height, in number of flowers and their hardiness and early and prolonged blooming. Focke made equally extensive observations and catalogues his own experiments with many of those made previously. His valuable book shows clearly that the phenomenon of heterosis is widespread and may be expected in the gymnosperms and pteridophytes as well as in the angiosperms. Both the works of Gärtner and of Focke have been so thoroughly reviewed in recent times (East and Hayes '12) in connection with the problem in hand that it would be a needless repetition to say more about their results here. Special points in their observations, as they supplement the experiments recorded here, will be referred to later.

While the work of Gärtner and Focke must always rank high as contributions to our knowledge of genetics one cannot refrain from remarking that they both missed by their extensive studies of many species the point which Mendel discovered by his intensive and careful study in one species.

Naudin ('65) next to Mendel will always be remembered, no doubt, as the first to conceive of a method in the uniformity of the first generation and the variability of the second. His conception of the segregation of parental qualities as a whole leads up naturally to Mendel's law whereby the characters of the parents segregate as units and when finally appreciated the chaotic observations of Gärtner, Focke and their contemporaries began to be understood as orderly facts. In Naudin's classical experiments there are many excellent examples of heterosis. Out of 36 interspecific crosses which he made in *Papaver*, *Mirabilis*, *Primula*, *Datura*, *Nicotiana*, *Petunia*, *Digitalis*, *Linaria*, *Luffa*, *Coccinea* and *Cucumis*, 24 show positive evidence of heterosis. Among the most notable crosses in this respect was that of *Datura Stramonium* with *D. Tatula* in which both reciprocal hybrids were twice as tall as either parent. Concerning the Datura crosses Naudin says:

> "A shape very much taller than the two parental types, and the premature falling off of the flowers in the first dichotomies, which leads to tardy fructification are the principal characteristics of this hybrid of which all the plants in the collection present the greatest uniformity. We shall see that these different characteristics appear in all the hybrids of this section of the genus Datura."

Mendel ('65) also records instances of heterosis in his pea hybrids as is shown in the following passage:

"The longer of the two parental stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different lengths are crossed. Thus, for instance, in repeated experiments, stems of 1 foot and 6 feet in length yileded without exception hybrids which varied in length between 6 feet and 7½ feet."

THE OBSERVATIONS OF DARWIN UPON PLANTS.

Of all the contributors to our knowledge of the effects of inbreeding and crossbreeding no one has collected as many facts as Darwin ('75, '77). Although undoubtedly much confusion and misunderstanding have resulted from Darwin's conclusions on this problem, one cannot but admire his painstaking efforts to accumulate facts from the behavior of many species of plants through many generations of crossing and selfing before advancing his conclusions. No one was more frank to acknowledge the discrepancies between the facts as he found them and the conclusions he drew from them. Those parts of his results which were not clear to Darwin are clearer to us through our knowledge of Mendelism of which he was not permitted to know. Since his method of experimentation, and the results obtained are familiar to all interested in the problem at hand no extensive review of his work is necessary. Only a brief summary of the results obtained and the conclusions which he drew from them will be given here, reserving a more detailed review of special parts for a later part of this paper.

Among animal breeders in Darwin's time it was a common belief that whatever evil effects resulted from more or less close inbreeding were due to the accumulation of abnormal, diseased, or morbid tendencies in the offspring of parents which possessed such tendencies. Darwin refused to ascribe any large part of the effects of inbreeding to this cause because he knew so many cases were weakened and reduced types of both plants and animals which gave vigorous progeny when crossed among themselves. Instead of an accumulation of the undesirable traits of both parents the very reverse seemed to be true. Had Darwin known of the way by which recessive characters may exist for many generations without making their appearance, doubtless his views on this point would have differed materially.

Darwin clearly thought that the evil effects of inbreeding kept on accumulating until eventually a plant or animal propagated

in that manner was doomed to extinction. His own results came far short of proving such an assumption. The two wild plants with which inbreeding was practiced the longest—*Ipomea* and *Mimulus*—showed very little further loss of vigor after the first generation. What these experiments did show, most clearly, was that there was segregation of the inbred stock into diverse types which differed in minor, visible, heriditary characters and which also differed in their ability to grow. In both species plants appeared which were superior to other plants derived from the same source and some were even equal or superior in vigor to the original cross-pollinated stock. They differed from this race, however, most noticeably in the uniformity of all visible characteristics.

After several generations of inbreeding Darwin found that it made no difference in the resulting vigor, whether the plants in an inbred lot were selfed or were crossed among themselves. This he correctly attributed to the fact that the members of such an inbred strain had become germinally alike. From his views on the effect of the environment on organisms, it is easy to see why he attributed this approach to similarity in inherited qualities to the fact that the plants were grown for several generations under the same conditions. This view he thought was supported by the fact that crosses of his selfed lines with the intercrossed lines (also inbred, but to a less degree) did not give as great increase in vigor as the crosses of either lines with a fresh stock from distant regions. The crosses between two inbred lines did give a noticeable increase in vigor, in many cases, equaling the original variety. This is illustrated in the *Dianthus* crosses in which the selfed line was crossed with the intercrossed line and with a fresh stock. The ratio of both crosses to the selfed plants in height, number of capsules and weight of seed produced is as follows:

	Selfed X Inter-crossed	Selfed X Fresh stock
Height, compared to selfed................	100:95	100:81
No. Capsules, compared to selfed...........	100:67	100:39
Weight of seed, compared to selfed..........	100:73	100:33

Like Darwin we now attribute the greater increase of vigor in a cross with distinct stocks to a greater germinal diversity although we may differ in our ideas as to the way in which that diversity was brought about. Whatever may be the explanation of that, credit is due Darwin for being the first to see that it was not the mere act of crossing which induced vigor but the union of different germinal complexes. This he states clearly in the following sentences (Cross and Self Fert., p. 270):

> "These several cases taken together show us in the clearest manner that it is not the mere crossing of any two individuals which is beneficial to the offspring. The benefit thus derived depends on the plants which are united differing in some manner, and there can hardly be a doubt that it is in the constitution or nature of the sexual elements. Anyhow, it is certain that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during the several generations to different conditions."

Recent Investigations with Plants.

Although Darwin was the first to attack the problem from the standpoint of determining the effects of inbreeding, it is doubtful if he clearly recognized that the same phenomenon was concerned in both inbreeding and crossbreeding. It remained for Shull ('08, '09, '10, '11 and '14), East ('08, '09) and East and Hayes ('12) to bring out clearly the fundamental similarity of both processes and to put the matter in such a light that a far clearer understanding of the nature of the effects of inbreeding has resulted.

Their conclusions in regard to the causes of the effects of inbreeding and crossing were for the most part entirely new and dependent for their support upon the Mendelian principle of the segregation and recombination of inherited qualities as independent units and upon Johannsen's genotype conception of heredity. Stated briefly their main tenets, based upon their own careful experiments and a survey of previous results bearing upon the problem, are as follows:

1. Inbreeding automatically sorts out into homozygous, pure breeding lines, the diverse and variating complex of hereditary characters found in a naturally cross-pollinated species.

2. Although complete homozygosity is difficult to attain in practice, after several generations of selfing, members of the resulting inbred lines are uniform among themselves but the respective lines may differ greatly among each other in visible hereditary characters. The strains may also differ in their power of development, some being larger, stronger and more productive than others at normal maturity. Some individuals are often isolated which are so lacking in necessary characters that they perish because of inability to reproduce themselves.

3. Those inbred strains which are able to survive finally become constant; no further reduction in vigor or change in visible characters is to be expected by continued inbreeding. These constant types are thus quite comparable to naturally self-fertilized species and may exist indefinitely.

4. When these pure breeding types are crossed there is commonly an immediate and striking increase in general size and vigor to be expected in the resulting first hybrid generation.

To account for this increase in development, following a cross, a physiological stimulation was postulated which accompanied heterozygosity of hereditary factors and disappeared as the organisms approached homozygosity. As an illustration the union of factor "A" with it allelomorph "a" was considered to evolve developmental energy which was lacking when either "A" or "a" were united with themselves. This stimulus to development was considered to be due to the union of unlike factors alone and to have an effect quite different from whatever part each factor had by itself in the development of the organism. Stated in their own words the main conclusions of East and Hayes ('12) are as follows (p. 8):

> "1. Mendel's law—that is, the segregation of character factors in the germ cells of hybrids and their chance recombinations in sexual fusions—is a general law.
>
> 2. Stimulus to development is greater when certain, or possibly all, characters are in the heterozygous condition than when they are in a homozygous condition.
>
> 3. This stimulus to development is cumulative up to a limiting point and varies directly with the number of heterozygous factors in the organism although it is recognized that some of the factors may have a more powerful action than others."

It was clearly apparent to recent investigators that many of the unfavorable characters which appear on inbreeding a naturally cross-pollinated species are recessive characters which are segregated out of the original complex. In a naturally crossed species, these are hidden from sight on account of being continually crossed with dominant characters. That dominance of factors could in any way be an essential factor in the vigor and excellence of hybrids, an idea first proposed by Keeble and Pellew ('10) and also by Bruce ('10), has not been accepted by most writers on this subject. They considered dominance to be totally inadequate to account for the widespread and almost universal occurrence of heterosis in plants and animals and the fact that nearly all naturally cross-fertilized domesticated species are reduced by inbreeding.

Collins ('10) has shown clearly that many crosses between varieties of Indian corn already widely crossed among themselves and grown in the same regions may not give any increase in productiveness, but when these same varieties are crossed with varieties from distinct geographical regions great increases in productiveness are obtained. Further evidence as to the occurrence of heterosis is seen in the many publications which have appeared from time to time urging the commercial utilization of this hybrid vigor as a method of increasing production in many plants. Among these are Beal ('76–'82), McCleur ('92), Morrow and Gardner ('93–'94), Swingle and Webber ('97), Hayes and East ('11), Hartley ('12), Wellington ('12), Hayes ('13), Hayes and Jones ('16).

In view of the innumerable cases in which an increase in development, in some character, results from crossing and the converse fact of reduction following subsequent inbreeding, of which the preceding paragraphs refer to only a small fraction, it is surprising to note such radically diverse opinions as are held by Burck ('08) and championed by Stout ('16).

Stout attributes the following statements to Burck: (p. 418)

> "That (1) plants that are regularly self-fertilized show no benefits from crossing and that (2) nowhere in wild species is there evidence of an injurious effect from self-fertilization, and that there is abundant evidence of continued vigor and high fertility resulting from long continued self-fertilization."

If by the first statement is meant that crossing between members of the same variety or between individuals of a uniform species does not give an increase in development such a result would be expected because of the germinal similarity brought about by long continued selfing and elimination by selection, either natural or artificial, of all but one type. On the other hand, there is abundant evidence to show that crossing between different varieties or between different wild species of self-pollinated plants often results in striking increases in size and vigor. It is only necessary to refer to the work of Kölreuter, Knight, Gärtner, Naudin and Mendel where many crosses between different species, or between distinct types of *Nicotiana*, *Pisum*, and *Lathyrus*—plants which are naturally self-fertilized—give unmistakable evidence of heterosis.

Turning to the effects of inbreeding, almost no long-continued experiments have been carried out with strictly wild cross-pollinated species of plants. Collins ('18) in a brief note states that teosinte, a semi-wild relative of maize, is not affected by inbreeding to the extent that maize is. That there is "abundant evidence of continued vigor and high fertility resulting from long continued self-fertilization" no one longer doubts. There is, however, hardly enough evidence from plants, so far on record, to justify the sweeping statement, which the quotation implies, that cross-fertilized wild species are never reduced by inbreeding.

What evidence there is indicates that naturally crossed wild species are not reduced by inbreeding to anything like the extent that domesticated races are. More will be said about this difference between wild and domesticated races later. There is some evidence, however, to show that strictly wild species are affected by inbreeding. Darwin compared the progeny of artificially self-fertilized plants with the progeny of artificially intercrossed plants of many wild species. Many of these species were such as were for one cause or another almost completely cross-fertilized in their natural state at all times. Although the difference may be slightly exaggerated there can be no question but that the difference in the first generation which Darwin obtained between the selfed plants and the intercrossed plants represents in many cases the effect which inbreeding has upon these plants. As examples of widely crossed wild species in which a reduction in the first generation of inbreeding was obtained by Darwin, one can, therefore, cite: *Digitalis purpurea*, *Linaria vulgaris*, *Sarothamnus scoparius* and *Reseda lutea*.

Moreover, no matter how much domestication may change plants from the wild, one cannot cast aside, as of no consequence, the results obtained from cultivated plants.

INVESTIGATIONS WITH ANIMALS.

According to Darwin, the mule, that classic example of hybrid vigor, was known in the time of Moses, when its hardihood and general good qualities doubtless endeared this animal to the Jews no less than to the Southern cotton planters of to-day. A similar cross of the ass with the wild zebra according to Riley ('10) gives a first generation hybrid animal of considerable merit.

In the early history of the establishment and fixation of breeds of livestock we note in Darwin's "Animals and Plants under Domestication" that certain crosses between different breeds often resulted in progeny excelling individuals of either parent breed; just as to-day it is not an uncommon practice for livestock raisers to cross certain well-established breeds to produce crossed animals to feed for market.

In looking over the reports of experiments designed to test the effects of crossing in both wild and domesticated animals there is little disagreement as to the results usually obtained. All are practically in accord that crossing diverse breeds or races of animals, if not too distantly related, may frequently result in vigorous, large and fertile offspring, excelling either parent in one or more respects. For example, Castle et al ('06) find that crossing diverse stocks of Drosophila results in an increase in fertility and that matings between different inbred lines give progeny with increased fertility up to or beyond that of the more fertile parental race. In Meriones Bonhote ('15) states that fertility and size are increased by crossing. Castle ('16) has crossed domesticated races of guinea-pigs with the wild species from Peru with the result that there is a noticeable increase in body weight over either pure parent. Gerschler ('14) crossed different genera of fishes and obtained large increases in size in the first hybrid generation. *Xiphophorus strigatus*, of which the males were 43.0 cm. long and the females 52.0 cm., when crossed with *Platypoecilius maculatus*, of which the males were 26.0 and the females 31.0 cm. in length, gave hybrid males 54.0 cm. and females 57.5 cm. He speaks of their "gigantic size."

Fischer ('13) in his study of the Rehoboth hybrids, a race in South Africa resulting from a mixture of Hottentots and Boers, states that their average height is somewhat greater than either the Hottentots or the Hollanders and South Germans of whom statistics are available. All the members of this new race are not first generation crosses by any means, but they are not many generations removed and crossing with the pure Hottentots, the shorter parental race, is frequent.

When, however, the literature on the effects of inbreeding in animals is examined one finds the greatest diversity of facts and opinions. We find the extreme views of Kraemer ('13) who states that "continued inbreeding always must result in weakened constitution, through its own influence" together with the equally extreme and biased opinion of Huth ('75) that in mankind there is no injurious effect resulting from consanguineous marriages which cannot be accounted for on other grounds.

Crampe ('83), Ritzema-Bos ('94), Guaita ('98), Fabre-Domengue ('98) and Weismann ('04) by inbreeding mammals and birds found that the process was accompanied by decreased fertility, attended more or less commonly by lack of vigor, diminution in size, and pathological malformations. Castle, Carpenter et al ('06) inbreeding extensively the fruit fly, Drosophila, maintained fertility by selection, so that at the end of 59 generations of brother and sister matings in one line the fecundity was no less at the end of the experiment than it was at the start. There was some indication of reduction in size of inbred flies when compared to normally crossed stock flies reared under the same conditions. Furthermore, fertility was increased by crosses between certain inbred lines and between the inbred lines and stock flies. From this fact and from the fact that their experiments show that the number of flies in a brood fluctuates greatly, due to temperature and food conditions, it is not positive that inbreeding was wholly without injurious effects. It is evident that their experiments do show clearly:

1. That inbreeding results in strains of unequal fertility.

2. That the occurrence of absolute sterility was pronounced in the first part of the experiment with the "A" line but almost entirely disappeared in the later part of the experiment. The figures as I have calculated them from their table I, p. 736, are as follows:

		Percent of matings totally sterile
Generations	6 to 24	17.80
"	25 to 42	18.47
"	43 to 59	3.37

This result is to be expected on the view that inbreeding isolates homozygous individuals and these whenever sterile are, of course, eliminated.

Moenkhaus ('11) and Hyde ('14) by similar inbreeding experiments with Drosophila have also found that sterility is increased in the first stages of inbreeding but tends to be eliminated after this process is long continued. Hyde found definite evidence that inbreeding caused reduction in size, vigor, rate of growth, longevity and fecundity and that there was a return to the normal condition on crossing. As in the other experiments Hyde found that selection was an effective agent in controlling sterility.

Both Whitney (12a) and A. F. Shull (12a) have shown that inbreeding and crossbreeding have considerable effect upon the rotifer, *Hydatina Senta*, in the size of family, number of eggs laid per day, rate of growth and in the difficulty of rearing the animals.

King ('16) has obtained results with albino rats which are quite in agreement with those of Castle. By growing about one thousand rats in each inbred generation, and selecting the best individuals for mating, animals have been carried through 22 generations of brother and sister matings without loss of size, fertility, longevity, resistance to disease and with constitutional vigor unimpaired. This writer states:

> "The results so far obtained with these rats indicate that close inbreeding does not necessarily lead to a loss of size or constitutional vigor or of fertility, if the animals so mated came from sound stock in the beginning and sufficient care is taken to breed only from the best individuals."

Here, as in Drosophila, inbreeding isolates diverse types of different degrees of excellence. In this case individuals are obtained which surpass the original stock before inbreeding. Thus we have "Goliaths" among inbred rats as Darwin found "Heroes" in morning-glories.

> Castle ('16) has found that in inbred rats "races of fair vigor and fecundity can be maintained under these conditions, but that when two of these inbred races are crossed with each other, even though they have their origin in a small common stock many generations earlier, an immediate and striking increase of fecundity occurs."

The evidence from relationship marriages in human stocks is even more conflicting and conclusions still more difficult to draw. Huth ('75) has certainly done a service in showing that consanguineous marriages seldom result in the disastrous effects usually attributed to them. He has shown that incest was not a rare custom and that races which have undergone such practices are many of them far from weak. Certainly, races have practiced close intermarriage for many generations with no marked deterioration. The Persians, Spartans, the ruling classes among the Egyptians and Polynesians are cited by Huth in support of this assertion. The data from human matings, however, are of little value since the close unions are seldom continued many generations in succession, and the results from isolated communities mean little, since often the original stock is exceedingly diverse so as to make the resulting races extremely heterogeneous in hereditary constituents. This is particularly true of the Rehoboths and the Pitcairn Islanders which are cited as instances of close intermarrying without loss of racial vigor.

Looking over the experiments upon animals it seems as unwise to expect that inbreeding may not have some deleterious effects, which, in some cases at least, cannot be overcome by the most rigid selection, as it is to hold that inbreeding must always result injuriously. It is to be expected that all breeds of domestic animals and wild species will not be equally affected by inbreeding. Domesticated animals in many cases are more widely crossed and diversified than wild species, and those characters affected by inbreeding are more accentuated. Certain wild species, which, by their mode of life, are forced to endure long periods of isolation, and consequently more or less close inbreeding, would be expected to show less change under artificial inbreeding. Finally, as I shall attempt to show that there is no longer a question as to whether or not inbreeding, *in itself*, is injurious, the effect which inbreeding will have on any organism depends solely on the hereditary constitution of that organism at the time the inbreeding process is commenced.

UNIVERSALITY OF HETEROSIS.

From the literature on the subject of crossbreeding it is to be observed, therefore, that the occurrence of an incentive to increased development accompanying germinal heterogeneity is widespread, as it has been noted in plants in the angiosperms, gymnosperms and pteridophytes, and according to Britton ('98) there is even some slight evidence that heterosis occurs in the sporophyte of the bryophytes.

In animals the mammals, birds, fishes, insects and rotifers show the phenomenon of heterosis although in some of the unicellular animals, as we shall see later, the evidence is not so clear.

I shall now take up, in some detail, experiments on inbreeding and crossbreeding in cultivated plants, principally in maize.

A Theoretical Consideration of Inbreeding.

Up to the present time it has been maintained that the effects of inbreeding were of two kinds, an isolation of homozygous biotypes together with a loss of a physiological stimulation which was considered to be roughly proportional to the number of heterozygous allelomorphs present in the organism at any time. The reduction of the number of heterozygous allelomorphs in an inbred population is automatic and varies with the closeness of inbreeding.

Pearl ('15) on the basis of the number of ancestors which make up the pedigree of any individual has worked out a coefficient of inbreeding which is an indication of the degree to which that individual has been inbred. The fewer the number of ancestors the greater the degree of inbreeding which may vary from no inbreeding, in which no one ancestor appears more than once in the pedigree of an individual, to the closest kind of inbreeding in which no more than one ancestor is concerned in any one generation in the production of an individual (self-fertilization). The latter degree is only approached by hermaphroditic plants and animals, which are capable of self-fertilization and in functionally bisexual animals and plants by brother and sister matings. This statement of inbreeding must, of course, leave out of consideration any germinal change which might take place by means other than hybridization and as Castle ('16) has pointed out is modified by the differences in heterozygosity of the ancestors making up the pedigree.

The automatic reduction in the number of heterozygous allelomorphic pairs in an inbred population, by self-fertilization, follows the well known Mendelian formula by which any heterozygous pair forms in the next generation 50 percent homozygotes and 50 percent heterozygotes in respect to that pair. Since the homozygotes must always remain homozygous and the heterozygotes are halved each time and one half added to the homozygotes the reduction in the number of heterozygous elements proceeds as a variable approaching a limit by one half the difference in each generation. The curve illustrating this condition is shown as No. 1 in Fig. I. Various formulæ dealing with inbreeding have been discussed by East and Hayes ('12), Jennings ('12, '16), Pearl ('15) and Bruce ('17).

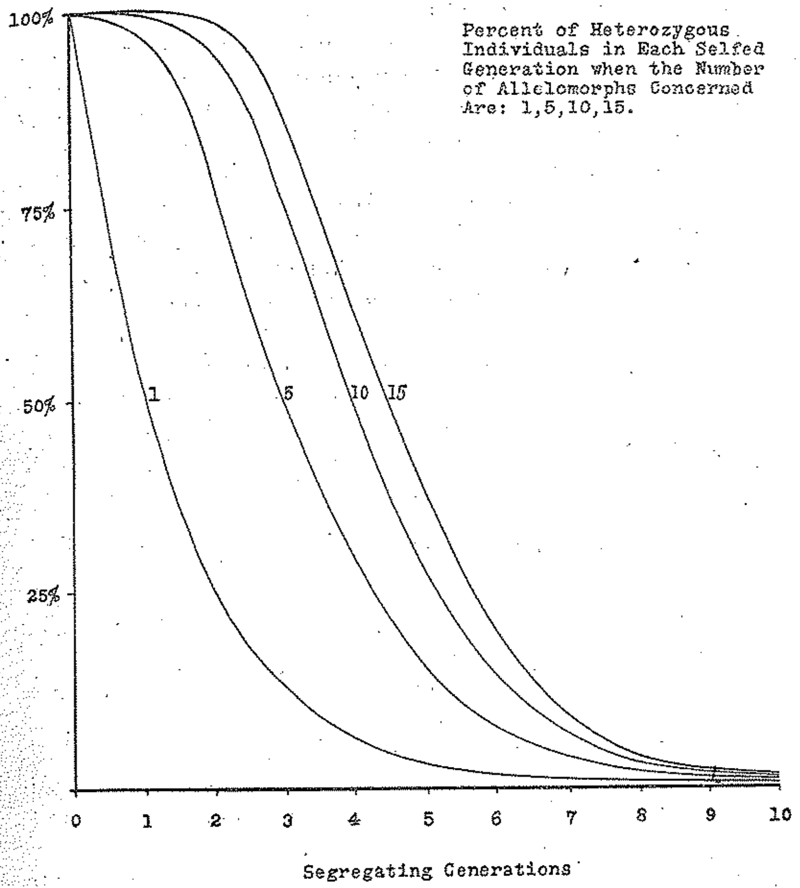

Figure I. The percent of heterozygous individuals and the percent of heterozygous allelomorphic pairs in the whole population in each generation of self-fertilization.

It should be remembered that this reduction applies only to the whole population in which every member is inbred and all the progeny grown in every generation. In practice, in an inbreeding experiment, only one individual in self-fertilization or two individuals in brother and sister matings are used to produce the next generation. Thus the rate at which complete homozygosis is approached depends on the heterozygosity of the individuals chosen. Theoretically in any inbred generation the progenitors of the next generation may either be completely homozygous or completely heterozygous or any degrees in between depending upon chance. The only condition which must follow in self-fertilization is that no individual can ever be more heterozygous than its parent but may be the same or less. Thus it is seen that inbreeding, as it is practiced, may theoretically never cause any reduction in heterozygosity, or it may bring about complete homozygosity in the first inbred generation. In other words the rate at which homozygosity is approached may vary greatly in different lines. However, as the number of heterozygous factors at the commencement of inbreeding increases the more nearly will the reduction to homozygosity follow the curve shown because the chance of choosing a completely homozygous or completely heterozygous individual in the first generations will become less.

In Table 1 is shown the theoretical classification of the progeny of a self-fertilized organism which was heterozygous with respect to 15 independent mendelizing units. It will be seen that the bulk of the individuals lie between classes 6 and 11 where none of the members are heterozygous for more than 10 factors nor less than 5. In other words any individual selected for the progenitor of the next generation would probably come from the middle classes and therefore it would be heterozygous for about half the factors that its parent was. The chance that this individual would not come from the mid-classes between 6 and 11 would be about 1 out of 10. The chance that it would be completely homozygous or completely heterozygous would be 1 out of 32,768. If 20 instead of 15 factors were concerned the chances would be 1 out of 1,048,576.

This condition by which the progenitor of each generation tends to be half as heterozygous as its parent holds true for any number of factors and in every generation. Also in Table 1 it can be seen that the progeny as a whole has an equal number of heterozygous factor pairs as homozygous factor pairs in respect to those

TABLE 1. THE THEORETICAL NUMBER AND RATIO OF INDIVIDUALS IN THE CLASSES OF DIFFERENT DEGREES OF HETEROZYGOSITY, AFTER RECOMBINATION, WHEN FIFTEEN MENDELIZING UNITS ARE INVOLVED.

Class No.	The total number of individuals in all the possible mendelian recombinations in F_2 when 15 factors are involved.	Ratio of individuals in the classes with different number of heterozygous and homozygous factors—coefficients $(a+a)^{15}$	The number of factors in respect to which the different classes are:		The total number of heterozygous and homozygous factor pairs in all the individuals in each class:	
			Heterozygous	Homozygous	Heterozygous factor pairs	Homozygous factor pairs
1	32,768	1	15	0	15	0
2	491,520	15	14	1	210	15
3	3,440,640	105	13	2	1,365	210
4	14,909,440	455	12	3	5,460	1,365
5	44,728,320	1,365	11	4	15,015	5,460
6	98,402,304	3,003	10	5	30,030	15,015
7	164,003,840	5,005	9	6	45,045	30,030
8	210,862,080	6,435	8	7	51,480	45,045
9	210,862,080	6,435	7	8	45,045	51,480
10	164,003,840	5,005	6	9	30,030	45,045
11	98,402,304	3,003	5	10	15,015	30,030
12	44,728,320	1,365	4	11	5,460	15,015
13	14,909,440	455	3	12	1,365	5,460
14	3,440,640	105	2	13	210	1,365
15	491,520	15	1	14	15	210
16	32,768	1	0	15	0	15
16 $(n+1)$	1,073,741,824 $(2^n)^2$	32,768 2^n	15 n	15 n	245,760 $\frac{1}{2}(n.2^n)$	245,760 $\frac{1}{2}(n.2^n)$

characters in which the parent was heterozygous. So it is that in practice the reduction in growth accompanying inbreeding (on the assumption that heterosis is correlated with heterozygosity) is greatest at first, rapidly becomes less and finally ceases for all practical purposes.

If there were no deviating factors the curve of reduction should, in the majority of cases, approximate curve 1 in Fig. I. However, it has never been assumed that the amount of heterosis was perfectly correlated with the number of heterozygous factors. Moreover, since the heterozygous individuals are more vigorous than the homozygous, selection, either unconscious or purposeful, would favor the more heterozygous so that the tendency might be that the actual approach to homozygosity would not proceed at as fast a rate as the theoretical curve would indicate.

Self-fertilization is the quickest and surest means of obtaining complete homozygosis for the reason that whenever any pair of allelomorphs becomes homozygous it must always remain so long as self-fertilization takes place, whereas in brother and sister mating a homozygote may be mated to a heterozygote. Thus we see from Jennings' ('16) tables that 6 generations of self-fertilization are more effective than 17 generations of brother and sister matings in bringing about homozygosis. The reduction in heterozygous allelomorphs in a population as a whole follows curve 1 in Fig I irrespective of the number of factors concerned, provided, as stated before, that a random sample of all the different classes of individuals are selfed and used as progenitors for the next generation and that there is equal productiveness and equal viability. If the heterozygotes are more productive, as in many cases they are, the reduction to complete homozygosity will be delayed.

The number of completely homozygous individuals in any generation, inbred by self-fertilization, differs according to the number of heterozygous factors concerned at the time that the inbreeding process is commenced. The curves showing the reduction in the number of individuals heterozygous in any factors, where, 1, 5, 10 and 15 factors are concerned at the start are given in Fig. I calculated from the formula given by East and Hayes ('12). The curve for the reduction in heterozygous individuals, where one factor only is concerned, is identical with the curve showing the reduction in heterozygous factors in an inbred population where any number of factors are concerned. In any case almost complete homozygosity is reached in about the tenth generation on the average, although theoretically it may be reached in the first generation, or may never be reached when a single individual is used in each generation to perpetuate the line.

Assuming, then, that the loss of the stimulation, accompanying heterozygosity, is correlated with the reduction in the number of heterozygous allelomorphs we should expect to find the decrease of heterosis greatest in the first generations, rapidly becoming less until no further loss is noticeable in any number of subsequent generations of inbreeding, and that, on the average, the loss will become negligible at about the eighth generation and from then on no further marked change will take place. Some cases are to be expected in which stability is reached before this generation and some cases in which it is not reached until later or may even theoretically never be reached. With these assumptions in mind let us see what are the actual results of long continued inbreeding in maize.

The Results of Inbreeding the Naturally Cross-pollinated Maize Plant.

The behavior of maize during six generations of inbreeding by self-fertilization has already been reported by East and Hayes ('12). The same inbred strains have been continued and in some cases the results up to the eleventh generation are given here.

In the previous publication it was stated that a loss of vegetative vigor has followed every case of inbreeding in maize. Some plants had been obtained which were unable to reproduce themselves. Those strains which were maintained became uniform but differed considerably from each other. It was considered at the end of the period of inbreeding that some strains were appreciably better than others in their ability to yield. Six additional years of inbreeding with this material has confirmed, in the main, these conclusions. A further appreciable reduction in productiveness, however, has taken place in all lines together with certain changes in various parts of the plants.

The original experiment began with four individual plants obtained from seed of a commercial variety of Leaming dent corn grown in Illinois. This variety was given the number 1 and the four plants which were self-pollinated and selected for continuation of the inbreeding experiment were numbered 1-6, 1-7, 1-9 and 1-12. These four strains were continued each year by self-pollination. In the second inbred generation two self-pollinated plants in the 1-7 line were saved for seed and from them two inbred lines were split off which therefore came originally from one line inbred two generations. These are numbered 1-7-1-1 etc. and 1-7-1-2 etc. In a similar way these, and the other inbred lines, were further split up in subsequent generations. After the experiment was started with the dent corn inbreeding was commenced with other material. Two inbred strains of floury corn, Nos. 10-3 and 10-4, originally from the same variety, have been maintained and also two strains of flint, Nos. 5 and 29, and two strains of popcorn Nos. 64 and 65. Chief attention has been paid to the inbred strains of Leaming corn (the longest inbred) and most of the data presented here have resulted from this material. Many other varieties besides these have been inbred for many generations in connection with other investigations and while they are not specifically mentioned the observations as a whole include these.

In Tables 2 and 3 the yield and height of some of these inbred strains are given. In 1916 seed of the original Leaming variety was obtained which had been grown in the meantime in the same locality whence it was originally secured and was grown for comparison with the inbred strains. This variety in Illinois in 1905 yielded at the rate of 88 bushels per acre, and in Connecticut in 1916 at the rate of 74.7 bushels. While there is no proof that any change has not taken place in the original variety there is no reason to suppose that it has changed to any great extent. Grown under the same conditions in 1916 the four inbred Leaming strains yielded from one-third to one-half as much as the original non-inbred variety.

With regard to rate of reduction in yield or the constancy of the varieties during the later generations it is difficult to draw conclusions from these figures owing to the fluctuation in yield from year to year due to seasonal conditions and to the difficulty of accurate testing in field plot work, which is recognized by all who have made such tests. As was stated in the first report the yields for 1909 were too low and in 1911 much too low on account of poor seasons. No yields were taken on any of the strains in

TABLE 2. THE EFFECT OF INBREEDING ON THE YIELD AND HEIGHT OF MAIZE.

Year grown	No. of generations selfed	Four inbred strains derived from a variety of Leaming dent corn.							
		1-6-1-3-etc.		1-7-1-1-etc.		1-7-1-2-etc.		1-9-1-2-etc.	
		Yield bu. per acre	Height inches	Yield bu. per acre	Height inches	Yield bu. per acre	Height inches	Yield bu. per acre	Height inches
1916	0	74.7	117.3	74.7	111.3	74.7	117.3	74.7	117.3
1905	0	88.0	....	88.0	....	88.0	....	88.0	....
1906	1	59.1	....	60.9	....	60.9	....	42.3	....
1908	2	95.2	....	^{1907}59.3	....	^{1907}59.3	....	51.7	....
1909	3	57.9	....	^{1908}46.0	....	^{1908}59.7	....	35.4	....
1910	4	80.0	....	63.2	....	68.1	....	47.7	....
1911	5	27.7	86.7	25.4	81.1	41.3	90.5	26.0	76.5
1912	6	....	....	....	....	....	....	^{1913}38.9	....
1913	7	41.8	....	39.4	....	....	....	^{1914}45.4	85.0
1914	8	78.8	96.0	47.2	83.5	58.5	88.0	^{1915}21.6	....
1915	9	25.5	....	24.8	....	....	....	^{1916}30.6	78.7
1916	10	32.8	97.7	32.7	84.9	19.2	86.9	^{1917}31.8	82.4
1917	11	46.2	103.7	42.3	78.6	37.6	83.8	....	....

TABLE 3. THE EFFECT OF INBREEDING ON THE YIELD OF MAIZE.

Year grown	No. of generations selfed	Two inbred strains of floury corn		One inbred strain of flint corn
		10-3-7-etc. Yield bu. per acre	10-4-8-etc. Yield bu. per acre	5-8-6-etc. Yield bu. per acre
1908	0	70.5	70.5	75.7
1909	1	56.0	43.0	47.5
1910	2	67.0	48.7	36.1
1911	3	39.1	29.3	11.5
1912	4	....	....	....
1913	5	32.2	49.5	30.4
1914	6	....	52.6	38.1
1915	7	....	....	....
1916	8	13.9	16.6	18.3
1917	9	26.6	24.0	......

1912. The yields in 1914 are too high and in 1915 too low for the same reasons. Also in 1915 the yields are unreliable because only a few plants were available to calculate yields from as most of them were used for hand pollination. During the last three years of the test samples of corn have been dried to a uniform moisture basis and the yields calculated to bushels of shelled corn per acre with 12 per cent. moisture. This has probably had a tendency to reduce the yields somewhat as these inbred strains are very late in maturing and consequently contain large amounts of water.

With these points in mind an examination of the table shows that from the beginning of the experiment to the ninth generation there has been a tremendous drop in productiveness, so that in that generation the strains are approximately only one-third as productive as the variety before inbreeding. From the ninth to the eleventh generation there has been at least no reduction in productiveness, and practically no change in visible plant or ear characters.

In the previous publication it was stated (U. S. Dept. of Agric., B. P. I. Bull. 243, pp. 23-24) that

> . . . . "strain No. 6, is a remarkably good variety of corn even after five generations of inbreeding. It yielded eighty bushels per acre in 1910. The yield was low in 1911, but since all yields were low that year it can hardly be doubted that this strain will continue to produce good normal yields of grain......The poorest strain, No. 12, is partially sterile, never fills out at the tip of the ear and can hardly exist alone. In 1911 it yielded scarcely any corn but will no doubt continue its existence as a partly sterile variety."

These statements will have to be modified somewhat. Although No. 6 is, in the eleventh generation, still the most vigorous inbred strain, as a producer of grain, however, it can hardly be considered to give "good normal yields." The plants, nevertheless, are perfectly healthy and functionally normal in every way except for an extreme reduction in the amount of pollen which they produce. The strain No. 12 was lost. Since the difficulty of carrying along any inbred strain is very great owing to failure to pollinate at the right time, attacks of fungus on the ear enclosed in a paper bag, and poor germination in the cold, wet weather common in New England at corn planting time, the loss of this strain might be easily accounted for without supposing that it simply ran out. It may be that this strain could have been perpetuated if sufficient effort had been put forth to do so. In view of the further reduction in the other strains, however, the maintaining of this strain would have been extremely difficult.

Complete records on the height of plant are wanting for many of the generations, and, unfortunately, in the first part of the inbreeding period. What figures are available certainly show that very little change in height has taken place in all four strains during the last seven generations. Strain No. 6 has increased in height, if anything. Height is less affected by environmental factors than is yield and in that respect is a more reliable indicator. However, great changes in the structure, size and productiveness may take place without height of plant being greatly altered.

From the figures given in Table 2 there is some evidence that these strains have reached about the limit of reduction in productiveness and that there has been very little change in the last three years. This, however, is not proven. The continuation of inbreeding is necessary for conclusive evidence on this point. As the crosses between individual plants within these inbred strains have given very little increase over the selfed strains, as will be shown later, and from the fact that almost no visible change has taken place in these four strains during the past three years that I have had them under observation, it seems apparent to me that the reduction in vegetative vigor and productiveness is very nearly at an end.

In Tables 4, 5, 6 and 7 are given the frequency distributions of height, length of ear, number of nodes and the number of rows of grain on the cob of the original, non-inbred Leaming variety and several inbred strains derived from this variety after nine or ten generations of selfing. All the plants from which the data were taken were grown on the same field in the same year. Four different plots of the variety were grown in different parts of the field and the data on these plots are given separately and totaled in the tables. It can be seen from these that no great variations in range, mean, standard deviation or coefficient of variability were caused by environmental factors. The pedigree numbers show the relationship of the several inbred strains to each other.

From these tables it can be seen that both height of plant and length of ear have been reduced, but in different degrees in different lines. In some strains reduction in height amounts to 40 inches and in length of ear to 3.5 inches. The reduction in

TABLE 4. FREQUENCY DISTRIBUTION OF HEIGHT OF PLANT OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Height of plant in inches.																		N.	A.	S. D.	C.
	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	113.5	118.5	123.5	128.5	133.5	138.5	143.5				
1 (Original	..	..	..	..	..	..	..	1	4	5	7	11	9	6	3	2	..	..	48	114.0±.91	9.40±.64	8.2
1 non-inbred	..	..	..	..	..	..	..	2	2	4	4	10	8	11	13	5	1	..	60	119.2±.91	10.50±.64	8.8
1 Leaming	..	..	..	..	..	..	..	1	1	4	15	8	9	6	7	3	0	1	55	116.3±.90	10.05±.65	8.6
1 variety)	..	..	..	..	..	..	..	1	0	4	7	8	6	10	8	3	3	..	50	119.3±.98	10.30±.69	8.6
Total..........	..	..	..	..	..	..	..	5	7	17	33	37	32	33	31	13	4	1	213	117.3±.48	10.33±.34	8.8
1-6-1-3-4-4-4-2-4-4-3	..	..	..	..	..	..	4	11	30	11	..	..	..	..	..	..	..	..	56	97.8±.36	4.05±.26	4.1
1-6-1-3-4-4-4-2-4-1-2	..	..	..	..	..	..	5	22	24	10	..	..	..	..	..	..	..	..	61	96.7±.37	4.25±.26	4.4
1-6-1-3-4-4-4-2-5-5-1	..	..	..	..	2	2	9	16	14	3	..	..	..	..	..	..	..	..	46	93.6±.57	5.75±.41	6.1
1-6-1-3-4-4-4-2-5-3-1	..	..	..	..	..	..	..	7	11	26	8	4	..	..	..	..	..	..	56	102.7±.47	5.25±.33	5.1
1-7-1-1-1-4-7-5-2-6-1	1	3	8	3	11	20	6	..	..	..	..	..	..	..	..	..	..	..	52	78.5±.71	7.65±.51	9.7
1-7-1-1-1-4-7-5-2-1-1	2	3	1	6	9	12	19	6	..	..	..	..	..	..	..	..	..	..	58	82.2±.77	8.75±.55	10.6
1-7-1-1-1-4-7-5-4-7-2	..	..	..	1	3	3	18	26	2	..	..	..	..	..	..	..	..	..	53	90.2±.46	4.95±.33	5.4
1-7-1-1-1-4-7-5-4-5-2	..	..	1	1	1	7	16	7	5	..	..	..	..	..	..	..	..	..	38	88.7±.70	6.45±.50	7.2
1-7-1-2-2-9-2-1-1-4-1	..	1	1	8	9	18	13	3	1	..	..	..	..	..	..	..	..	..	54	82.6±.61	6.65±.43	8.0
1-7-1-2-2-9-2-1-1-1-3	..	..	1	1	2	8	8	18	11	2	..	..	..	..	..	..	..	..	51	91.2±.68	7.25±.48	7.9
1-9-1-2-4-6-7-5-6-4	2	2	2	14	26	12	1	..	..	..	..	..	..	..	..	..	..	..	59	77.0±.52	5.95±.37	7.7
1-9-1-2-4-6-7-5-3-3	..	..	..	10	22	25	3	..	..	..	..	..	..	..	..	..	..	..	60	80.3±.35	4.05±.25	5.0

2

TABLE 5. FREQUENCY DISTRIBUTION OF LENGTH OF EAR OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Length of ear in inches											N.	A.	S. D.	C. V.
	2	3	4	5	6	7	8	9	10	11	12				
1 (Original	..	..	..	7	12	20	13	3	1	0	1	57	7.0±.12	1.33±.08	19.00±1.24
1 non-inbred	..	..	2	6	9	12	11	7	3	1	..	51	7.2±.15	1.61±.11	22.36±1.55
1 Leaming	..	..	2	1	7	19	19	9	3	1	..	61	7.6±.11	1.31±.08	17.24±1.08
1 variety)	..	..	1	1	4	14	18	18	3	..	..	59	7.9±.10	1.20±.08	15.19± .96
Total............	..	..	5	15	32	65	61	37	10	2	1	228	7.5±.06	1.43±.05	19.07± .63
1-6-1-3-4-4-4-2-4-4-3	..	1	5	8	16	29	..	..	..	..	..	59	6.1±.09	1.05±.07	17.17±1.18
1-6-1-3-4-4-4-2-4-1-2	..	..	2	7	29	19	1	..	..	..	..	58	6.2±.07	.81±.05	13.06± .82
1-6-1-3-4-4-4-2-5-5-1	..	2	7	11	7	8	10	1	..	..	..	46	6.0±.16	1.57±.11	26.17±1.95
1-6-1-3-4-4-4-2-5-3-1	..	..	3	5	6	25	16	1	..	..	..	56	6.9±.10	1.12±.07	16.23±1.05
1-7-1-1-1-4-7-5-2-6-1	..	7	27	28	..	..	..	..	..	..	..	62	4.3±.06	.67±.04	15.58± .96
1-7-1-1-1-4-7-5-2-1-1	3	5	25	22	1	..	..	..	..	..	..	56	4.2±.08	.84±.06	20.00±1.31
1-7-1-1-1-4-7-5-4-7-2	5	10	24	18	..	..	..	..	..	..	..	57	4.0±.08	.91±.06	22.75±1.51
1-7-1-1-1-4-7-5-4-5-2	..	9	12	14	1	..	..	..	..	..	..	36	4.2±.09	.83±.07	19.76±1.62
1-7-1-2-2-9-2-1-1-4-1	1	3	10	11	14	4	..	..	..	..	..	43	5.1±.12	1.19±.09	23.33±1.77
1-7-1-2-2-9-2-1-1-1-3	..	1	6	15	18	2	..	..	..	..	..	42	5.3±.09	.85±.07	16.04±1.20
1-9-1-2-4-6-7-5-6-4	..	..	3	8	25	19	..	..	..	..	..	55	6.1±.08	.84±.06	13.77± .90
1-9-1-2-4-6-7-5-3-3	..	..	1	9	44	5	..	..	..	..	..	59	5.9±.05	.55±.04	9.32± .58

TABLE 6. FREQUENCY DISTRIBUTION OF THE NUMBER OF NODES OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Number of nodes											N.	A.	S. D.	C. V.
	8	9	10	11	12	13	14	15	16	17	18				
1 (Original	..	..	..	..	4	12	19	22	1	3	1	62	14.3±.10	1.21±.07	8.46±.51
1 non-inbred	..	..	..	2	9	15	15	11	5	0	1	58	13.8±.12	1.40±.09	10.14±.63
1 Leaming	..	..	..	1	0	9	26	15	3	4	1	59	14.4±.10	1.20±.08	8.33±.52
1 variety)	..	..	2	2	10	13	19	12	2	5	1	66	13.8±.14	1.66±.10	12.03±.71
Total............	..	..	2	5	23	49	79	60	11	12	4	245	14.1±.06	1.42±.04	10.07±.31
1-6-1-3-4-4-4-2-4-4-3	..	..	..	2	25	28	3	..	..	..	..	58	12.7±.06	.65±.04	5.12±.32
1-6-1-3-4-4-4-2-4-1-2	..	..	1	30	30	..	..	..	..	..	..	61	11.5±.05	.53±.04	4.61±.28
1-6-1-3-4-4-4-2-5-5-1	..	..	..	6	24	13	6	..	..	..	..	49	12.4±.08	.86±.06	6.94±.47
1-6-1-3-4-4-4-2-5-3-1	..	1	0	6	34	18	..	..	..	..	..	59	12.2±.06	.73±.05	5.98±.37
1-7-1-1-1-4-7-5-2-6-1	..	1	2	11	35	5	..	..	..	..	..	54	11.8±.07	.74±.05	6.27±.40
1-7-1-1-1-4-7-5-2-1-1	1	1	7	15	21	14	..	..	..	..	..	59	11.6±.10	1.12±.07	9.66±.60
1-7-1-1-1-4-7-5-4-7-2	..	..	1	5	34	14	3	..	..	..	..	57	12.2±.07	.76±.05	6.23±.39
1-7-1-1-1-4-7-5-4-5-2	..	..	1	2	13	18	5	1	..	..	..	40	12.7±.10	.95±.08	7.48±.56
1-7-1-2-2-9-2-1-1-4-1	..	1	1	14	18	21	1	..	..	..	..	56	12.1±.09	.96±.06	7.93±.50
1-7-1-2-2-9-2-1-1-1-3	..	..	1	1	12	23	15	..	..	..	..	52	13.0±.08	.88±.06	6.77±.45
1-9-1-2-4-6-7-5-6-4	..	..	..	3	15	27	13	1	..	..	..	59	12.9±.07	.86±.06	6.67±.41
1-9-1-2-4-6-7-5-3-3	..	..	..	2	6	39	13	..	..	..	..	60	13.1±.06	.67±.04	5.11±.31

TABLE 7. FREQUENCY DISTRIBUTION OF THE NUMBER OF ROWS OF GRAIN ON THE EAR OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Number of rows on the ear.								N.	A.	S. D.	C. V.
	12	14	16	18	20	22	24	26				
1 (Original	..	2	14	18	14	5	2	2	57	18.7±.23	2.64±.17	14.12±.91
1 non-inbred	..	1	15	21	8	3	3	..	51	18.2±.21	2.26±.15	12.42±.84
1 Leaming	2	6	7	19	17	7	2	..	60	18.4±.23	2.70±.17	14.67±.93
1 variety)	1	5	15	17	13	6	0	2	59	18.2±.24	2.76±.17	15.16±.96
Total............	3	14	51	75	52	21	7	4	227	18.4±.12	2.62±.08	14.22±.46
1-6-1-3-4-4-4-2-4-4-3	..	7	24	22	6	..	..	..	59	16.9±.14	1.66±.10	9.83±.61
1-6-1-3-4-4-4-2-4-1-2	..	12	42	4	..	..	..	..	58	15.7±.09	1.02±.06	6.48±.40
1-6-1-3-4-4-4-2-5-5-1	5	34	7	..	..	..	..	..	46	14.1±.10	1.02±.07	7.23±.51
1-6-1-3-4-4-4-2-5-3-1	6	37	13	..	..	..	..	..	56	14.3±.10	1.14±.07	7.96±.50
1-7-1-1-1-4-7-5-2-6-1	..	..	..	5	13	30	12	2	62	21.8±.16	1.84±.11	8.43±.51
1-7-1-1-1-4-7-5-2-1-1	..	..	..	6	14	14	19	3	56	22.0±.20	2.22±.14	10.10±.64
1-7-1-1-1-4-7-5-4-7-2	..	..	..	1	16	23	11	1	52	21.8±.15	1.63±.11	7.48±.49
1-7-1-1-1-4-7-5-4-5-2	..	..	1	10	13	11	1	..	36	20.1±.20	1.80±.14	8.94±.71
1-7-1-2-2-9-2-1-1-4-1	..	12	22	8	1	..	..	..	43	15.9±.15	1.49±.11	9.40±.68
1-7-1-2-2-9-2-1-1-1-3	..	12	20	10	..	..	..	..	42	15.9±.15	1.45±.10	9.06±.66
1-9-1-2-4-6-7-5-6-4	..	20	30	3	2	..	..	..	55	15.5±.13	1.43±.09	9.21±.59
1-9-1-2-4-6-7-5-3-3	..	19	40	..	..	..	..	..	59	15.4±.08	.94±.06	6.08±.38

length of ear is even more than it seems from this table because the variety contained plants which produced two ears of which the second is usually smaller than the first; whereas the inbred strains almost never produce more than one ear to a plant.

The number of nodes per plant is reduced but as compared to height and length of ear this reduction is very much less. In the number of rows of grain on the cob there is a reduction in some lines and an increase in others. These tables show in the clearest manner that inbreeding has a greater effect on some characters than on others, and that segregation of characters has occurred. Perhaps the most noticeable effect of inbreeding as shown by these tables is the reduction in variability as brought out by the range and statistical constants. This reduction in variability is most apparent in the characters which are the least reduced by inbreeding—number of nodes and number of rows of grain on the ear—although the low variability is also apparent in height and length of ear. In variability, also, there is a difference between different lines.

The variability in height and length of ear of the inbred strains is higher than it should be, owing to the fact that it was difficult to obtain a perfect stand of plants, on account of poor germination of the seeds of the inbred strains. The aim was to have three plants in a hill. From four to eight seeds were planted as far as a limited supply of seed would permit, and later, thinned to three plants. In spite of this precaution it was extremely difficult to get anything like a perfect stand, so missing plants were replanted as soon as possible. These replants, owing to their late start, never entirely caught up with the other plants and are shorter in height and have smaller ears in consequence. It is unfortunate that this practice was followed because it is believed that much more reliable results would have been obtained otherwise. On the other hand missing plants introduce another source of error—that of unequal opportunity to grow. Because there was abundant seed of the variety, and it germinated well, practically complete stands of these plants were obtained.

The reduction in variability is more apparent in the details of the structure of the plants and ears which cannot be expressed statistically. The beautiful uniformity of these plants in all characteristics at the present time is one of their most striking features. This can be seen fairly well in the accompanying photographs. (Plates I to V).

In view of this fact of great uniformity and constancy as a result of inbreeding one is astonished at the statement made recently by Stout ('16) in a discussion of the results obtained from inbreeding in maize by East and Hayes. Stout says (pp. 420–421):

> "strains similar in homozygosity show widest variation indicative of spontaneous variation in natural vigor which is suggested that in such highly cultivated varieties such as corn extreme sporadic variations may be constantly occurring, a condition which is well shown by the numerous and well-known results of the ear to row test."

Several curious misconceptions are to be noted in this statement. In the first place, it has never been maintained by anyone to my knowledge that an equal number of generations of inbreeding produce an equal amount of homozgosity in different lines. Secondly, it has never been proposed that the degree of heterozygosity determined the form or structure of any organism, but that such a condition was accompanied by a stimulus to development which merely increased the expression of many hereditary factors. This stimulus is considered to be without any great effect *in itself* on variability. Granted that the inbred strains were equal in homozygosity at that time, that was no reason why they should be similar in vigor or in any other respect—in fact the expectation is exactly the reverse of this. With regard to "spontaneous" and "sporadic" variation these inbred strains show unmistakably that there is practically no sporadic or spontaneous variation, that the individuals making up an inbred strain are remarkably constant and uniform after some degree of homozygosity is obtained and that the diversity between different lines can be perfectly accounted for on the basis of segregation of characters. Also, in the following paragraphs in his paper Stout fails to see the distinction between crosses of diverse inbred lines and between crosses of non-inbred commercial varieties. Because Collins ('14) and Hayes ('14) failed to obtain increases in all crosses between commercial varieties of similar type Stout would question whether crossing in maize was ever beneficial. It is quite to be expected that there are many varieties already so widely crossed that further crossing does not result in greater heterozygosity, but may even reduce it. It is only in crosses between somewhat different varieties, like flint and dent (Jones and Hayes '17) or between varieties from different geographical regions (Collins '10) that any great amount of heterosis in naturally widely crossed varieties is to be expected.

Although there has been a striking reduction in size of plant, general vegetative vigor and productiveness in these inbred strains of maize, and in comparison with non-inbred varieties the inbred plants are more difficult to grow, emphasis must be put on the fact that the plants are normal and healthy. The monstrosities which are common in every field of maize, such as the occurrence of seeds in the tassels, anthers in the ears, dwarf plants, completely sterile plants, mosaic and albino plants and other similar anomalies never appear in these inbred strains. Furthermore, in the details of the size, shape, structure and position of the tassels, leaves, stalks and ears, these inbred strains show the most striking uniformity. These minor details which characterize each of these groups of plants are difficult to describe but are perhaps the most noticeable feature about them. The stalks, the tassels or the ears of all of these four Leaming strains if mixed together could be separated without the slightest difficulty by anyone familiar with them. Some of the differences which characterize the ears of these four strains are shown in Plate Ib. It is to be noticed in this photograph that Nos. 1–7–1–2 and 1–7–1–1, which were originally from the same line, both have flat cobs. In one of them, however, it is colored, in the other uncolored. Other differences are to be seen in shape and color of seeds.

The segregation of row number accompanied by a reduction in variability in these two strains is shown in Table 8 and Fig II. Data previous to the third generation are not available but since then a noticeable change in average row number has taken place without any selection one way or the other. The variability of each line has decreased at the same time. Whether the increase in variability, after the eighth generation, has any significance is not known. It is possibly due to the fact that both lines have become irregular in row number so that the correct determination of the row number has been rendered more difficult in the later generations. Also the number of plants grown in the generations from the 7th to the 10th are much too few to base accurate conclusions upon. The sharp increase in average row number and decrease in variability in the 8th generation are probably due to the unusually favorable growing conditions of that year.

TABLE 8. REDUCTION IN VARIABILITY AND SEGREGATION OF EAR ROW NUMBER IN INBRED STRAINS OF MAIZE.

Year grown.	Generations selfed.	Pedigree number.	Number of rows of grain on the ear.									N.	A.	C. V.
			12	14	16	18	20	22	24	26	28			
1908	3	1-7-1-1	3	3	4	6	27	7	4	1	2	57	19.7±.30	17.00±1.10
1908	3	1-7-1-2	..	..	..	..	..	..	..	..	..	..	....	....
1910	4	1-7-1-1-1	..	2	5	11	17	19	6	1	..	61	20.2±.22	12.67± .78
1910	4	1-7-1-2-2	..	..	2	8	14	9	5	1	..	39	20.5±.25	11.20± .86
1911	5	1-7-1-1-1-4	..	..	3	4	10	16	4	1	..	38	20.9±.25	10.92± .85
1911	5	1-7-1-2-2-9	..	..	14	29	21	1	..	..	..	65	18.3±.13	8.34± .49
1912	6	1-7-1-1-1-4-7	..	..	..	..	..	..	..	..	..	..	....	....
1912	6	1-7-1-2-2-9-2	..	..	..	..	..	..	..	..	..	..	....	....
1913	7	1-7-1-1-1-4-7-5	..	..	1	3	5	1	..	..	..	10	19.2±.34	8.33±1.26
1913	7	1-7-1-2-2-9-2-1	..	4	12	2	..	..	..	..	..	18	15.8±.18	7.16± .80
1914	8	1-7-1-1-1-4-7-5-4	..	..	..	1	9	16	6	..	..	32	21.7±.18	4.72± .40
1914	8	1-7-1-2-2-9-2-1-1	..	..	17	20	6	..	..	..	..	43	17.5±.14	7.83± .57
1915	9	1-7-1-1-1-4-7-5-4-5	..	..	..	1	14	4	2	..	..	21	20.7±.21	6.90± .72
1915	9	1-7-1-2-2-9-2-1-1-4	..	6	16	7	..	..	..	..	..	29	16.1±.17	8.33± .74
1916	10	1-7-1-1-1-4-7-5-4-5-2	..	..	1	10	13	11	1	..	..	36	20.1±.20	8.94± .71
1916	10	1-7-1-2-2-9-2-1-1-4-3	..	12	22	8	1	..	..	..	..	43	15.9±.15	9.40± .68
1917	11	1-7-1-1-1-4-7-5-4-5-2-1	..	..	3	20	43	22	7	..	..	95	20.2±.13	9.15± .45
1917	11	1-7-1-2-2-9-2-1-1-4-3-1	3	23	45	22	2	..	..	..	..	95	15.9±.11	10.39± .51

pollen suffices for fertilization when conditions are right. For that reason unconscious selection for good ovule production has been much more rigid than for pollen production. That is the reason, I believe, that more inbred strains now show a greater reduction in the staminate function than in the pistillate.

A significant feature of the effect of inbreeding upon sterility is that some inbred strains are perfectly normal in their production of pollen, and the amount of pollen produced is only a little less than non-inbred plants, owing to the reduced vigor and size of the plants which produce the tassels. Out of about twenty-five inbred strains carried through at least seven generations, three of them are perfectly normal in the structure and function of their staminate parts. One of the Leaming strains (No. 1–9) produces more pollen than many non-inbred varieties growing nearby. In every case, however, those plants which produce the best developed ears are the poorest producers of pollen, and those strains which produce abundant pollen have ears which are poorly developed. In other words, inbreeding is bringing about a tendency for maize to change from a functionally monoecious plant to a functionally dioecious plant although, morphologically, both staminate and pistillate parts are still present. This is illustrated in Plates VI, a and b, where tassels and ears of four of the inbred strains are shown.

Although no systematic selection has been practiced throughout the inbreeding experiment a great deal of selection upon many characters has been unavoidable as it is unavoidable in any inbreeding experiment. In maize, the difficulties of hand pollination result in the selection of plants whose staminate and pistillate parts are matured synchronously. Any great differences in this respect, particularly towards proterandry, would render self-fertilization difficult or impossible, as pollen, according to Andronescu ('15) has very short viability, which fact my own experience confirms. Of course, all plants which are weak, sterile, diseased or in any way abnormal tend to become eliminated wherever these causes reduce the chance of obtaining seed. This unconscious selection becomes more rigid as reduction in vigor and productiveness increases in the later generations of inbreeding. The small amount of seed produced by hand pollination, under the most favorable circumstances necessitates the using of the best ears obtained for planting in order to have enough plants upon which to make any fair observations.

In every case inbreeding in maize has so far resulted in a reduction in size, vigor and productiveness. Some thirty or forty inbred strains have been observed, many of which are additional to the ones reported previously.

From the preceding statements in regard to the effect of inbreeding it can be said that this process produces types which differ in their power of development as follows:

1. Plants which cannot be perpetuated.
2. Plants which fail to complete normal development and can be propagated only with the greatest difficulty.
3. Plants which are perfectly normal but varying in the amount of growth they attain at maturity.

These normal inbred plants, so far obtained in maize, are not as a rule as large, vigorous or productive as the original cross-fertilized plants. It is theoretically possible to obtain such plants, which cannot be reduced in vigor in a homozygous condition as will be explained later. There is some evidence from the experiments of Darwin, that such plants have been obtained by inbreeding in other material, for example, in Ipomea and Mimulus. Selection will help to obtain these vigorous, unreduceable individuals but may not be fully effective in doing so. More or less unconscious selection is unavoidable in any inbreeding experiment.

These homozygous, normal, inbred strains, after the reduction in growth has ceased, are quite comparable to plants of a naturally self-fertilized species. Darwin found that self-pollination caused no reduction in vigor in Nicotiana, Pisum, Lathyrus, Phaseolus and other genera which are naturally self-fertilized to a large extent. Hayes and Jones ('17) have found similar results with the tomato. The only effect that inbreeding may have on such plants is merely to isolate pure lines, which are quite uniform among themselves, but may be diverse from one another, as shown by soy beans (Jones and Hayes ('17), but which show no reduction in vigor on continued artificial inbreeding. These results are perfectly in accord with Johannsen's genotype conception.

The Approach to Complete Homozygosity.

It now remains to be seen whether or not these inbred strains are reaching the limit of reduction. There are two ways of determining this, one is by growing two successive inbred generations side by side in the same year, the other is by crossing different plants within the same inbred strain.

In Table 9 the results from two successive generations grown side by side in the same year are compared. On the whole, an additional year of inbreeding after the sixth produces very little change. In Table 10 are given the height, yield and length of ear of selfed and sib-crossed plants which were grown in 1917. In 1916, in each of the strains of which figures are given in the table, some plants were selfed and some were crossed by another plant within the same strain. Since all the plants grown that year in any one strain came from one individual of the preceding generation, that generation is the significant one. In other words if the plant in that generation was homozygous, no increase of the sib-crossed plants over the selfed plants would be expected. The figures show that there is, on the whole, a slight increase in all the characters studied. The increase, however, is no greater in the cases where the common ancestor was inbred for seven generations than in the cases where it was inbred nine generations.

Shull ('11) compared sib-crosses with selfed plants in which the significant generation, as I understand it, was the fourth, and found that the crossed plants slightly excelled the selfed plants in height, number of rows on the ear and yield of grain. Similarly the F_1 × Sibs exceeded F_1 × self in yield, showing that in the fourth generation complete homozygosis had not been attained.

Whether or not complete homozygosis has been attained by some or all of the strains shown in Table 10 cannot be stated positively from the data given. In most cases the increase of the sib-crosses over the selfs is slight and probably of no significance as there are about an equal number of cases in which the reverse condition is shown. A few of the sib-crosses are, however, considerably greater than the selfs in all three characters and it may very well be that these strains have not attained the degree of homozygosity that the other strains have. More data are needed to establish this point with certainty as environmental factors which favored a certain plot in one character would also favor the other character as well.

Table 9. The yield, height and length of ear of two successive inbred generations of maize both grown side by side in the same year.

Pedigree number in the Nth generation	Generations compared		Yield: bu. per acre		Difference of (N+1) above N	Height of plant in inches		Difference of (N+1) above N	Length of ear in inches		Difference of (N+1) above N
	N	(N+1)	N	(N+1)		N	(N+1)		N	(N+1)	
65-8-2-2-6-5-2...	6	7	20.9	28.4	+ 7.5	53.3 ± .47	54.3 ± .41	+1.0 ± .62	5.4 ± .12	5.6 ± .09	+.2 ± .15
1-9-1-2-4-6-7-5-3..	8	9	28.8	30.5	+ 1.7	78.0 ± .57	80.3 ± .35	+2.3 ± .67	6.1 ± .08	5.9 ± .05	—.2 ± .09
1-7-1-2-2-9-2-1-1-4	9	10	26.3	20.0	— 6.3	83.9 ± .45	82.6 ± .61	—1.3 ± .76	5.4 ± .09	5.1 ± .12	—.3 ± .15
1-7-1-1-1-4-7-5-2-1	9	10	44.5	30.4	—14.1	84.8 ± .64	82.2 ± .77	—2.6 ± 1.00	4.7 ± .07	4.2 ± .08	—.5 ± .11
1-7-1-1-1-4-7-5-4-5	9	10	....	....	......	88.5 ± .47	88.7 ± .70	+ .2 ± .84	4.4 ± .08	4.2 ± .09	—.2 ± .12
1-6-1-3-4-4-4-2-4-4	9	10	46.3	34.9	—11.4	100.6 ± .44	97.8 ± .36	—2.8 ± .57	6.2 ± .08	6.1 ± .09	—.1 ± .12
1-6-1-3-4-4-4-2-5-3	9	10	29.7	31.5	+ 1.8	98.2 ± .44	102.7 ± .47	+4.5 ± .64	6.4 ± .12	6.9 ± .10	+5. ± .16
Average.......			32.8	29.3	— 3.5	83.9	84.1	+ .2	5.5	5.4	—.1

TABLE 10. A COMPARISON OF THE HEIGHT, YIELD OF GRAIN AND LENGTH OF EAR OF SELFED STRAINS OF MAIZE WITH CROSSES BETWEEN INDIVIDUAL PLANTS WITHIN THE STRAINS.

Pedigree number	Significant generation	Height of plant in inches			Yield of grain in lbs. per plant			Length of ear in inches		
		Selfed strains	Sib crosses	Difference of sib crosses above selfed	Selfed strains	Sib crosses	Difference of sib crosses above selfed	Selfed strains	Sib crosses	Difference of sib crosses above selfed
10-3-7-3-9-7-5-1-1......	7	91.3±.58	93.4±.50	+2.1±.77	.25	.20	−.05	5.8±.02	6.4±.08	+.6±.08
10-3-7-3-9-7-5-4-2......	7	93.1±.53	94.2±.52	+1.1±.74	.26	.31	+.05	6.4±.06	6.1±.06	−.3±.08
10-4-8-3-5-3-4-8-2......	7	89.6±.53	87.1±.73	−2.5±.90	.31	.40	+.09	5.3±.07	5.0±.06	−.3±.09
10-4-8-3-5-3-4-5-2......	7	94.4±.56	95.9±.46	+1.5±.73	.38	.34	−.04	5.6±.08	5.9±.07	+.3±.09
1-9-1-2-4-6-7-5-6-2....	8	82.7±.29	81.6±.29	−1.1±.41	.24	.19	−.05	5.7±.06	4.9±.06	−.8±.08
1-9-1-2-4-6-7-5-3-2....	8	82.0±.33	84.2±.37	+2.2±.50	.20	.19	−.01	5.3±.05	5.7±.04	+.4±.06
1-6-1-3-4-4-4-2-4-4-2...	9	103.0±.42	109.4±.36	+6.4±.55	.33	.47	+.14	6.1±.08	6.9±.06	+.8±.10
1-6-1-3-4-4-4-2-4-1-3...	9	113.5±.37	109.9±.58	−3.6±.69	.44	.36	−.08	7.5±.04	7.2±.04	−.3±.06
1-6-1-3-4-4-4-2-5-3-2...	9	102.6±.53	103.4±.36	+ .8±.64	.40	.44	+.04	7.2±.06	7.3±.06	+.1±.08
1-6-1-3-4-4-4-2-5-5-2...	9	95.6±.50	95.2±.63	− .4±.80	.37	.40	+.03	6.9±.08	6.6±.10	−.3±.13
1-7-1-2-2-9-2-1-1-4-3...	9	83.8±.63	85.9±.57	+2.1±.85	.20	.26	+.06	4.5±.08	4.9±.07	+.4±.11
1-7-1-1-1-4-7-5-4-5-2...	9	83.8±.53	81.5±.60	−2.3±.80	.23	.24	+.01	3.9±.07	3.8±.05	−.1±.09
1-7-1-1-1-4-7-5-4-7-1...	9	76.1±.72	81.2±.53	+5.1±.89	.15	.23	+.08	3.5±.06	3.7±.05	+.2±.08
1-7-1-1-1-4-7-5-2-1-1...	9	78.7±.60	80.2±.55	+1.5±.81	.29	.19	−.10	4.1±.07	3.8±.06	−.3±.09
1-7-1-1-1-4-7-5-2-6-1...	9	75.6±.49	78.3±.55	+2.7±.74	.26	.35	+.09	3.8±.05	3.9±.06	+.1±.08
Average..............		89.7	90.8	+1.1	.29	.30	+.01	5.4	5.5	+.1

THE EFFECT OF HETEROZYGOSIS ON VEGETATIVE LUXURIANCE.

The most noticeable manifestation of heterosis in plants is a general increase in vegetative luxuriance. In maize this is particularly noticeable in increased height of plant, diameter of stalk, root development, length of ear and productiveness of grain (see Plates III, V, VII, VIII, IX, X and XII). In crosses between inbred strains of maize the amount of heterosis shown is inversely proportional to the degree of relationship as shown in Table 11. Montgomery ('12) has obtained similar results.

Some characters are much more affected by heterozygosis than others. In comparing Tables 12, 13 and 14 with Tables 15 and 16 it will be noticed that the yield of the crosses is increased 180 per cent., height is increased 27 per cent. and length of ear 29 per cent. over the average of their parental lines. On the other hand, the number of nodes per plant and number of rows of grain on the ear is increased only 6 and 5 per cent. respectively. In other words, heterozygosis does not increase the number of parts to anything like the extent that it increases the size of those parts. Those parts of the plants which are more or less indeterminate in size, like internodes, ears and seeds are augmented by crossing as the result of an increase in the rapidity and rate of cell division. The increase in size of parts is probably brought about by an increase in size of cells as well as an enormous increase in number of cells. Tupper and Bartlett ('16) have shown that *gigas* mutants in *Oenothera* have larger cells than the non-mutant type, so that a change in cell size may accompany a germinal change.

From Table 11 it will also be seen that some first generation hybrids may even surpass the original variety in yield, height or length of ear, although the comparison is rather unfair as the Leaming variety was not acclimatized as were the inbred strains. The return of vigor realized in the first generation crosses is often enormous, and the same is true of crossing inbred strains derived from totally different types of maize as is shown in Table 17.

Although there is an immediate and striking return to the vigorous condition of the non-inbred stock there is not a return in variability as shown in Tables 18, 19, 20, 21 and 22. The first generation crosses are no more variable than the inbred strains by which they are produced, in many cases less variable, and show striking differences when compared to the original stock. The coefficient of variability is entirely inadequate in bringing out

TABLE 11. THE DEGREE OF RELATIONSHIP AND THE AMOUNT OF HETEROSIS SHOWN BY INBRED STRAINS WHEN CROSSED.

Pedigree number	Significant generation	Yield bu. per acre	Increase above ave. yield of parents	Height inches	Increase above ave. height of parents	Length of ear inches	Increase above ave. length of parents
1-6-1-3-4-4-4-2-4-4-3	..	34.9	......	97.8± .36	......	6.1±.09	......
1-7-1-1-1-4-7-5-4-7-2	..	30.3	......	90.2± .46	......	4.0±.08	......
1-7-1-2-2-9-2-1-1-4-1	..	20.0	......	82.6± .61	......	5.1±.12	......
1-9-1-2-4-6-7-5-3-3	..	30.5	......	80.3± .35	......	5.9±.05	......
(1-6-1-3-4-4-4-2-4-1)×(1-6-1-3-4-4-4-2-4-4)	7	19.2	−15.7	88.4±1.12	− 9.4	5.3±.09	− .8
(1-7-1-1-1-4-7-5-2-6)×(1-7-1-1-1-4-7-5-2-1)	7	31.1	+ .8	79.2± .64	−11.0	4.5±.10	+ .5
(1-7-1-2-2-9-2-1-1-1)×(1-7-1-2-2-9-2-1-1-4)	7	23.9	+ 3.9	86.0± .63	+ 3.4	5.5±.10	+ .4
(1-9-1-2-4-6-7-5-3)×(1-9-1-2-4-6-7-5-6)	6	....	......	66.8± .48	−13.5	4.1±.10	−1.8
(1-6-1-3-4-4-4-2-4-4)×(1-6-1-3-4-4-4-2-5-5)	6	43.9	+ 9.0	103.4± .47	+ 5.6	6.7±.09	+ .6
(1-6-1-3-4-4-4-2-5-5)×(1-6-1-3-4-4-4-2-4-4)	6	....	......	98.1±1.12	+ .3	5.7±.15	− .4
(1-7-1-1-1-4-7-5-4-7)×(1-7-1-1-1-4-7-5-2-1)	6	17.5	−12.8	88.1± .74	− 2.1	4.7±.09	+ .7
(1-7-1-1-1-4-7-5-4-7)×(1-7-1-2-2-9-2-1-1-4)	1	70.9	+45.7	102.4± .44	+16.0	6.4±.12	+1.8
(1-7-1-2-2-9-2-1-1-1)×(1-7-1-1-1-4-7-5-2-6)	1	55.9	+30.7	103.1± .44	+16.7	6.3±.09	+1.7
(1-7-1-2-2-9-2-1-1-1)×(1-7-1-1-1-4-7-5-4-5)	1	58.4	+33.2	103.0± .50	+16.6	6.5±.08	+1.9
(1-6-1-3-4-4-4-2-4-1)×(1-7-1-2-2-9-2-1-1-1)	0	101.0	+73.5	121.9± .46	+31.7	7.9±.10	+2.3
(1-7-1-2-2-9-2-1-1-4)×(1-9-1-2-4-6-7-5-3)	0	82.1	+56.8	109.5± .76	+28.0	7.6±.13	+2.1
(1-9-1-2-4-6-7-5-3)×(1-6-1-3-4-4-4-2-4-1)	0	71.5	+38.8	110.5± .58	+21.4	7.6±.09	+1.6
1 Non-inbred variety	...	80.8	......	116.3± .90	......	7.6±.11	......

TABLE 12. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE YIELD OF GRAIN.

Pedigree number of strain—A	Yield of bushels per acre				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	34.9	99.1	99.9	30.3	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	34.9	112.9	....	37.4	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	34.9	82.4	....	30.7	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	31.9	101.0	....	18.3	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	16.8	88.1	84.4	30.3	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	16.8	106.2	106.7	20.0	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	16.8	91.0	....	30.7	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	31.5	94.8	....	30.4	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	30.5	63.9	....	31.5	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	30.5	71.5	....	31.9	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	30.5	58.0	....	30.4	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	30.5	52.5	100.5	18.9	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	30.5	59.6	82.1	20.0	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	30.7	66.3	....	18.3	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	20.0	84.9	....	34.9	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	37.4	40.5	....	16.8	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	30.4	59.4	....	31.9	1-6-1-3-4-4-4-2-4-1
Average	28.8	78.4		27.2	
Increase		50.4			
Percent increase		180.00			

TABLE 13. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE HEIGHT OF PLANT.

Pedigree number of strain—A	Height of plant in inches				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	97.8±.36	117.3± .61	117.2±.44	90.2±.46	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	97.8±.36	117.6± .38	....	78.5±.71	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	97.8±.36	115.4± .56	....	77.0±.52	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	96.7±.37	121.9± .46	....	91.2±.68	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	93.6±.57	112.9±1.04	109.9± .77	90.2±.46	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	93.6±.57	116.1± .41	113.4± .51	82.6±.61	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	93.6±.57	113.8± .40	....	77.0±.52	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	102.7±.47	116.0± .42	....	82.2±.77	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	80.3±.35	111.1± .61	....	102.7±.47	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	80.3±.35	110.5± .58	....	96.7±.37	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	80.3±.35	109.2± .76	94.0±1.36	82.2±.77	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	80.3±.35	110.9± .60	114.1± .55	88.7±.70	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	80.3±.35	108.1± .50	109.5± .76	82.6±.61	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	77.0±.52	111.1± .58	....	91.2±.68	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	82.6±.61	114.9± .68	....	97.8±.36	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	78.5±.71	98.7± .78	....	93.6±.57	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	82.2±.77	105.2± .71	....	96.7±.37	1-6-1-3-4-4-4-2-4-1
Average	88.0	112.4		88.3	
Increase		24.2			
Percent increase		27.44			

TABLE 14. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE LENGTH OF EAR.

Pedigree number of strain—A	Length of ear in inches				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.1±.11	7.3±.10	4.0±.08	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.5±.11	....	4.3±.06	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.8±.08	....	6.1±.08	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	6.2±.07	7.9±.10	....	5.3±.09	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.0±.16	7.5±.12	6.8±.15	4.0±.08	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.0±.16	8.2±.08	8.0±.09	5.1±.12	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.0±.16	7.8±.08	....	6.1±.08	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	6.9±.10	7.6±.09	....	4.2±.08	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.9±.05	7.7±.09	....	6.9±.10	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.9±.05	7.6±.09	....	6.2±.07	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.9±.05	6.5±.12	5.5±.11	4.2±.08	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.9±.05	6.5±.10	7.6±.09	4.2±.09	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.9±.05	7.1±.12	7.6±.13	5.1±.12	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	6.1±.08	7.1±.11	....	5.3±.09	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	5.1±.12	7.6±.14	....	6.1±.09	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	4.3±.06	5.5±.12	....	6.0±.16	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	4.2±.08	6.0±.10	....	6.2±.07	1-6-1-3-4-4-4-2-4-1
Average..........	5.8	7.2		5.3	
Increase..........		1.6			
Percent increase....		28.57			

TABLE 15. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE NUMBER OF NODES.

Pedigree number of strain—A	Number of nodes				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	12.7±.06	13.6±.07	13.2±.07	12.2±.07	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	12.7±.06	13.3±.04	....	11.8±.07	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	12.7±.06	14.0±.05	....	12.9±.07	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	11.5±.05	14.0±.05	....	13.0±.08	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	12.4±.08	12.9±.08	13.2±.05	12.2±.07	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	12.4±.08	13.5±.06	13.1±.06	12.1±.09	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	12.4±.08	13.4±.06	....	12.9±.07	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	12.2±.06	13.3±.06	....	11.6±.10	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	13.1±.06	12.8±.03	....	12.2±.06	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	13.1±.06	12.9±.06	....	11.5±.05	1-6-1-3-4-4-4-2-4-3
1-9-1-2-4-6-7-5-3	13.1±.06	13.2±.06	12.5±.13	11.6±.10	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	13.1±.06	13.3±.06	14.0±.06	12.7±.10	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	13.1±.06	13.3±.07	13.7±.07	12.1±.09	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	12.9±.07	13.7±.06	....	13.0±.08	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	12.1±.09	13.6±.06	....	12.7±.06	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	11.8±.07	11.3±.07	....	12.4±.08	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	11.6±.10	12.6±.07	....	11.5±.05	1-6-1-3-4-4-4-2-4-1
Average..........	12.5	13.2		12.3	
Increase..........		.8			
Percent increase....		6.45			

TABLE 16. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE NUMBER OF ROWS OF GRAIN ON THE EAR.

Pedigree number of strain—A	Number of rows of grain on the ear				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	16.9±.14	19.5±.15	20.8±.15	21.8±.15	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	16.9±.14	19.5±.13	....	21.8±.16	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	16.9±.14	17.2±.13	....	15.5±.13	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	15.7±.09	18.4±.13	....	15.9±.15	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	14.1±.10	17.4±.11	18.3±.14	21.8±.15	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	14.1±.10	16.9±.10	18.2±.13	15.9±.15	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	14.1±.10	17.0±.10	....	15.5±.13	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	14.3±.10	19.4±.15	....	22.0±.20	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	15.4±.08	15.7±.11	....	14.3±.10	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	15.4±.08	16.7±.12	....	15.7±.09	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	15.4±.08	19.9±.20	18.7±.25	22.0±.20	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	15.4±.08	17.8±.14	19.0±.17	20.1±.20	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	15.4±.08	16.8±.17	16.2±.09	15.9±.15	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	15.5±.13	16.2±.14	....	15.9±.15	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	15.9±.15	19.3±.17	....	16.9±.14	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	21.8±.16	17.6±.14	....	14.1±.10	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	22.0±.20	19.8±.16	....	15.7±.09	1-6-1-3-4-4-4-2-4-1
Average..........	16.2	17.9		17.7	
Increase..........		.9			
Percent increase....		5.29			

TABLE 17. THE EFFECT OF CROSSING INBRED STRAINS DERIVED FROM DIFFERENT TYPES OF MAIZE.

Type	Pedigree number	Yield bu. per acre	Increase above ave. of parents	Height inches	Increase above ave. of parents	Length of ear inches	Increase above ave. of parents
Dent..........	1-6-1-3-4-4-4-2-4-4-3	34.9	....	97.8	....	6.1	....
Floury........	10-3-7-3-9-7-5-4-3.....	10.4	....	75.5	....	6.1	....
Flint..........	29-5-2-3-8..........	9.2	....	88.7	....	5.9	....
Pop..........	65-8-2-2-6-5-2-4......	28.4	....	54.3	....	5.6	....
Dent×Floury..	(1-6-1-3)×(10-3-7-3)..	90.4	+67.7	122.8	+36.1	9.1	+3.0
Dent×Flint...	(1-6-1-3)×(29-5-2-3)..	94.6	+72.5	117.5	+24.2	8.9	+2.9
Floury×Dent..	(10-3-7-3)×(1-6-1-3)..	43.3	+20.6	108.2	+21.5	7.4	+1.3
Floury×Flint..	(10-3-7-3)×(29-11-4-4)	61.1	+51.3	104.5	+22.4	9.7	+3.7
Flint×Dent...	(29-5-2-3)×(1-6-1-3)..	80.7	+58.6	115.7	+22.4	9.6	+3.6
Flint×Floury..	(29-5-2-3)×(10-3-7-3).	73.0	+63.2	112.9	+30.8	10.0	+4.0
Pop×Dent....	(65-8-2-2)×(1-6-1-3)..	73.1	+41.4	88.9	+12.8	7.2	+1.3
Pop×Flint....	(65-8-2-2)×(5-8-6-3)..	51.3	......	79.5	......	7.1	.....

TABLE 18. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE HEIGHT OF PLANT.

Pedigree number of strain—A	Coefficient of variability of height				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	4.14±.26	6.10±.37	4.01±.26	5.49±.36	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	4.14±.26	3.74±.23	....	9.75±.64	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	4.14±.26	5.55±.34	....	7.73±.48	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	4.40±.27	4.22±.27	....	7.95±.52	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.14±.43	9.92±.66	7.32±.50	5.49±.36	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.14±.43	4.09±.25	5.20±.32	8.05±.52	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.14±.43	4.00±.25	....	7.73±.48	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	5.11±.32	4.05±.26	....	10.64±.67	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.04±.31	6.66±.39	....	5.11±.32	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.04±.31	6.15±.38	....	4.40±.27	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.04±.31	7.78±.49	12.61±1.04	10.64±.67	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.04±.31	6.18±.38	5.48±.34	7.27±.56	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.04±.31	5.27±.33	7.94±.49	8.05±.52	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	7.73±.48	6.26±.38	....	7.95±.52	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	8.05±.52	6.27±.41	....	4.14±.26	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	9.75±.64	8.81±.56	....	6.14±.43	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	10.64±.67	7.41±.47	....	4.40±.27	1-6-1-3-4-4-4-2-4-1
Average..........	5.98	6.03		7.11	

TABLE 19. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE LENGTH OF EAR.

Pedigree number of strain—A	Coefficient of variability of length of ear				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	17.17±1.18	19.86±1.18	16.99±1.05	22.75±1.51	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	17.17±1.18	17.33±1.02	....	15.58± .96	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	17.17±1.18	11.92± .74	....	13.77± .90	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	13.06± .82	14.94± .93	....	16.04±1.20	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	26.17±1.95	17.73±1.11	25.88±1.65	22.75±1.51	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	26.17±1.95	11.71± .72	12.37± .77	23.33±1.77	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	26.17±1.95	12.44± .76	....	13.77± .90	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	16.23±1.05	13.55± .85	....	20.00±1.31	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	9.32± .58	14.16± .87	....	16.23±1.05	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	9.32± .58	13.82± .84	....	13.06± .82	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	9.32± .58	20.46±1.36	15.45±1.47	20.00±1.31	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	9.32± .58	17.69±1.15	13.55± .83	19.76±1.62	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	9.32± .58	18.87±1.23	20.26±1.26	23.33±1.77	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	13.77± .90	18.73±1.16	....	16.04±1.20	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	23.33±1.77	19.87±1.30	....	17.17±1.18	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	15.58± .96	24.91±1.66	....	26.17±1.95	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	20.00±1.31	18.83±1.21	....	13.06± .82	1-6-1-3-4-4-4-2-4-1
Average..........	16.39	16.87		18.40	

TABLE 20. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE NUMBER OF NODES.

Pedigree number of strain—A	Coefficient of variability of number of nodes				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	5.12±.32	5.88±.36	5.91±.37	6.23±.39	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	5.12±.32	3.68±.22	....	6.27±.40	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	5.12±.32	4.50±.27	....	6.67±.41	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	4.61±.28	4.00±.25	....	6.77±.45	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.94±.47	6.82±.43	4.09±.27	6.23±.39	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.94±.47	5.48±.32	5.34±.33	7.93±.50	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.94±.47	5.67±.35	....	6.67±.41	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	5.98±.37	5.19±.32	....	9.66±.60	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.47±.33	....	5.98±.37	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.11±.31	5.66±.35	....	4.61±.28	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.53±.34	8.72±.73	9.66±.60	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.41±.34	4.93±.30	7.48±.56	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.11±.31	5.86±.36	6.20±.38	7.93±.50	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	6.67±.41	5.62±.34	....	6.77±.45	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	7.93±.50	5.15±.33	....	5.12±.32	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	6.27±.40	7.61±.47	....	6.94±.47	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	9.66±.60	6.67±.42	....	4.61±.28	1-6-1-3-4-4-4-2-4-1
Average..........	6.05	5.54		6.80	

TABLE 21. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE NUMBER OF ROWS OF GRAIN ON THE EAR.

Pedigree number of strain—A	Coefficient of variability of number of rows				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	9.83±.61	9.73±.55	8.68±.52	7.48±.49	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	9.83±.61	8.50±.48	....	8.43±.51	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	9.83±.61	8.79±.54	....	9.21±.59	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	6.48±.40	7.96±.49	....	9.06±.66	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	7.23±.51	7.31±.45	9.24±.55	7.48±.49	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	7.23±.51	6.62±.40	8.11±.49	9.40±.68	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	7.23±.51	6.60±.40	....	9.21±.59	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	7.96±.50	8.92±.55	....	10.10±.64	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	6.08±.38	8.00±.48	....	7.96±.50	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	6.08±.38	8.36±.50	....	6.48±.40	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	6.08±.38	11.11±.72	10.32±.98	10.10±.64	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	6.08±.38	8.92±.56	10.62±.65	8.94±.71	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	6.08±.38	11.35±.72	7.02±.42	9.40±.68	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	9.21±.59	10.42±.63	....	9.06±.66	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	9.40±.68	9.68±.63	....	9.83±.61	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	8.43±.51	8.75±.56	....	7.23±.51	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	10.10±.64	8.84±.56	....	6.48±.40	1-6-1-3-4-4-4-2-4-1
Average..........	7.83	8.82		8.58	

E 22. FREQUENCY DISTRIBUTION OF HEIGHT OF PLANT OF A NON-INBRED VARIETY OF MAIZE, OF SEVERAL INBRED STRAINS DERIVED FROM THIS VARIETY AND FIRST GENERATION CROSSES BETWEEN THESE INBRED STRAINS.

Pedigree number	Height of plant in inches																	N.	A.	C. V.
	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	113.5	118.5	123.5	128.5	133.5	138.5	143.5			
....	..	..	..	..	..	..	1	1	4	15	8	9	6	7	3	0	1	55	116.3 ± .90	8.64 ± .55
3-4-4-4-2-4-4-3....................	..	..	..	..	..	4	11	30	11	..	..	..	..	..	..	..	..	56	97.8 ± .36	4.14 ± .26
1-1-4-7-5-4-7-2....................	..	..	1	3	3	18	26	2	..	..	..	..	..	..	..	..	..	53	90.2 ± .46	5.49 ± .36
2-2-9-2-1-1-4-1....................	1	1	8	9	18	13	3	1	..	..	..	..	..	..	..	..	..	54	82.6 ± .61	8.05 ± .52
2-4-6-7-5-3-3......................	..	..	10	22	25	3	..	..	..	..	..	..	..	..	..	..	..	60	80.3 ± .35	5.04 ± .31
-3-4-4-4-2-4-4) × (1-7-1-1-1-4-7-5-4-7).	..	..	..	..	..	..	2	2	1	2	9	27	17	1	..	..	..	61	117.3 ± .61	6.10 ± .37
-3-4-4-4-2-4-1) × (1-7-1-2-2-9-2-1-1-1).	..	..	..	..	..	..	1	0	0	1	2	10	39	4	..	..	..	57	121.9 ± .46	4.22 ± .27
-3-4-4-4-2-4-4) × (1-9-1-2-4-6-7-5-6)...	..	..	..	..	1	0	0	1	2	3	20	26	6	..	..	..	..	59	115.4 ± .56	5.55 ± .34
-1-1-4-7-5-2-6) × (1-6-1-3-4-4-4-2-5-5).	..	1	0	2	3	3	5	14	20	8	..	..	..	..	..	..	..	56	98.7 ± .78	8.81 ± .56
-1-1-4-7-5-4-5) × (1-9-1-2-4-6-7-5-3)...	..	..	..	..	..	..	..	2	6	6	19	19	6	..	..	..	..	58	114.1 ± .55	5.48 ± .34
-2-2-9-2-1-1-4) × (1-6-1-3-4-4-4-2-4-4).	..	..	..	..	..	..	2	0	2	9	13	18	4	3	..	..	..	51	114.9 ± .68	6.27 ± .41
-2-2-9-2-1-1-4) × (1-9-1-2-4-6-7-5-3)...	..	..	1	0	1	0	1	3	10	14	23	6	..	..	..	..	..	59	109.5 ± .76	7.94 ± .49
-2-4-6-7-5-3) × (1-6-1-3-4-4-4-2-5-3)...	..	..	..	..	..	3	2	0	5	16	23	17	..	..	..	..	..	66	111.1 ± .61	6.66 ± .39
-2-4-6-7-5-3) × (1-7-1-1-1-4-7-5-2-1)...	..	..	..	..	..	2	2	9	5	8	18	12	1	..	..	..	..	57	109.2 ± .76	7.78 ± .49
-2-4-6-7-5-3) × (1-7-1-2-2-9-2-1-1-4)...	..	..	..	..	..	2	1	4	7	25	19	1	..	..	..	..	..	59	108.1 ± .50	5.27 ± .33

the beautiful uniformity of these crosses between inbred strains. In every respect each plant is a replica of the other. A collection of such vigorous and uniform maize plants in the field is a novel sight (see Plates IIIb and Vb).

Shull ('14) has pointed out that vigorous plants may be less susceptible to the effect of the environment than weaker types and that first generation hybrids, between uniform strains, may even show a reduction in variability.

The results obtained show this quite noticeably. Particularly was this true of several F_1's grown between their parental strains in a demonstration plot on rich low ground. During both seasons (1916–'17) when they were grown on this piece of ground, the weather was especially unfavorable when the plants were just starting, the ground being saturated with water most of the time. The germination in the selfed lines was extremely poor and many plants which did grow were stunted, and remained so throughout the season and never attained full height nor did they produce either tassels or ears. The variability of height, in these plants, was far greater than in many non-inbred varieties. Several plants, when killed by frost in the fall, were not over 30 inches tall while the average height of this strain is from 80 to 85 inches. The hybrids also had a poorer start than non-inbred varieties grown on the same ground on account of the small seed, but were able to overcome their handicap and in a few weeks were quite uniform. At the end of the season the difference in variability between the F_1 on the one hand and the inbred strains and the varieties on the other was striking. These plants were not used in the statistical work given here. The crosses and parents which were used and which were apparently quite uniform show a slight reduction in variability, in the number of nodes and in height in the F_1's as compared with their parents as can be seen in Tables 18 and 20. As Shull also pointed out, the variability of some characters may be increased by heterosis. This is shown in number of rows on the ear. The inbred strains rarely or never produce a second ear. The vigorous hybrids almost always do, and as the data have been obtained by counting all the ears gathered from a plot, the variability of the crosses, as shown in Tables 19 and 21, consequently seems greater than it really is as the second ear on nearly every plant is smaller and contains a fewer number of rows.

Although reciprocal crosses are on the whole nearly equal in respect to the degree in which heterosis is shown, there is some evidence, from Table 12, that this is not always so. Observations from the crosses in the field showed clearly that those in which strain Number 1-6 was used as the female, were usually more vigorous and productive than the others. In Table 23 the yields of all the crosses and reciprocal crosses (from 1 to 4 of each) having the same parental races are averaged. An average of all those crosses in which each strain was used as the male and in which each was used as the female parent shows some striking results. Those crosses on the whole in which strain Number 1–9 was used as the female gave the lowest yield. Those crosses in which strain Number 1–6 was used as the female are clearly the most productive. Strain Number 1–6 is the one which has the largest seeds and in which the pistillate inflorescence is the best developed of the four strains and at the expense of the staminate inflorescence.

TABLE 23. YIELD OF RECIPROCAL CROSSES AMONG INBRED STRAINS OF MAIZE.

(All crosses grown 1916. Yield given as bushels per acre.)

	1-9-1-2 ♀	1-7-1-2 ♀	1-7-1-1 ♀	1-6-1-3 ♀	Average ♂
1-9-1-2 ♂		82.1	100.5	86.7	89.8
1-7-1-2 ♂	63.0		70.9	103.6	79.2
1-7-1-1 ♂	55.3	57.2		98.7	70.4
1-6-1-3 ♂	67.7	95.8	92.2		85.2
Average ♀	62.0	78.4	87.9	96.3	
Yield selfed:- (1917)	31.8	37.6	42.3	46.2	
(1916)	30.6	19.2	32.7	32.8	
Ave. weight of seed-cg.	16.6	27.9	19.9	34.1	

Strain Number 1–9 is just the reverse of this. It is the best developed of all the inbred strains in its staminate inflorescence, always producing abundant pollen, but has the smallest seeds, and is one of the poorest in the development of its pistillate inflorescence. Approximately a uniform stand of plants was obtained in all these crossed plots. They were all grown side by side in the same field in the same year.* There seems, therefore, to be a marked correlation in the development of the pistillate inflorescence between the mother and her hybrid progeny. The high yield of the crosses in which Number 1–9 was used as the male is due to the fact that its average yield was not pulled down by the low yielding crosses in which it was used as a female. The crosses in which 1–7–1–1 and 1–7–1–2 were used cannot be compared fairly with the other two because these two strains are more closely related. This correlation bears a close relationship with the size and development of the seed which produces first generation hybrid plant. The seeds of strain 1–9 are the poorest developed, those of Number 1–6 are the best. Hence, the plants of crosses (1–6) x (1–9) have a better start than the plants of the reciprocal cross. This assumption is borne out by the fact that the second generation starting from large fully developed seeds grown on vigorous F_1 plants are larger at the start than the F_1 plants grown from small, poorly developed seeds produced on inbred plants. This is shown in Fig. III and Plate IX. The second generation, however, is surpassed by the first before the end of the season, as shown in Fig. III and Plate X. Somewhat similar results have been obtained by Castle ('16) in guinea-pigs. F_2 animals, out of vigorous F_1 females, are larger at the start than either parent but do not surpass the F_1 individuals as in this case. It will be seen from this that in plants or animals which are reduced by inbreeding, the F_1 is handicapped in comparison with the F_2 and the immediately following generations.

It is not certain that the differences between reciprocal crosses can be accounted for on a purely nutritional basis. There is the possibility of unequal germinal reactions with different cytoplasms.

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*The crossed strains were not grown between their inbred parental strains as was the case in the yields reported in U. S. Dept. of Agric., B. P. I. Bull. 243. This accounts in part for the extraordinarily large yields obtained at that time.

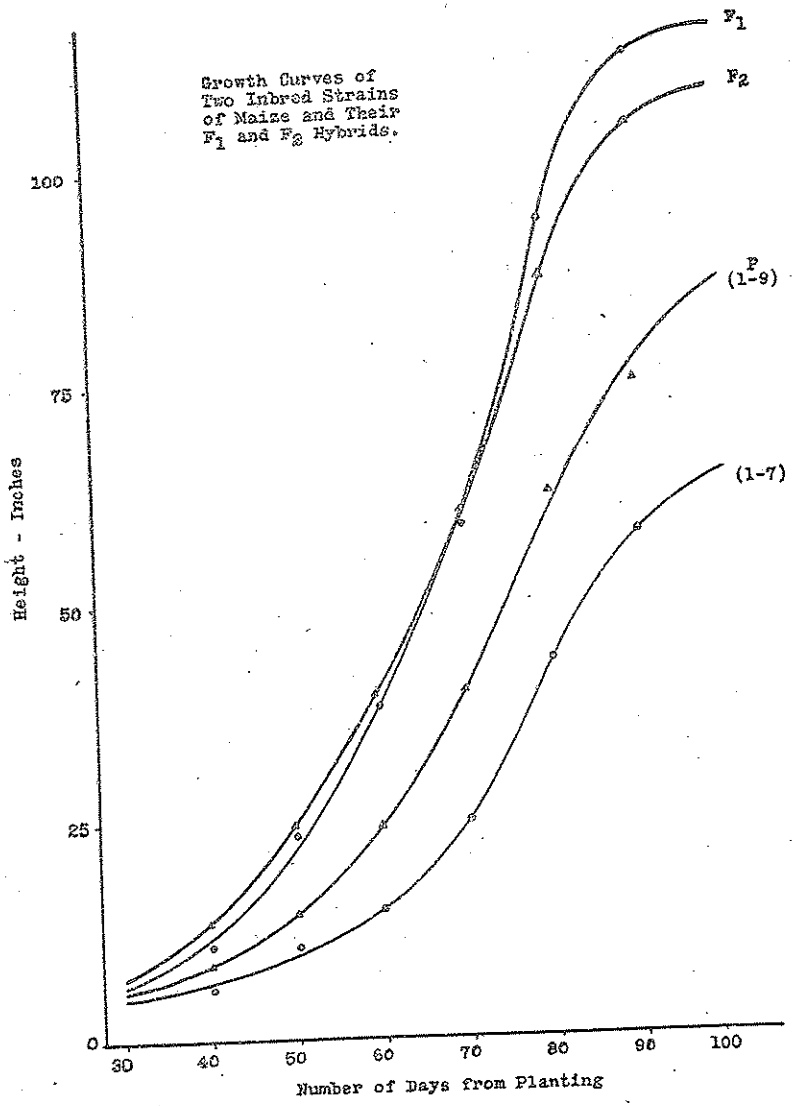


Figure III. Growth curves of two inbred strains of maize and their first and second generation hybrids.

The Value of Inbreeding in Plant and Animal Improvement.

These inbreeding and crossbreeding experiments on corn have considerable theoretical importance in the improvement of cultivated plants and domesticated animals. We have seen that inbreeding results in the elimination of abnormal, pathological and undesirable characters in general. This result has been obtained with a loss of size, vigor and productiveness. When these inbred strains are crossed, however, vigor and productiveness are returned in increased amount due to the uniform excellence of the individuals freed from undesirable characters. In this way a new variety or breed can be synthesized from the purified inbred strains of an old stock. A great sacrifice is thus made to attain a great good. Of course such a variety would have to be fixed by selection during a number of generations. The common practice of crossing in animals and plants already extremely heterozygous in order to obtain further improvement is like trying to solve a picture puzzle in the dark. It is only by resolving a naturally crossed species into homozygous types by inbreeding that it can be best analyzed and its desirable characters most surely selected for the recreation of an improved type.

The practical value of inbreeding has long been recognized by the breeders of domesticated animals. To gain uniformity and the highest expression of certain desirable characters they often practice inbreeding until the vigor of the breed is frequently impaired. From the results obtained with maize it seems that they stop just before the greatest good is to be accomplished. What if vigor is lost? It can always be regained immediately by crossing. There is no surer way of eliminating undesirable characters and discovering the best that there is in a stock than by a process of rigid inbreeding followed by subsequent testing in different crosses. This is not offered as a practical plan of procedure for the improvement of animals. It is merely intended to call attention to a principle which has probably not been used to its fullest extent. It may be that many domesticated breeds of animals cannot endure inbreeding to the extent that maize can. The cost of obtaining such pure types might very easily be prohibitive. The writer believes, however, that the splitting up of a breed of animals or a naturally crossed variety of plants by long continued inbreeding of the closest kind possible followed by the recombination of the most desirable inbred types, obtained in sufficient numbers to insure that nothing of value present in the stock at the start, is lost, is a valuable, practicable method of improvement in many animals and plants. According to this method a variety or breed would be re-created and then continued in a naturally crossed condition just as it was before. The value of this procedure as a method for plant improvement is now being tested. It is, of course, a long time proposition and one that must be carried on extensively to promise results.

With a few plants which are easily crossed it is possible to utilize hybrid vigor to the fullest extent by growing only first generation plants. Attention has been repeatedly called to this method of increasing the productiveness, particularly of maize and tomatoes. The greatest amount of hybrid vigor is shown in maize when the plants have been previously inbred. Unfortunately, when the inbreeding is carried on for several generations the reduction in the vigor of the resulting plants is so great that the small size and low vitality of the seeds borne on inbred plants seriously handicaps the hybrid plants grown from these seeds as just shown. So what is gained by an increased amount of heterosis may be partly lost by the poor start which the plants have. This handicap, in comparison with normally-crossed varieties, the F_1 may not be able to overcome entirely even though it is far more uniform and free from barren, mal-formed and otherwise undesirable plants—factors which count heavily in maximum production.

A way to overcome this handicap suggests itself which is to cross two vigorous first generation hybrids whose composition is such that the resulting cross will not be less heterozygous than either parent and, therefore, theoretically no less vigorous and productive. This is easily accomplished by taking four distinct inbred strains which are of such a composition that a cross between any two of them gives a vigorous product. Now by crossing two of these strains to make one first generation hybrid, and at the same time crossing the other two to make another, and then by combining the two first generation hybrids there should be no reduction in heterozygosity. These doubly crossed plants, however, starting from large seeds produced on large, vigorous hybrid plants would be freed from the handicap which their parents had and although somewhat less uniform should be more productive. While it may be out of place to say anything about this method

until it has been thoroughly tested it is a method which is more promising than the plan originally advocated because by this method crossed seed for general field planting is produced much more abundantly than when non-vigorous inbred strains are crossed.

THE EFFECT OF HETEROZYGOSIS UPON ENDOSPERM DEVELOPMENT AND SELECTIVE FERTILIZATION.

Together with the increase in size of other parts of the plant there is also an appreciable increase in the size and weight of seeds of maize immediately resulting from cross-pollination. This has been shown clearly by Collins and Kempton ('13) by pollinating several ears of maize with a mixture of the plant's own pollen and that of a different variety. Roberts ('12), Carrier ('13) and Wolfe ('15) have also shown that in maize the endosperm is increased by crossing. The writer ('18) has shown that this increase in endosperm development appears even more strikingly in reciprocal crosses between different inbred strains of maize. At that time reciprocal crosses had not been obtained between different individual plants. In Table 24 are given the distributions of the weights of the seeds shown in Plate XIa. Two plants were pollinated with a mixture of pollen obtained from these same two plants. One of the plants had white seeds and the other yellow and the selfed and crossed seeds on each ear could be easily distinguished. The same pollen mixture was also applied to a third plant of an inbred strain different from either of the other two but more nearly related to one than to the other. The average difference in weights between the selfed and crossed seeds on each ear are large. The two out-crossed lots of seeds on the third ear do not differ as greatly but the heavier seeds resulted from the wider cross.

Table 25 gives a number of averages of the weights of seeds from similar pairs of ears each having selfed and reciprocally crossed seeds. In every case there is a noticeable increase in weight as the result of crossing. In Table 26 the weights of the out-crossed seeds resulting from some of the same pollen mixtures are given. Here again the heavier seeds are those which have resulted from the wider cross. A and C are two inbred strains derived from one variety at the start while B is derived from a

TABLE 24. THE IMMEDIATE EFFECT OF POLLINATION ON THE WEIGHT OF SEEDS OF MAIZE AS SHOWN BY SELFED, RECIPROCALLY CROSSED AND OUT-CROSSED SEEDS OBTAINED FROM A MIXTURE OF POLLEN FROM TWO PLANTS OF TWO DIFFERENT INBRED STRAINS.

Type	Color of seeds	Weight of seeds in centigrams																N.	A.	Difference
		12.3	14.2	16.1	18.0	19.9	21.8	23.7	25.6	27.5	29.4	31.3	33.2	35.1	37.0	38.9	40.8			
A	White..................	..	1	0	0	0	6	7	35	66	60	10	..	..	..	..	..	185	27.6 ± .11	....
A×B	Light yellow............	..	..	..	..	..	1	2	4	6	15	35	87	25	3	..	..	178	32.3 ± .12	4.7 ± .16
B×A	Light yellow............	..	1	0	1	5	5	9	11	15	18	19	18	8	11	6	1	128	29.9 ± .31	6.1 ± .34
B	Dark yellow............	..	2	2	3	9	41	49	39	19	4	0	0	0	1	..	..	169	23.8 ± .15	....
C×A	White..................	1	2	10	17	27	16	14	8	3	..	..	..	..	..	..	..	98	20.5 ± .22	....
C×B	Light yellow............	..	..	..	1	13	57	56	26	5	1	..	..	..	..	..	..	159	23.1 ± .10	2.6 ± .24

TABLE 25. THE IMMEDIATE EFFECT OF POLLINATION UPON THE WEIGHT OF SEEDS OF MAIZE. (Selfed and reciprocally crossed seeds from the same ears.)

Pollen mixture number	Pedigree number of parent plant—A	A	A×B	B×A	B	Pedigree number of parent plant—B
		Selfed	Crossed	Crossed	Selfed	
		White	Light yellow		Yellow	
1	21-3-13-9-7-57-1	27.0	32.1	30.3	22.3	14-10-30-4-3-7-11-4
2	21-3-13-9-7-57-2	20.3	21.9	25.2	21.4	14-10-30-4-3-7-11-3
3	21-3-13-9-7-57-3	26.0	31.1	30.9	22.5	14-10-30-4-3-7-11-10
4	21-3-13-9-7-57-5	22.2	24.3	31.4	25.3	14-10-30-4-3-7-11-2
5	21-3-13-9-7-57-7	26.9	31.1	35.2	28.3	14-10-30-4-4-2-7-6
6	21-3-13-9-7-57-10	27.8	32.4	29.9	23.7	14-10-30-4-3-7-11-1
7	21-3-13-9-7-57-14	28.0	30.3	39.4	29.5	14-10-30-4-4-2-7-3
8	21-3-13-9-7-57-20	30.9	35.5	21.6	21.1	14-10-30-6-11-3-11-3
9	21-3-13-9-7-57-24	28.5	33.0	29.1	25.5	14-10-4-6-4-7-8-5
10	21-3-13-9-7-57-25	24.6	29.7	36.6	30.1	14-10-4-6-16-2-12-8
11	21-3-13-9-7-57-29	32.4	38.4	24.1	19.3	14-10-30-4-3-7-11-7
12	21-3-13-9-7-57-31	14.7	17.3	24.3	20.5	14-10-30-4-3-7-11-8
13	21-3-13-9-7-57-33	16.5	18.9	23.6	18.5	14-10-30-4-3-7-11-9
14	21-3-13-9-7-57-35	19.2	23.6	31.3	25.5	14-10-30-4-3-7-11-18
15	21-3-13-9-7-57-36	22.3	25.1	36.4	28.9	14-10-30-4-4-2-7-14
16	21-3-13-9-7-57-43	20.6	22.7	34.5	27.3	14-10-30-4-4-2-7-2
Average..............		24.2	28.0	30.2	24.4	
Increase of crossed above selfed........			3.8	5.8		
Percent increase.......			15.70	23.77		

TABLE 26. THE IMMEDIATE EFFECT OF POLLINATION UPON THE WEIGHT OF SEEDS OF MAIZE. (Out-crossed seeds resulting from some of the same pollen mixtures used in Table 25.)

Pedigree number of parent plant—C	Pollen mixture number	Average weight of seeds in centigrams				
			Cross C×A		Cross C×B	
20A-8-5-35-8.......	1			20.5		24.5
20A-8-5-35-3.......	2			19.7		23.7
20A-8-5-35-4.......	3			25.4		25.0
20A-8-5-35-11......	6			20.3		22.9
20A-8-5-35-24......	8			27.3		27.5
20A-8-5-35-26......	9			25.9		27.7
20A-8-5-35-6.......	13			20.2		20.1
20A-8-5-35-13......	16		20.1		25.8	
20A-8-5-35-15......			23.9		27.5	
20A-8-5-35-18......			21.6		20.9	
20A-8-5-35-21......			20.2		18.9	
20A-8-5-35-30......			21.7		21.2	
20A-8-5-35-37......			21.6		21.0	
		Ave.	21.5	21.5	22.6	22.6
Average........................				22.7		24.3
Increase of (C×B) over (C×A)....						1.6
Percent increase............						7.05

different variety. All the data taken together clearly show that an increase in endosperm development in maize is one of the common manifestations of heterosis.

Since the crossed seeds receive a noticeable impetus in development it seemed quite likely that the foreign pollen might be more efficient in fertilizing than the self pollen and hence a greater number of crossed seed than selfed would be produced. Such is not the case, however, as an examination of a large amount of data has shown.

In performing the mixed pollinations no attempt was made to have more than approximately equal quantities of pollen. It is impossible to get a mixture of equal quantities of functional pollen because it varies so in respect to viability. Since the same mixture of pollen was applied to both plants the ratio of the seeds resulting from "yellow" pollen to the seeds produced by the "white" pollen should be the same on both ears. Thus if there were no selective fertilization the percent of white seeds on one ear plus the percent of dark yellow seeds on the other, selfed seeds in both cases, should equal the sum of the percents of the crossed seeds on each ear. An excess of crossed seeds would then indicate a selective fertilization in favor of the crossed pollen. As a small excess of selfed seeds was obtained any selective fertilization in favor of the foreign pollen certainly did not take place.

The numbers of the crossed and selfed seeds, of which the weights are given in Tables 25 and 26, together with a large amount of similar data are not given here for fear of unduly burdening this publication with tables but they show, on the whole, a small excess of selfed seeds instead of crossed seeds. The results of an experiment designed to test this point in a somewhat different way are given in Table 27. Here instead of taking a mixture of pollen from two plants of two different strains a large amount of pollen was collected from an approximately equal number of plants of two long inbred and exceedingly uniform strains of maize. The two lots of pollen were sifted to obtain pure pollen and equal quantities of each were carefully measured out, thoroughly mixed together and applied to a number of ears of each of the two strains which furnished the pollen—A and B— and to a third strain—C—distinct from either. Although the tassels were bagged on the same day and the pollen collected two days later and equal quantities of each taken there

TABLE 27. THE NUMBER AND PROPORTION OF SELFED, RECIPROCALLY CROSSED AND OUT-CROSSED SEEDS OBTAINED BY MEANS OF A MIXTURE OF POLLEN FROM TWO DIFFERENT INBRED STRAINS OF MAIZE.

	Plant number	Selfed seeds from yellow pollen	Crossed seeds from white pollen	Plant number	Crossed seeds from yellow pollen	Selfed seeds from white pollen	Plant number	Out-crossed seeds from yellow pollen	Out-crossed seeds from white pollen
		A	A×B		B×A	B		C×A	C×B
	A1	317	1	B1	319	5	C1	361	10
	A2	189	2	B2	224	9	C2	429	15
	A3	270	7	B3	369	10	C3	421	13
	A4	389	8	B4	348	26	C4	445	1
	A5	332	8	B5	330	6	. .	. . .	. .
	A6	260	1	. .	. . .	. .	. .	. . .	. .
Total number		1757	27		1590	56		1656	39
Actual proportion, percent		98.49	1.51		96.60	3.40		97.70	2.30
Closest perfect proportion, percent		97.545	2.455		97.545	2.455		97.545	2.455
Deviation		+.945	−.945		−.945	+.945		+.155	−.155
Probable error		±.195			±.301			±.246	
Ave. wt. per seed in centigrams		13.8	18.1		18.0	15.7		20.5	20.3
Increase		. .	4.3		2.3	. .		.2	. .
Percent increase			30.4		14.6			1.0	

Note: The yellow seeded plants A = 1-9-1-2-4-6-7-5-6-2-1; the white seeded plants B = 10-4-8-3-5-3-4-8-2-1 and the yellow seeded plants C = 1-6-1-3-4-4-4-2-4-4-2-5. All seeds resulted from one mixture of pollen obtained from approximately equal numbers of plants of the two strains—A and B.

was not equal quantities of functional pollen as the number of seeds given in Table 27 show. The great inequality of functional pollen may have been due to the fact that the pollen of the B strain was more moist and tended to aggregate into a flocculent mass while the pollen of the other was perfectly dry and each grain remained separated from the others. For this reason it was difficult to measure the two lots of pollen equally and the dry pollen clustered about the fine lumps of moist pollen when the two kinds were mixed and was probably first to gain access to the stigmas. The difference between the two kinds of pollen was not due to any external differences, as far as could be seen, and indicate differences in the rate of maturing after shedding.

Whatever may be the cause of the great difference in fertilizing power this does not effect the point under investigation. However different the pollen may be, the seeds resulting from "yellow" pollen should be in the same ratio to the seeds resulting from the "white" pollen on one ear as the ratio of the same two kinds of seeds on the other ear within the limits of the error of random sampling if there is no selective fertilization one way or the other. And both these ratios should be the same as the third ratio obtained when this same mixture of pollen is used to produce seeds on a plant of a different variety of maize. Let us see what the figures given in Table 27 show. Of the reciprocal crosses and selfs the proportion, expressed as percent, is as follows:

Seed color carried by pollen............	Yellow		White		Yellow		White
Type of Seeds........................	Selfed		Crossed		Crossed		Selfed
Actual proportion obtained.....	98.490	:	1.510	::	96.600	:	3.400
Closest perfect proportion.......	97.545	:	2.455	::	97.545	:	2.455
Deviation	+.945		−.945		−.945		+.945

The deviation from the closest perfect proportion is in favor of the selfed seeds. This theoretical ratio agrees very closely with the actual ratio obtained from the out-crossed seeds as shown in Table 27 although there is considerable difference in the results from the different ears. Letting S stand for selfed and C for crossed the probable error of the determination $\frac{S}{S+C}$ is $\pm \frac{.6745}{S+C} \sqrt{\frac{(S)(C)}{S+C}}$. The fraction $\frac{S}{S+C}$ gives the percent of selfed seeds and the probable error is stated as percent. Likewise the fraction $\frac{C}{S+C}$ gives the percent of crossed seeds and the probable error is the same as for the percent of selfed seeds.

This same experiment was repeated with about the same number of plants with the result of a similar excess of selfed seeds greater than would be expected from the probable error on the assumption that there is no selective fertilization. Does this mean that there is a selective fertilization in favor of a plant's own pollen and that the plant discriminates against foreign pollen even though the seeds resulting from that foreign pollen are greatly increased in size, weight, viability and the rate of growth of the ensuing plants? Unless there has been a constant error in classifying the seeds this seems to be the necessary conclusion to be drawn from the results so far given by maize. A sufficient number of plants will be grown from this seed to determine definately whether or not there has been any error in the separation of the seeds so that this question can be answered with a high degree of certainty.

In the meantime there is little doubt but that there is no great selective fertilization in favor of cross-pollination, if any, however much that cross-pollination may benefit the resulting seeds and the plants grown from them. If this is true crossing is without effect until the zygote is formed at the time of the union of the male and female nuclei.

In a consideration of selective fertilization it should be remembered that there are two different conditions which may be included in the term selective fertilization. One may be said to be the selection of different germ-plasms; the other the selection of different cytoplasms. For example a heterozygous plant produces pollen grains with different germinal compositions but all enclosed in the same cytoplasm. On the other hand pollen from different plants may differ in the nature of the cytoplasm as well as in hereditary factors carried in the nuclear material. East and Park ('18) have demonstrated that in tobacco there is no selective fertilization between gametes coming from one plant although the pollen grains differ in factors which determine fertility or sterility of the ensuing plants. The case is quite similar to that of the shape of pollen grains in peas which may be either all round or all cylindrical according to the germinal composition of the sporophyte which produced them and not according to the factors which they carry. Where pollen grains differ both in the factors which they carry and in the plants from which they come, as is the case with these experiments with maize, the conditions are quite different. It would not be surprising that there should be selective fertilization in one case and not in the other. East and Park have shown that a tobacco plant which was self-sterile, pollinated with a mixture of its own and pollen from another plant with which it was fertile, gave all crossed seeds—a maximum of selective fertilization.

Darwin (" Cross and Self Fertilization ") found that there was a selective fertilization in favor of foreign pollen in different plants. Many of Darwin's experiments, however, were made in such a way as to be open to doubt whether or not he really did obtain such an effect. His experiments, in applying foreign pollen sometime after self-pollination had taken place, in which he obtained in some cases many or all apparently crossed progeny, are open to other interpretations. The purity of the plants pollinated was not known. External conditions influencing fertilization were not guarded against. Taken as they stand, however, his experiments with *Mimulus*, *Iberis*, *Brassica*, *Raphinus*, *Allium* and *Primula* do indicate that in these plants there may be a selective fertilization in favor of foreign pollen. It is to be expected that plants which show partial self-incompatibility would show selective fertilization when a mixture of self and foreign pollen was applied. In maize, however, as mentioned before, the sterility shown is in the nature of pollen and ovule abortion, and whenever well formed pollen is produced it seems to be able to fertilize equally any plants if not too distinct in type. A distinction should be made, then, between self-fertile plants and self-sterile plants when dealing with selective fertilization.

Hyde ('14) has shown clearly that in Drosophila both males and females of inbred lines are more productive of offspring when mated to an individual of a different line than when mated to one of their own. Both males and females, therefore, produce more functional gametes than are utilized when individuals of the same inbred lines are paired. Hence a female, impregnated with a mixture of two kinds of spermatozoa from the same and from different lines would produce more hybrid progeny than inbred progeny even if equal quantities of both types of spermatozoa were available for fertilization. In other words there would be selective fertilization in favor of cross-fertilization.

Whether or not there may be a similar condition in other animals I do not know. Even in Drosophila, fertilization by the two types of sperm may take place equally, and a greater proportion of close-fertilized eggs, than cross-fertilized, fail to hatch, due to lesser vigor or lethal factors. In Hyde's experiments the type of fertilization had no marked effect on the number of eggs laid, only on the percentage which hatched.

In maize, and possibly all plants which show no self-incompatibility, the fact seems clear that crossing is wholly without effect until the fertilization process is completed.

Although there is apparently no effect of crossing in maize until the zygote is formed, such an effect is apparent immediately afterwards. In addition to the increase in endosperm development there is also an increase in the vigor of the embryo. Whether or not the size of the embryo in the seed is increased has not been actually determined, other than by inspection, but it undoubtedly is, along with the endosperm. When crossed and selfed seeds from the same ear, grown on a plant which has been inbred previously for several generations, are planted a striking difference is soon apparent. The crossed seedlings appear from one to two days before the selfed seedlings and may be two or three inches above ground before any of the selfed plants begin to appear. (See Plate XIb). From then on the superiority of the crossed over the selfed plants increases rapidly as shown by the curves in Figure III.

The Effect of Heterozygosis upon Longevity, Hardiness and Viability.

An increased longevity, viability and endurance against unfavorable climatic conditions have been frequently noted in hybrids. Kölreuter and Wiegmann both mention this fact. Gärtner in his book "Bastarderzeugung im Pflanzenreich" devotes considerable attention to this feature. Under the heading "Ausdauer und Lebenstenacität der Bastardpflanzen" he makes the following statements.

> "There is certainly no essential difference between annual and biennial plants and between these and perennials in regard to their longevity; for it is not seldom that different individuals of the same species have a longer life at times as, for example, *Draba verna*, which has annual and

biennial forms; the longevity of a plant furnishes thereby no specific differences but signifies at most a variability as Prof. W. D. I. Koch has shown. However, in hybrids this difference deserves special consideration. In most hybrids an increased longevity and greater endurance can be observed as compared with their parental races even if they come into bloom a year earlier. The union of a annual, herbaceous female plant with a perennial, shrubby species through hybridization does not shorten the life cycle of the forthcoming hybrid as the union of *Hyoscyamus agrestis* with *niger*, *Nicotiana rustica* with *perennis*, *Calceolaria plantaginea* with *rugosa* shows; and so also in reciprocal crosses when the perennial species furnishes the seed and the annual species supplies the pollen, as *Nicotiana glauca* with *Langsdorfii*, *Dianthus caryophyllus* with *chinensis*, *Malva sylvestris* with *Mauritiana* or biennials with perennials and reciprocally as *Digitalis purpurea* with *Ochroleuca* or *lutea* and *lutea* with *purpurea* or *ochroleuca* with *purpurea*. From the union of two races of different longevity comes usually a hybrid into which the longer life of one or the other of its parent races is carried whether it comes from the male or female parent species."

Many more instances are given by Gärtner from his own observations and those of others to enable him to reach the following conclusion:

"These examples support the statement of Kölreuter's that the longer life of hybrid plants is to be counted among their usual properties."

With regard to the resistance of hybrids to unfavorable weather conditions he goes on to say:

"With their longevity stands, in the closest relation, the fairly common property of hybrids to withstand lower temperatures than their parental races without injury to their growth and vegetative life. Kölreuter first observed that *Lycium barbara-afrum* in south Germany withstood the winter in the open field; although *Lycium afrum* must be wintered over, at least, in a cold frame. The cross of *Nicotiana Tabaco-undulata*, according to Sageret in France had an increased life, although in a protected place, in open field. W. Herbert reports that *Rhododendron altaclarae*, which is a hybrid union of *R. pontica-cantawbiense* ♀ with the very sensitive *Nepalense arboreum coccineum* ♂, has been grown in the open in England; also Robert Sweet confirms the same result by a hybrid *crinum* and many other hybrids of bulbous plants grown in open field whose parental species must be grown in the hothouse.

"*Lobelia syphilitica-cardinalis* wintered over with a light covering in the winter of 1832-1833 with 5°F in open field. *Lychnicucubalus albus* and *ruber* lasted three years in open field although *cucubalus viscosus* in south Germany did not survive in open field. All hybrids of genus *coccineum* stood over the winter of 1842-1843 with 5°F. in the open, although the pure species seldom lives through our usual winters of 43° to 9.5° F. Prof. Wiegmann reports similar results.

"Very frost sensitive species of Nicotiana and their hybrids did not withstand, under the same conditions, such low temperatures as the afore-mentioned plants; but we have flowered and carried over part of them wherever they were well covered with snow, for example, *N. quadri-valvis glutinosa*, *rustica-quadrivalvis*, these withstood 25° F. and yet have continued blooming although *N. glutinosa*, *quadrivalvis*, *paniculata*, *Tabacum* and *rustica* were already frozen by 32° F. Moreover other crosses of very sensitive and tender species of this genus as *paniculata-Langsdorfii*, *vincaeflora-Langsdorfii*, *vincae-flora-quadrivalvis* have been carried over in an active growing condition two to three years, and *glauca-Langsdorfii* three years in a cold house with 39° to 42°. The hybrid *N. paniculatarustica-paniculata* was kept over in a cold house in the cold winter of 1839-40 but its leaves were yellow. Among all the species of this genus the cross of *N. suaveolenti-macrophylla* showed itself to be the most hardy. On the 16th of October of its first year (1828) its top was frozen but it did not suffer from this, and 12 days later put out a new shoot from the root and its leaves lasted through the winter in a cold house in a fresh, green condition although the other species were yellow and this plant was the first to start into growth in the spring. The same endurance Sageret observed in *Nicotiana suaveolenti-virginica*. All these plants in the last year of their vegetative life seemed to die off more as the result of the unfavorableness of the weather than of old age."

Exceptions are noted by Gärtner in that some species which were not resistant to cold did not give resistant hybrids. In many cases the hybrids were weak because of the distant relationship of the parental races.

Sargent ('94) reports a remarkably vigorous and hardy hybrid tree supposed to be a cross of the tender English walnut, *Juglans regia* and the common butternut *Juglans cinerea*. He says: p. 434

"My attention was first called to the fact by observing that a tree which I had supposed was the so-called English walnut—*Juglans regia*, in the grounds connected with the Episcopal School of Harvard College at Cambridge, was not injured by the cold of the severest winters, although *Juglans regia* generally suffers from cold here— and rarely grows to a large size. This individual is really a noble tree; the trunk forks ab u five feet above the surface of the ground into limbs and girths, at the point where its diameter is smallest, fifteen feet and two inches. The divisions of the trunk spread slightly and form a wide, round-topped head of pendulous branches and unusual symmetry and beauty, and probably sixty to seventy feet high."

Heterosis is also shown in a resistance to bacterial and fungus diseases. Some of the inbred strains of maize are very susceptible to the bacterial leaf-wilt and in some years at the end of the season all the plants of these strains appear as if they had been scorched by fire while other strains in adjoining rows are untouched. Other strains have quite a large percentage of plants attacked by smut. Crosses, however, of these susceptible strains with those which are not affected by these parasitic organisms are only slightly or not at all affected.

TABLE 28. SUSCEPTIBILITY TO SMUT (*Ustilago zeae*) OF A NON-INBRED VARIETY OF MAIZE, SEVERAL INBRED STRAINS DERIVED FROM THIS VARIETY AND THE FIRST AND SECOND GENERATION CROSSES BETWEEN THE MOST SUSCEPTIBLE AND THE LEAST SUSCEPTIBLE STRAINS.

Pedigree number	Percent of plants affected			Total number of plants grown	Total percent of plants affected
	Plot I	Plot II	Plot III		
1	....	....	1.75	114	1.75
1-9-1-2-4-6-7-5	0	.27	.56	596	.34
1-7-1-2-2-9-2-1	2.17	.35	0	408	.49
1-7-1-1-1-4-7-5	8.79	10.16	5.77	950	9.79
1-6-1-3-4-4-4-2	0	0	0	992	0
(1-6-1-3) × (1-7-1-1) F_1	....	2.48	0	439	2.28
(1-6-1-3) × (1-7-1-1) F_2	....	....	5.15	97	5.15

In Table 28 are given the per cent. of plants affected by smut (*Ustilago zea,* Beck. Ung.) of the original, non-inbred Leaming variety of maize previously spoken of and four inbred strains derived from this variety by ten or eleven generations of self-pollination. Seed of the four inbred strains was planted in three rather widely separated plots in the same field in 1917. Two of the strains showed only a small infection by this parasite; one showed about 10 per cent infection and one had not a single plant affected in all three plots in a total of nearly one thousand plants. Since the differences which these four strains show are fairly consistent in the different places grown it can hardly be doubted but that segregation of susceptibility to parasitism has occurred in the inbreeding process. The first generation hybrid between the most resistant and the most susceptible strain was free from smut in one plot and but slightly affected in another. The second generation hybrid grown side by side with first generation showed considerably more infection although the number of plants grown was small. This is fairly good evidence that resistance to smut in maize tends to dominate in crosses between plants which differ in this respect.

Tisdale, according to L. R. Jones ('18) also finds that in flax disease resistance tends to be dominant although the hybrids are more or less intermediate in this respect and the method of inheritance is rather complex. Biffen ('12), on the other hand, concluded that the resistance to rust in wheat was recessive. Likewise, Weston ('18) states that maize and teosinte-maize hybrids are extremely susceptible to a downy mildew (*Peronospora Maydis,* Rac.) in Java and other places, although teosinte (*Euchlaena mexicana,* Schrad.) is immune.

Data from another source have been obtained from the garden radish (*Raphanus sativus,* L.). A white-rooted variety of radish was allowed to go to seed alongside a red-rooted radish. Seed collected from the white-rooted plants was sown thickly in a flat and when they came up it was seen that a number of the seedlings were crossed from their red colored stems. The seedlings were quite badly attacked by the "damping-off" fungus and large numbers of them were killed, but a far less number of the crossed seedlings were affected as shown by the decay of the tissues at the base of the stem. The figures obtained are given in Table 29.

TABLE 29. COMPARATIVE SUSCEPTIBILITY TO "DAMPING-OFF" DISEASE OF SELFED AND CROSSED RADISH SEEDLINGS.

Variety of Radish	White Seedlings, Selfed			Red Seedlings, Crossed		
	Number grown	Number affected	Percent affected	Number grown	Number affected	Percent affected
Short, white	349	142	40.7	30	4	13.3
Long, white	76	28	36.8	7	0	0

Gernert ('17) reports a case of immunity to aphis attack of teosinte-maize hybrids in which the maize parent was badly infested whereas the teosinte parent and the hybrid entirely escaped injury.

Together with these manifestations of heterosis in its influence on hardiness there is an increase in the viability of crossed seeds as compared to selfed seeds from the same ears as shown in Table

TABLE 30. THE EFFECT OF HETEROZYGOSIS UPON GERMINATION—A COMPARISON OF CROSSED AND SELFED SEEDS FROM THE SAME EARS OF MAIZE

Pedigree number of female parent	Pedigree number of male parent	Percent increase in weight of crossed seeds over selfed	Number of seeds planted of each	Number of selfed seeds germinated	Number of crossed seeds germinated	Percent selfed seeds germinated.	Percent crossed seeds germinated.	Excess of percent crossed seeds germinated over selfed
21-3-13-9-7-57-13	14-10-30-6-2-13-5-13	8.2	121	24	46	19.8	38.0	18.2
21-3-13-9-7-57-17	14-10-30-6-11-3-11-17	18.8	39	26	37	66.7	94.9	28.2
21-3-13-9-7-57-21	14-10-30-6-11-3-11-4	7.1	32	28	29	87.5	90.6	3.1
21-3-13-9-7-57-38	14-10-30-4-4-2-7-38	68.0	22	14	22	63.6	100.0	36.4
21-3-13-9-7-57-39	14-10-30-4-4-2-7-7	18.3	33	16	26	48.5	78.8	30.3
21-3-13-9-7-57-54	14-10-30-4-4-2-7-7	3.9	97	19	27	19.6	27.8	8.2
21-3-13-9-7-57-58	14-10-4-6-4-7-8-15	8.8	100	43	68	43.0	68.0	25.0
21-3-13-9-7-57-59	14-10-4-6-4-7-8-10	10.0	12	9	12	75.0	100.0	25.0
21-3-13-9-7-57-63	14-10-4-6-4-7-8-29	17.5	31	26	30	83.9	96.8	12.9
21-3-13-9-7-57-64	14-10-4-6-4-7-8-29	13.3	14	9	14	64.3	100.0	35.7
21-3-13-9-7-57-65	*	13.5	47	41	45	87.2	95.7	8.5
14-10-30-4-4-2-7-12	21-3-13-9-7-57-38	8.3	87	84	86	96.6	98.9	2.3
	Total	16.3	635	339	442	53.4	69.6	16.2

* Seeds crossed but number of parent unknown.

30. Seeds which were secured from some of the mixed pollinations, reported previously, were sown in flats. Without exception the crossed seeds showed a higher percentage of germination than the selfed seeds from the same ears as can be seen in Plate XIb. These seeds were planted two months after ripening. Whether or not an increase in age would show greater differences in viability is not known but it is quite likely that the difference might become even greater with age up to a certain point. The low germination of both crossed and selfed seeds in some of the ears was due to the fact that they were moldy on account of late ripening and damp weather.

The increased vegetative vigor as manifested by an increased facility of vegetative propagation in hybrids has been repeatedly spoken of. Kölreuter, Wiegmann, Sageret and Focke make a special mention of this phenomenon.

Moreover there is no positive evidence that plants which are propagated vegetatively lose any of their hybrid vigor which they may have, no matter how many generations of asexual reproductions take place. Undoubtedly most varieties of cultivated fruits, flowers, ornamental plants and field crops which are commonly propagated vegetatively, owe their excellence in part to heterosis.

From time to time the supposed degeneration of plants in long-continued vegetative propagation has been much disputed. Knight ('99) and Van Mons ('36) contended that they did degenerate, but Lindley ('52) reviewing Knight's work thought that the evidence did not support such a view. Gärtner states that the characteristics of a hybrid do not change throughout the whole life cycle of the individual, even when it is propagated and disseminated by buds, cuttings or layers.

Darwin believed that a degeneration took place largely for the same reason that he thought long continued self-fertilization was injurious. Asa Gray ('76), in reviewing Darwin's opinions on this matter, says (p. 347):

> "The conclusion of the matter, from the scientific point of view is, that sexually propagated varieties of races, although liable to disappear through change, need not be expected to wear out and there is no proof that they do, but that non-sexually propagated varieties, though not especially liable to change, may theoretically be expected to wear out, but to be a very long time about it."

Gray, however, cites cases of horticultural varieties propagated since the time of the Romans with no apparent loss of vigor. Whitney ('12a, b, c) and A. F. Shull ('12b) believe that an actual degeneration takes place in parthenogenetic reproduction in the rotifers. The work of Enriques ('07), Woodruff ('11) and Jennings ('12) on Paramecium proves almost beyond doubt that there is no degeneration in this organism although reproduction by fision in the infusoria may be considerably different from vegetative propagation in the higher plants. Hedrick ('13), from the evidences of long-continued varieties of fruits, and East ('08) working with potatoes and reviewing extensively the whole question believe that there is no evidence that a real degeneration takes place which cannot be accounted for on the basis of the accumulation of disease or other external effects. East ('10), however, suggested that such a degeneration, if ever proven, might be accounted for on the basis of a decreasing effect of the physiological stimulation assumed to be derived from heterozygosity. A. F. Shull (12a) holds a similar opinion. From the nature of the problem it can hardly be settled satisfactorily one way or the other by experimental means. As it stands at present there is no clear evidence that there is a degeneration in long continued asexually propagated plants. The burden of proof rests with the positive side.

THE EFFECT OF HETEROZYGOSIS UPON THE TIME OF FLOWERING AND MATURING.

Many investigations have indicated that there is a hastening of the time of maturity due to heterozygosis. That there is an acceleration in the rate of growth is, of course, evident from the great increase in size shown by hybrids grown in the same season with their parents. There is, moreover, considerable evidence from previous work and from the data to be given here to show that hybrids not only grow to a larger size but complete their growth in a shorter time than the parents take to complete a smaller amount of growth. In other words, heterozygosis tends to hasten the time of maturity as well as to increase size.

The investigations of Kölreuter, Gärtner, Focke and Darwin show a large number of specie- and variety-crosses wherein the hybrid flowers before either of the parents. Both Kölreuter and Gärtner give instances of perennials which commonly bloom in the second or third year whose hybrids bloom in the first year.

The most extensive observations bearing on this relation of heterosis to time of flowering are those given by Darwin in his "Cross and Self Fertilization in the Vegetable Kingdom." He gives the time of flowering of 28 crosses between different strains within many different species—which show positive evidence of hybrid vigor. Of these 28 crosses 81 per cent. flower before the parents. Four cases are given where the crosses are less vigorous than the parents and in each of these the parents flowered first.

Recent experiments in hybridization show, almost without exception, that crosses which result in an increase in vigor also result in a hastening of the time of flowering. One exception to this statement must be noted in the cross between a large dent and a small pop variety of corn reported by Emerson and East ('13). This cross showed distinct evidence of hybrid vigor in an increase in internode length over that of both parents. The parents differed in time of flowering by 25 days. The first generation of the cross grown the same year as the parents was "distinctly intermediate" in time of flowering. There was an increase in the rate of growth necessarily as the plants were larger than the average of the parents.

Data bearing upon the relation of heterozygosis to the time of maturing has been secured from two different plants, tomatoes and corn. A large part of the data on tomatoes was collected by Prof. H. K. Hayes, now at the Minnesota College and Station.

Four commercial varieties of tomatoes were successively self-pollinated for four years. Two first generation crosses between these varieties were grown in each of the four years and compared as to yield of fruit and time of production with the two selfed parents. In every case the same plants which were used to produce the selfed seed for the next generation were also used to make the crosses. For this reason and because tomatoes are naturally self-pollinated and are hence in a homozygous condition the first generation crosses can be compared strictly with their parents.

From thirty to fifty plants of each variety and cross were grown each year. The fruit was picked as it ripened at intervals of from 3 to 5 days and the average production per plant was determined. One of the crosses was between varieties which had approximately the same time of ripening. This first generation cross did not exceed, in total yield, the average of the two parents and did not differ from them in respect to time of production.

The other cross, however, yielded, each year, an average of 16 percent above the better parent. The two varieties used in making this cross differed in time of production by an average of five days. The first generation cross while yielding 16 percent more than the late parent was each year fully as early as the early parent. Although the difference in time of production between these varieties is small the consistent results obtained in four successive years are certainly significant.

Similar results were secured with sweet corn. A first generation cross between an early variety of sweet corn, Golden Bantam and a late variety, Evergreen, was grown in 1916 together with the two parental varieties and compared in time of flowering, number of ears per plant and in height. They were all planted at the same time but rather late in the season so that the early and late varieties bloomed at more nearly the same time than is usually the case. About half of the plants of the early variety were showing silks before the late variety commenced to silk out. The first generation cross was slightly earlier than the early parent in producing silks. The cross was noticeably affected by vigor of crossing in that it was fully as tall as the taller parent and averaged more ears per plant than either parent although the ears were not as large as those of the Evergreen variety.

Much more extensive and authoritative data have been secured from a comparison of inbred strains of corn with their first generation crosses. Forty-two strains of corn which had been continuously selfed for from 5 to 11 generations and 100 first generation crosses representing different combinations between these selfed strains were grown under the same conditions as to time of planting and culture. Both the inbred strains and their crosses were exceedingly uniform in time of flowering and maturing. All the plants in any selection flowered and matured within a few days. About 60 plants of each were grown. At intervals of one week during the flowering season the number of selections of the selfs and crosses which had flowered by that time were noted. Similarly at the end of the season the selections which were mature were noted at intervals. Although the time of maturity can not be so definitely determined as the time of flowering all the plants in a selection were uniform in this respect. For the flint varieties the glazing of the ears and for the dent varieties the denting of the kernels were taken as indications of maturity. The crosses yielded, on the average, 180 per cent more than their parents.

Together with this increase in the amount of growth there was a noticeable hastening of both the time of flowering and maturing. In time of flowering the crosses were four days and in maturing eight days earlier than the average of their parents. Since the crosses gave a large increase in the total amount of growth and produced this growth in a somewhat shorter time than their inbred parents it is all the more evident that heterozygosis increases the rapidity of growth. See Plates VII a and b.

The Relation of the Effects of Heterozygosis and of the Environment.

East ('16) has stated that heterozygosis "affects a result comparable to favorable external conditions." In a cross between two varieties of *Nicotiana* he found that the first generation gave a noticeable increase in the amount of growth as shown by the height and general size of the plant as the result of heterozygosis. The corolla length of the flowers, which is very little affected by environmental factors, was not increased above the average of the two parents.

The similarity of the effects of heterozygosis to the environmental effects is also shown in the affect of crossing on the number of nodes and internode lengths of corn. As was noted from Tables 15 and 13 the number of nodes is increased only 6 percen while the height of plant is increased 27 percent. This is exactly the effect that nutritional factors have. The height of plant is reduced under poor conditions by a reduction in internode length without reducing appreciably the number of nodes.

In general it is evidently true that heterozygosis affects many characters in the same way as the environment, but it should be noted that in time of maturity these two factors have directly opposite effects. It is generally recognized, I believe, that favorable external conditions such as increased moisture or fertility, where these are limiting factors, which result in a greater total amount of growth tend to prolong both the time of flowering and the completion of growth. Conversely unfavorable external conditions which stunt the plants and limit their growth tend to hasten their period of flowering and maturity. There are, of course, certain exceptions to this statement.

Whether or not the effect of heterozygosis in hastening maturity can manifest itself independent of any increase in vegetative luxuriance or other manifestations of hybrid vigor is not known. The results given here would indicate that the vigor derived from crossing enables the plant to carry on its life processes more easily and more efficiently and thus to accomplish its task in a shorter time.

With regard to the effects of heterozygosis in animals much the same relation is shown with the external environmental effects as in plants although the rate of growth and size obtained at maturity may be more definitely fixed in animals than in plants. According to Castle ('16) there is an increase in the rate of growth as well as the attainment of a larger size at maturity in hybrid guinea-pigs. Hyde ('14) also finds an increase in rate of growth and hastening of sexual maturity on crossing in Drosophila. These effects in animals are probably greater than could be obtained by any amount of feeding or care just as it is the case in plants.

It may be stated briefly that the effects of heterozygosis in both animals and plants, not too distantly related, all together contribute towards an increased reproductive ability and this effect has probably been of fundamental importance in evolution in establishing sex.

In the foregoing account of some of the most noticeable effects of crossbreeding upon development we have been dealing only with crosses among closely related organisms. It is of course, well known that in crosses between distantly related forms the beneficial effects of crossing may disappear and the effects become increasingly more injurious as the degree of dissimilarity becomes greater. The most frequent, pronouncedly injurious effect is the reduction or complete loss of fertility. This may or may not be accompanied by a great acceleration of growth. This is shown in many plants, notably by Gravatt's Radish-Cabbage hybrid and by Wichura's Willow hybrids as well as by many good illustrations given by Gärtner and Focke. It is perhaps not surprising that the reproductive ability should be the first to suffer since reproduction is the most difficult task the organism has to perform. The failure of the reproductive mechanism might divert the energies into bodily growth and thus in part account for the large size and great vigor of some sterile hybrids but, as all are agreed, this can not entirely account for the great increases in size nor obviously does it apply to the more common cases where both size and productiveness are increased at the same time.

To sum up one can therefore say that, in plants, crossing may have a great range of effects, according to the degree of relationship of the parents, from a condition in which: the cross is not possible and no seed produced; seed may be produced but fail to germinate; plants may be produced which are either very weak, normal or very vigorous without being able to reproduce themselves; plants which are both more vigorous and more productive than their parents; to a condition in which they are so closely related that the crossed plants do not differ appreciably from selfed plants. A similar series can be arranged with animals.

SUMMARY OF THE EFFECTS OF INBREEDING AND CROSSBREEDING.

Before taking up a theoretical consideration of the cause of hybrid vigor and its importance in the establishment of sex it is well to summarize briefly some of the main conclusions, with regard to the effects of inbreeding and crossbreeding on development, to be arrived at from a study of the investigations discussed.

EFFECTS OF INBREEDING.

1. Continued inbreeding results in the segregation of a variable complex into a number of diverse types which are uniform within themselves.
2. The segregates which differ in visible, qualitative characters also differ in quantitative characters; types with abnormalities appear which cannot reproduce themselves; others appear which are perpetuated with difficulty; others are obtained which are perfectly normal in structure and function. These latter are usually less well developed, but may be as well or better developed than the original stock from which they are derived.
3. The change in size, structure, or function and reduction in variability is most noticeable in the earlier generations of inbreeding, rapidly becomes less and the surviving inbred strains are uniform and constant.
4. The rate of approach to uniformity and constancy differs in different lines.
5. These uniform and constant inbred strains are quite comparable to naturally self-fertilized species.
6. No single effect can be attributed to inbreeding other than the reduction in variability.
7. All these results are in conformity with Mendel's law and Johannsen's genotype conception.

THE EFFECTS OF CROSSBREEDING.

1. Heterosis accompanies heterogeneity in germinal constitution whether or not the organisms crossed are from the same or diverse stocks.
2. Heterosis is widespread in its occurrence throughout the plant and animal kingdoms.

3. Heterosis is shown as an increase in the size of parts rather than an increase in the number of parts.

4. Cross-fertilization is without effect until the zygote is formed; from that time on heterosis may be apparent throughout the life of the individual.

5. Heterozygosis has an undiminished effect on plants propagated vegetatively.

6. Heterozygosis may have a stimulating effect on some characters and a depressing effect on others in the same organism.

A MENDELIAN INTERPRETATION OF HETEROSIS.

It is due to the work of G. H. Shull ('08, '09, '10, '11) and of East ('08, '09) and East and Hayes ('12), supplemented and confirmed by the results given here, that we no longer believe that inbreeding is a process of continuous degeneration. Also these investigators first demonstrated clearly that the same principle was involved in the loss of vigor accompanying inbreeding and the increase in vigor resulting from crossing.

To account for this well nigh universal loss of vigor when domesticated races of plants and animals are inbred, they thought it necessary to assume a physiological stimulation which was present when unlike germplasms were united and which disappeared as homozygosis was brought about automatically by inbreeding. Part of the effects of inbreeding were due, according to their views, to the segregations into pure lines of different hereditary complexes and the appearance of previously hidden recessive characters, and part were due to the loss of this stimulation.

G. H. Shull's ('14) opinion as to the way germinal heterogeneity induces vigor is stated briefly as follows (p. 126):

> "The essential features of the hypothesis may be stated in more general terms as follows: The physiological vigor of an organism, as manifested in its rapidity of growth, its height and general robustness, is positively correlated with the degree of dissimilarity in the gametes by whose union the organism has been formed. In other words, the resultant heterogeneity and lack of balance produced by such differences in the reacting and interacting elements of the germ-cells act as a stimulus to increased cell-division, growth, etc. The more numerous the differences between the uniting gametes—at least within certain limits—the greater, on the whole, is the amount of stimulation. These differences need not be Mendelian in their inheritance, although in most organisms they probably are Mendelian to a prevailing extent."

Both the view stated above and that of East and Hayes assume that the increase in development is due to a reaction between different elements in the nucleus and that this stimulus disappears when homozygosity is reached. A. F. Shull ('12a) has proposed a slightly different idea in that he assumes the stimulus to be due to the reaction of new elements in the nucleus, brought in by cross-fertilization, to the maternal cytoplasm. According to his view there might still be a stimulation even after complete homozygosity is attained. Also in asexual propagation he supposes that the cytoplasm might become gradually accustomed to a heterozygous nucleus, hence long continued asexual reproduction might lead to a gradual reduction in vigor which this writer finds does occur in the rotifer, *Hydatina senta*. ('12b).

It should be remembered, however, that both these hypotheses, as to the effect of germinal differences, postulate a stimulation to account for an increase in development as the facts demand. It would have been even more plausible to postulate a depressing effect had the facts been otherwise. The only basis for a stimulation of this kind is in the fact that fertilization initiates the development of the egg. Heterozygosis, however, is not concerned with the starting of the development of the egg, but only with the rate of development after growth is commenced. Is it not more plausible that "a lack of balance" occasioned by the union of unlike germplasms would retard development rather than stimulate it?

Keeble and Pellew ('10) first suggested that dominance of characters contributed by both parents might be a factor in the increased vigor of hybrids. They illustrated this conception by a cross between two varieties of peas which possessed features of both parents, and were taller than either.

Bruce ('10) has shown that the total number of dominant factors is greater in a hybrid population than in either parental population and that there is consequently a correlation between the number of dominant factors and hybrid vigor. As far as I know, Bruce has never followed up this suggestion. He did not show why it was that the presence of a greater number of dominant factors brought about an increase in growth, nor did he show why it was that all the dominant features could rarely or never be accumulated in certain individuals and races which would therefore show no reduction in vigor when inbred.

East and Hayes ('12) attempting to distinguish between dominance and the effects of heterozygosis make the following statement (p. 31):

> "The term vigor has hitherto been used with the general meaning which the biologist readily understands. We will now endeavor to show in what plant characters this vigor finds expression. It is not an easy task because of the possibility of confusing the phenomenon of Mendelian dominance with the physiological effect due to heterozygosis. The confusion is due to a superficial resemblance only. Dominance is the expressed potency of a character in a cross and affects the character as a whole. A morphological character, like the pods of individual maize seeds, or the product of some physiological reaction like the red color of the seed pericarp in maize, may be perfectly dominant, that is, it may be developed completely when obtained from only one parent. Size characters, on the other hand, usually lack dominance or at least show incomplete dominance. The vigor of the first hybrid generation theoretically has nothing to do with these facts. This is easily demonstrated if one remembers that the increased vigor manifested as height in the F_1 generation cannot be obtained as a pure homozygous Mendelian segregate, which would be possible if due to dominance. Furthermore, the universality with which vigor of heterozygosis is expressed as height shows the distinction between the two phenomena. If the greater height were the expression of the meeting of two factors (T_2, t_2, x t_1, T_2) both of which were necessary to produce the character, one could not account for the frequency of the occurrence. Nevertheless, in practice the confusion exists, and while we have considerable confidence in the conclusions drawn from our experiments, we have no intention of expressing them dogmatically."

G. H. Shull's statements of the way in which crossing brings about increased development, and the relation that this stimulation of growth has to dominance of Mendelian characters is fairly stated, I believe, in the following passage ('11, pp. 244–245):

> "In 1908 I suggested a hypothesis to explain the apparent deterioration attendant upon self-fertilization, by pointing out that in plants, such as maize, which show superiority as a result of cross-fertilization, this superiority is of the same nature as that so generally met with in F_1 hybrids. I assumed that the vigor in such cases is due to the presence of heterozygous elements in the hybrids, and that the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous. I do not believe that this correlation is perfect, of course, but approximate, as it is readily conceivable that even though the general principle should be correct, heterozygosis in some elements may be without effect upon vigor, or even depressing. The presence of unpaired genes, or the presence of unlike or unequal paired genes, was assumed to produce the greater functional activity upon which larger size and greater efficiency depend. This idea has been elaborated by Dr. East and shown to agree with his own extensive experiments in self-fertilizing and crossing maize. He suggests that this stimulation due to hybridity may be analogous to that of ionization.
>
> Mr. A. B. Bruce proposes a slightly different hypothesis in which the degree of vigor is assumed to depend upon the number of dominant elements present, rather than the number of heterozygous elements. While all of my data thus far are in perfect accord with my own hypothesis, and I know of no instance in which self-fertilization of a corn-plant of maximum vigor has not resulted in a less vigorous progeny, it is quite possible that I have still insufficient data from which to distinguish between the results expected under these two hypotheses. However, for the purpose of the present discussion, it is not necessary to decide which of these two hypotheses (if either) is correct. Both of them are based upon the view that the germ-cells produced by any plant whose vigor has been increased by crossing are not uniform, some possessing positive elements or genes not possessed by others."

A. F. Shull does not consider dominance as an adequate means of accounting for heterosis, agreeing with East and Hayes and G. H. Shull, as the following quotation shows: ('12a, p. 10)

> "The view that vigor depends upon heterozygosis of the individual seems to me inherently more probable than that it is due to the presence of certain dominant genes. The former view admits of a plausible foundation in cell physiology, and the essence of it may be extended to cases of decrease of vigor in which there is no change in genotypic constitution, and which are therefore without the pale of either theory."

Castle is also in accord with the general belief that heterosis is not due to dominance of factors and draws a distinction between the effects of inherited characters and the stimulus resulting from crossing. In speaking of the increase in size in crosses between diverse races of guinea-pigs he says: ('16, p. 212.)

> "So far as heredity is concerned, the inheritance is blending, but F_1 shows an increase in size due to hybridization. This increased size, however, does not persist into F_2. It seems to be due not to heredity at all."

(And again on pages 223 and 224.)

> "Cross breeding has, then, the same advantage over close breeding that fertilization has over parthenogenesis. It brings together differentiating gametes, which, reacting on each other, produce greater metabolic activity. Whether or not the uniting gametes differ by Mendelian unit-characters

is probably of no consequence. That they *differ chemically* is doubtless the essential thing in producing added vigor. Heterozygosis is mentioned merely as an evidence of such chemical difference."

These quotations suffice to show that a distinction is held by biologists at the present time between the effects of inbreeding and cross breeding and of heredity in development, and they believe that dominance of hereditary factors is inadequate to account for the widespread, if not universal phenomenon of heterosis. The reason why biologists in general have refused to believe that dominance was in any way responsible for the increased vigor of hybrids has been due to two objections which have seemed to make this hypothesis untenable. They thought that if hybrid vigor was due to the dominance of definitely inherited characters that all these favorable characters which bring about heterosis could be easily recombined into a homozygous individual which would show no reduction on subsequent inbreeding. Since no clear case was known in maize where a plant did not lose vigor on inbreeding this seemed to be a convincing argument. Another objection to dominance as a means of accounting for heterosis was raised by Emerson and East ('13) in that the distribution in F_2 should be unsymmetrical in respect to those characters in which heterosis was shown in F_1. Since the usual frequency distributions in cases of this kind are symmetrical, this objection appeared to be valid.

How both of these objections do not hold when linkage of heredity factors is taken into consideration, the writer has attempted to show in a recent publication ('17). Because of linkage, characters tend to pass from one generation to the next in groups and are not easily recombined. Furthermore, on account of linkage skewness is not expected in the second hybrid generation. All of the recently acquired knowledge of heredity makes it seem highly probable that heterosis may be largely, if not entirely, accountable on the basis of dominance of linked factors.

In considering these two hypotheses, both attempting to account for heterosis, the following facts about dominance should be kept in mind:

1. Partial dominance of characters is a widespread occurrence in plants and animals.
2. Dominance, of course, does not appear until after the zygote is formed.

3. In most cases dominance does not change throughout the life of the individual and remains the same through innumerable clonal generations.

While none of these features of dominance offers any definite means of proving the truth of the hypothesis advanced, is it only a coincidence that they fit in exactly with what the facts of heterosis demand? It remains to show that those characters which enable a plant or animal to obtain the best development are, for the most part at least, partially dominant over those characters which retard or prevent maximum growth.

The essential difference between the two hypotheses may be stated briefly. According to the previous view the hybrid combination of factors Aa carried the ability to stimulate development because of the union of unlike elements. This stimulation was absent in either of the homozygous combinations AA and aa, and this stimulation had no direct relation to the part that either A or a had in development as hereditary entities. According to the conception of dominance, first proposed by Keeble and Pellew and carried out more fully by the writer, the hybrid union of AAbb with aaBB, resulting in the heterozygous combination of Aa Bb, increases development because two dominant characters are present here together, whereas each parent has only one dominant character. A similar factorial arrangement has been proposed by Hyde ('14) to account for the increased fertility of his crosses among partially sterile strains of Drosophila.

In crosses between different types of domesticated animals and of cultivated plants it has frequently been noted that there is a tendency towards a return to the characters of the wild species from which they were derived. Sageret ('26) makes particular note of this point. It is well known that crosses between different breeds of pigeons is quite apt to bring back the wild-type of plumage. The hybrid between radish and cabbage described by Gravatt ('14) illustrates this point strikingly. The hybrid produced had neither a succulent "head" like its cultivated male parent nor a fleshy root like its female parent. In other respects, as well, it showed this return to wild-type characters. It was also exceedingly vigorous, but sterile, like so many hybrids between diverse stocks.

Drosophila furnishes the best illustration of the appearance of wild type characters in the first hybrid generation. Of the more than one hundred mutations found in Drosophila by far the largest number of these are recessive. Almost all of them are characters which are less favorable to development. It is stated that any attempt to collect a large number of the recessive characters into one race is rendered difficult by the weakened constitution of the flies possessing any great accumulation of recessive characters (Muller, '16). Whenever crosses are made between diverse types the first generation fly is in many of its characters more like the wild stock and hence more vigorous than its parents. All lethal factors, well illustrated in Drosophila, furnish additional support to the hypothesis of dominance as a means of accounting for heterosis. Muller ('17) has shown that a condition of "balanced lethals" may be brought about in which only the heterozygotes can live. As dominant lethal factors are always eliminated as soon as they occur, so, also, is there always a strong tendency for selection to eliminate any dominant character which is at all unfavorable to the organism's best development. Unfavorable recessive factors also tend to be eliminated, but much more slowly.

If the results obtained in Drosophila are applicable to other animals and to plants we must infer that recessive mutations occur the most commonly. Hence recessive mutations make up the characters, to a large degree, that man has selected in the production of domesticated animals and plants. Just as in Drosophila, crosses between diverse domesticated types tend to result in the reappearance of wild-type characters which are more useful to the plant or animal whose chief aim in life is, apparently, to reproduce itself.

This is well shown in an illustration from maize. As stated before, inbred strains have been obtained which are markedly deficient in root development. On these plants the large brace roots which commonly appear when the plants begin to need extra support, are almost completely lacking. Consequently, the plants are blown over when they become heavy at the time of ear formation. I have observed these strains three years and each time they have fallen down. This character is not determined by soil conditions or insect damage or any external conditions as far as can be seen. Other plants on either side are perfectly upright. When these strains are crossed with other strains, inbred for an equal or longer period, which have well developed brace roots, the first hybrid generation has remarkably well developed brace roots, and usually does not show the slightest tendency to go down, as shown in Plates XIIa and b. Emerson ('12) describes similar plants in which the root deficiency is also recessive. Another striking feature is shown in this illustration. The inbred strain which lacks brace roots is derived from a floury variety of corn and shows a decided tendency to branch at the base of the stalk. These branches form stalks with tassels and ears and many of them are fully as well developed as the main stalk. In this way two or three stalks may be developed from one seed. The other parent of the cross shown never branches in this way and never even develops small branches or "suckers." The first hybrid generation shows this tendency to branch even more strongly developed than the branching parent. The plants shown are from three hills grown side by side and each hill is the product of three seeds. Thus it will be seen that both parents have contributed characters to the hybrid. Both these characters are such as to enable the plants to attain a greater development in general vegetative luxuriance than would be possible if either were lacking. Emerson ('12) gives an even better illustration of two extremely unproductive types of maize which give a vigorous hybrid, one of the parents contributing tall stature, the other green chlorophyll.

Many more illustrations of a similar operation of hereditary factors favoring a hybrid in its development might be cited. I believe that enough have been given to clear the way towards the acceptance of the doctrine that hybrid vigor is due largely to the normal functioning of definable, hereditary factors.

It is recognized that the characters used as illustrations here are superficial in nature. The characters which are really concerned in heterosis are those deep-seated, fundamental, physiological processes which govern metabolism and cell-division. As to the mode of inheritance of these characters we, as yet, know little. There is no reason to believe, however, but that many or all of them are Mendelian in mode of inheritance and that many of them operate in the same way to enable hybrid progeny to attain a more complete development than their parents. If this hypothesis, as to the way in which heterosis is brought about, is in its essential features correct, it points the way towards a more fundamental application of Mendelism to the physiological processes of growth than is generally acceded.

There now remains to be discussed the part that crossing-over or breaks in the linkage of hereditary factors would play according to this hypothesis. If any large number of characters are concerned and the dominant and recessive genes are equally apportioned between the two parents, and distributed at random on the chromosomes, the chance of crossovers occurring in such a way as to bring all the dominant factors in one individual at one time would be almost inconceivably small, especially when the phenomenon of interference is taken into consideration. However, when crossing-over does occur in such a way as to bring about more fortunate combinations in certain individuals, those individuals would be the ones selected by man in domesticated races, or by nature in the wild. Partial linkage does not prevent recombination but merely adds to the complexity of the process. The chance of fortunate recombinations would be greater in the more widely crossed animals and plants but such combinations would be again broken up by further crossing. The tendency would be, however, for the best combination of characters to survive and gradually supplant the others in time. In naturally selfed plants, most of which are crossed at more or less infrequent intervals, a fortunate homozygous combination would be fixed and the plants possessing such combinations would in time supplant their less fortunate relations.

Thus there would always be the tendency for all the more favorable characters to be gathered together and the others eliminated. In time all the individuals of a locality would tend to become equal in their hereditary characters and crossing between individuals in a given locality would not accumulate any greater number of favorable characters than the parents possessed and hence would not show any evidences of heterosis.

That this is the condition which is brought about Darwin has shown. Individuals from the same locality derive little or no benefit from crossing while crosses between individuals from different geographical regions show a greater effect of crossing. The work of Collins ('10) and the results obtained at the Connecticut Station (Jones and Hayes '17) show this also—varieties of maize of similar characters and from the same region give less increase when crossed than do varieties of diverse type or from widely separated geographical regions.

If by crossing-over and subsequent recombination the characters which bring about the great development in F_1 can all be accumulated in a homozygous condition in an individual, that individual should show a greater development even than the F_1 as A. F. Shull ('12) has pointed out. This is on the assumption that most characters which play a part in heterosis are not fully dominant. That a factor in the diploid condition has a greater effect than when in the haploid condition is indicated by the work of Hayes and East ('15) on endosperm characters in maize. Their results show that in reciprocal crosses a double dose of one allelomorph in the maternal endosperm fusion nucleus overcomes a single dose in the paternal endosperm nucleus. In other words factors have an accumulative effect.

The evidence that such superior individuals have been obtained by inbreeding is not very convincing it must be admitted. Darwin, however, in Ipomea obtained plants—"Hero" and its descendants—which were certainly no less vigorous than any plants at the beginning of the inbreeding period and the same thing occurred in Mimulus. These are the two species which were the most extensively inbred. Miss King, as mentioned before, has obtained inbred rats which are larger and more vigorous than individuals present in the original stock. Nothing of this kind has occurred in maize and on account of the small chance of recombining many of the most desirable characters in one plant, it is not at all surprising that such individuals have not as yet been produced.

The production of individuals by inbreeding which excel any of the original crossbred stock offers some means of deciding between the two hypothesis attempting to account for heterosis. According to the hypothesis of a physiological stimulation it would be difficult to see how individuals more vigorous than the parents could be produced by inbreeding.

The hypothesis of dominance also, possibly, makes it easier to understand why naturally crossed wild species, which have not been outcrossed with fresh stocks for long periods of time, may not show any markedly injurious effects from artificial inbreeding. According to the former view different characters of equal value to the organism which might persist indefinitely in a species, would supply a stimulation when united in a heterozygous combination. This stimulation would be lost whenever individuals were reduced to homozygosity by artificial self-fertilization. According to the view of dominance if the allelomorphs were all equal in their contributions to development there might be differences in a species and still no loss of vigor would result from inbreeding. It is assumed that the less favorable characters have been eliminated by selection. On either hypothesis there would be no reduction from inbreeding if all the members of species were exactly alike whether they are naturally crossed or naturally self-fertilized.

The hypothesis of physiological stimulation also implies the assumption that naturally crossed species of cultivated plants are inherently more efficient as producers than naturally selfed plants. This is hardly justified when we recall such vigorous and productive plants as wheat, oats, barley, rice, peas, beans, tobacco, tomatoes and many others which are usually self pollinated. It is, however, difficult to make a fair comparison on this basis.

To sum up, it may then be stated briefly that dominance of characters as opposed to the former idea of an indefinable physiological stimulation makes more understandable the facts that:

1. Heterozygosis produces a stimulating, and not an indifferent or depressing effect in crosses between related stocks and that the reverse is true in widely diverse stocks.
2. Heterozygosis operates throughout the lifetime of the individual even through many generations of vegetative propagation.
3. Inbreeding may result in individuals more vigorous than the original cross-bred stock.
4. Inbreeding may not bring about a reduction in some naturally crossed wild species.

Whether or not dominance of factors is wholly adequate to account for all of the immediate effects of exogamy remains to be seen. The former view that dominance was not concerned at all has been maintained so insistently that I have taken the extremely opposite view in order to show that dominance at least can be held responsible for a large part of the increased development shown by hybrids. The treatment of the subject in this light has been dogmatic. That cross-fertilization may produce some effect which can never be attained in self-fertilization or a sexual reproduction is still possible. The view of the problem which is presented here makes certain heretofore indefinite effects more intelligible. It is not meant to preclude entirely any beneficial physiological stimulation resulting from germinal diversity, if such an effect can be demonstrated.

The difference between the two hypotheses are not as great as might seem at first sight. The older hypothesis is general in its application and does not commit itself to the interpretation of specific effects. The view presented here is specific in its application and may be shown to be inadequate for the interpretation of all phases of the problem of increased development following cross-fertilization.

The greatest progress in our knowledge of inbreeding and crossbreeding was made when their effects were linked with Mendelian phenomena. This was the big step forward. The two ways of interpreting these effects discussed here, differ only in minor features and it is not putting the matter fairly to hold them up as two rival hypotheses, one to be chosen from the other. Placing the effects of inbreeding and cross-breeding entirely on a Mendelian basis is merely the logical outgrowth of the older view as knowledge of the methods of inheritance increased.

THE PART THAT HETEROSIS HAS PLAYED IN THE ESTABLISHMENT OF SEX.

Since heterosis is widespread in its manifestation it can hardly be doubted that it has played some part in the initiation and maintenance of sexual differentiation in organisms. Jennings ('13), however, has shown that conjugation in Paramecium does not result, immediately, to the advantage of the organism. The rate of reproduction is actually diminished and many of the organisms perish. The advantage which is derived from conjugation, he considers with Weismann, is due to the fact that biparental inheritance makes possible a greater variability and consequently a greater chance of recombinations, some of which are better able to persist. Hence, while many offspring from conjugating paramecia die, some may be able to survive. Conjugation therefore makes possible a greater elasticity in adaptiveness to new and varied surroundings.

If this immediately depressing effect found in Paramecium is general in the lower animals, heterosis would probably have played no part in the inauguration of sex. Both A. F. Shull ('12a) and Whitney ('12a) have shown, however, that heterosis occurs in the rotifer, *Hydatina senta*.

In the lower plants heterosis would have significance only in spore formation, as the main life of the plant is carried on in the haploid condition where heterozygosis could not, of course, operate. As organisms became more differentiated and specialized the accumulation of factors in the zygote from two somewhat different parents would have increasing significance. If, for example, an organism should vary in a character A by one new dominant mutation A′, the heterozygote AA′, according to the hypothesis of dominance, would be superior to the combination AA but not to the combination A′A′. According to the former view of a physiological stimulation the heterozygous combination AA′ might be superior to either homozygous combination. The matter is not so simple as this, however. The breeding facts show that recessive unfavorable variations are far more common than dominant favorable ones. The chances would be that those individuals which varied by dominant mutations would also vary from the parental stock, sooner or later, by recessive mutations as well, so that any hybrid union would tend to accumulate more favorable factors than either parental individual possessed and hence show heterosis. Heterosis would be an immedate factor for natural selection to work upon.

Moreover it seems possible that heterosis has had considerable to do with the rise of the sporophyte and the decline of the gametophyte in plants. Recombination of characters can take place as well when the dominant generation is the haploid as well as when it is diploid in respect to the chromosome arrangement. From the standpoint of adaptiveness through recombination of characters it might even be to the organism's advantage to retain the haploid generation as the one in which the principal life processes were carried on, since the different combinations would then be more surely tested and the best more easily selected in the simplex than in the duplex condition. Heterosis can only operate in the sporophyte. The union of different hereditary complexes gives to the sporophyte an advantage over the gametophyte in that all new favorable variations work together whereas segregation in the formation of the gametophyte reduces the efficiency of this generation. On the basis of the complimentary action of factors according to the dominance hypothesis of heterosis the gametophyte would practically always be at a disadvantage as compared to the sporophyte as long as variations were occurring so that heterosis must have played some part in these important changes.

Either on the basis of inducing variability or stimulating development, sex would be a creation of no value to organisms which are never cross-fertilized. It may be questioned if many such exist. In either case the sexual mechanism is so complex and deep-seated in the life of the organism that it is not to be discarded easily. Whenever the best possible combination of factors for a given environment is produced, it is to the advantage of the organism possessing that combination to give up cross-fertilization and resort to either self-fertilization or some form of sexual reproduction, for the reason that these are more efficient means of propagation. When the environment changes, those organisms which are not cross-fertilized may either be doomed to extinction or handicapped in becoming adapted to new conditions and the perpetuation of the sexual mechanism thereby accounted for.

Whatever may be the value or significance of heterosis, to account for this phenomenon it is, for the most part, unnecessary to assume that there is an indefinite stimulating effect of hybridization along with the expression of definable hereditary factors. Hence the distinction is no longer needed between the effects of self-fertilization and cross-fertilization and of heredity in development. The heretofore indefinite physiological stimulation resulting from heterozygosis and the related effects accompanying the loss of this stimulation following inbreeding can therefore be given a strictly Mendelian interpretation.

This being so there is no longer a question as to whether or not inbreeding *per se* is injurious. Whether good or bad results from inbreeding depends solely on the constitution of the organisms before inbreeding is commenced. Inbreeding is concerned only with the manifestation of conditions pre-existing. As a means of analyzing and of purifying a cross-bred stock by the elimination of undesirable qualities, inbreeding is therefore a method of first importance in plant and animal improvement.

LITERATURE CITED.

Andronescu, D. I., 1915. The physiology of the pollen of *Zea Mays* with special regard to vitality. Thesis, Univer. of Illinois.

Beal, W. J., 1876–1882. Reports, Michigan Board of Agriculture, 876, 1877, 1881 and 1882.

Biffen, R. H., 1912. Studies in the inheritance of disease resistance. Jour. Agr. Science 4:421–429.

Bonhote, J. L., 1915. Vigour and heredity. pp. xii+263. London: West, Newman and Co.

Britton, E. G., 1898. A hybrid moss. Plant World 1: 138.

Bruce, A. B., 1910. A Mendelian theory of heredity and the augmentation of vigor. Science, N. S. **32**: 627–628.

1917. In-breeding. Jour. Gen. **6**: 195–200.

Burck, W., 1908. Darwin's Kreuzungsgesetz und die Grundlagen der Blütenbiologie. Rec. Trav. Bot. Néerl. 4: 17–118.

Carrier, L., 1913. The immediate effect on yield of crossing strains of corn. Virginia Agr. Exp. Sta. Bull. 202, pp. 11.

Castle, W. E., 1916. Genetics and eugenics. pp. vi+353. Cambridge: Harvard Univer. Press.

Castle, W. E., Carpenter, F. W., Clark, A. H., Mast, S. O., and Barrows, W. M., 1906. The effects of inbreeding, cross-breeding and selection upon the fertility and variability of Drosophila. Proc. Am. Acad. of Arts and Sciences **41**: 731–786.

Collins, G. N., 1910. The value of first generation hybrids in corn. U. S. Dept. of Agr., Bur. of P. I. Bull. 191.

1910. Increased yields of corn from hybrid seed. Yearbook, U. S. Dept. of Agr., 1910, pp. 319–328.

1914. A more accurate method of comparing first generation hybrids with their parents. Jour. Agric. Research **3**: 85–91.

1918. Maize: its origin and relationships. Notes of the 123d regular meeting of the Botanical Society of Washington by H. N. Vinall. Jour. Wash. Acad. of Sciences **8**: 42–43.

Collins, G. N., and Kempton, J. H., 1913. Effects of cross-pollination on the size of seed in maize. U. S. Dept. of Agr., Cir. 124.

Crampe, H., 1883. Zucht-Versuche mit zahmen Wanderratten. Landwirtsch. Jahrbücher **12**: 389–458.

Darwin, C., 1875. The variation of animals and plants under domestication. 2 vols. 1898, New York: Appleton and Co.

1877. The effects of cross- and self-fertilization in the vegetable kingdom. pp. viii+482. London: Appleton and Co.

East, E. M., 1908a. Inbreeding in corn. Connecticut Agr. Exp. Sta. Report for 1907. pp. 419–428.

1908b A study of the factors influencing the improvement of the potato. Illinois Agr. Exp. Sta. Bull. 127. pp. 375–456.

1909. The distinction between development and heredity in inbreeding. Am. Nat. **43**: 173–181.

1910a. A Mendelian interpretation of variation that is apparently continuous. Am. Nat. **44**: 65–82.

East, E. M., 1910b. Inheritance in potatoes. Am. Nat. **44**: 424–430.

1915. The chromosome view of heredity and its meaning to plant breeders. Am. Nat. **49**: 457–494.

1916. Studies on size inheritance in Nicotiana. Genetics **1**: 164–176.

East, E. M., and Hayes, H. K., 1912. Heterozygosis in evolution and in plant breeding. U. S. Dept. of Agr., Bur. of P. I. Bull. 243, pp 58.

East, E. M., and Park, J. B., 1917. Studies on self-sterility I. The behavior of self-sterile plants. Genetics **2**: 505–609.

Emerson, R. A., 1912. The inheritance of certain "abnormalities" in maize. Report Am. Breeders' Assoc. **8**: 385–399.

Emerson, R. A., and East, E. M., 1913. The inheritance of quantitative characters in maize. Nebraska Agr. Exp. Sta. Research Bull. 2, pp. 120.

Enriques, P., 1907. La coniugazione e il differenziamento negli Infusoria. Archiv. f. Protistenkünde **9**:195–296.

Fabre-Domengue, P., 1898. Unions consanguines chez les Colombins. L'Intermédiarie des Biologistes **1**: 203.

Fischer, E., 1913. Die Rehobother Bastards und das Bastardierungsproblem beim Menschen. Jena. Reviewed in Jour. Her., 1914, **5**: 465–468.

Focke, W. O., 1881. Die Pflanzen-Mischlinge. pp. iv+569. Berlin: Borntraeger.

Gärtner, C. F., 1849. Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich, pp. xvi+791. Stuttgart: Hering & Comp.

Gernert, W. B., 1917. Aphis immunity of teosinte-corn hybrids. Science, N. S. **46**: 390–392.

Gerschler, M. W., 1914. Über alternative Vererbung bei Kreuzung von Cyprinodontiden-Gattungen. Zeitschr. f. ind. Abst. u. Vererb **12**: 73–96.

Gravatt, F., 1914. A radish-cabbage hybrid. Jour. Her. **5**: 269–272.

Gray, A., 1876. Darwiniana: essays and reviews pertaining to Darwinism. xii+396. New York: Appleton and Co.

Guaita, G. von, 1898. Versuche mit Kreuzungen von verschiedenen Rassen der Hausmaus. Ber. naturf. Gesellsch. zu Freiburg **10**: 317–332.

Hartley, C. P., Brown, E. B., Kyle, C. H., and Zook, L. L., 1912. Cross-breeding corn. U. S. Dept. of Agr., Bur. of P. I. Bull. 218.

Hayes, H. K., 1914. Corn improvement in Connecticut. Connecticut Agr. Exp. Sta., Part vi of the Annual Report for 1913. pp. 353–384.

Hayes, H. K., and East, E. M., 1911. Improvement in corn. Connecticut Agr. Exp. Sta. Bull. 168, pp. 21.

1915. Further experiments on inheritance in maize. Connecticut Agr. Exp. Sta. Bull. 188, pp. 31.

Hayes, H. K., and Jones, D. F., 1917. The effects of cross- and self-fertilization in tomatoes. Connecticut Agr. Exp. Sta., Part v of the Annual Report for 1916, pp. 305–318.

Hedrick, U. P., and Howe, G. H., 1913. Apples: old and new. New York Agr. Exp. Sta. Bull. 361, pp. 79–135.

Huth, A. H., 1875, The marriage of near kin, pp. lxvii+359. London: Churchill.

Hyde, R. H., 1914. Fertility and sterility in *Drosophila ampelophila*. i–iv, Jour. Exper. Zool., Vol. 17.

Jennings, H. S., 1912a. Age, death and conjugation in the light of work on lower organisms. Pop. Science Monthly **80**: 563–577.

1912b. The production of pure homozygotic organisms from heterozygotes by self-fertilization. Am. Nat. **46**: 487–491.

1913. The effect of conjugation in Paramecium. Jour. Exper. Zool. **14**: 279–391.

1916. The numerical results of diverse systems of breeding. Genetics **1**: 53–89.

Jones, D. F., 1917. Dominance of linked factors as a means of accounting for heterosis. Proc. Nat. Acad. of Sciences **3**: 310–312 and also Genetics **2**: 466–479.

1918. Bearing of heterosis upon double fertilization. Bot. Gaz. **65**: 324–333.

Jones, D. F., and Hayes, H. K., 1917. Increasing the yield of corn by crossing. Connecticut Agr. Exp. Sta., Part v of the Annual Report for 1916, pp. 323–347.

1917. The purification of soy bean varieties. Same, pp. 348–353.

Jones, L. R., 1918. Disease resistance in cabbage. Proc. of the Nat. Acad. of Sciences **4**: 42–46.

Keeble, F., and Pellew, C., 1910. The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*). Jour. Gen. **1**: 47–56.

Kempton, J. H., 1913. Flower abnormalities in maize. U. S. Dept. of Agr., Bur. of P. I. Bull. 278, pp. 16.

King, H. D., 1916. (Experiments of Miss King on inbreeding rats for 22 generations discussed in Jour. Her. **7**: 70–76.)

Knight, T. A., 1799. An account of some experiments on the fecundation of vegetables. Philosophical Transactions of the Royal Society of London **89**: 195–204.

1841 A selection from the physiological and horticultural papers published in the Transactions of the Royal and Horticultural Societies.

Kraemer, H., 1913. Über die ungünstigen wirkungen naher Insucht. Mitteilung der Deutsches Landwirtschafts Gesellschaft, 6 and 13 Sept., 1913. Translated in Jour. Her. **5**: 226–234.

Kölreuter, J. G., 1766. Dritte Fortsetzung der Vorläufigen Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Gleditschen Handlung. Reprinted 1893 in Ostwald's Klassiker der Exakten Wissenschaften, No. 41. Leipzig: Engelmann.

Lindley, J., 1852. The theory of horticulture. pp. 20–364. 2d Amer. Edition by A. J. Downing, New York: Wiley.

Mendel, G., 1865. Experiments in plant-hybridisation. Translated in Castle's Genetics and Eugenics, 1916, pp. vi+353. Cambridge: Harvard Univ. Press.

McCluer, G. W., 1892 Corn crossing. Illinois Agr. Exp. Sta. Bull. 21, pp. 82–101.

Moenkhaus, W. J., 1911. The effects of inbreeding and selection on the fertility, vigor and sex-ratio of *Drosophila ampelophila*. Jour. Morph. **22**: 123–154.

Montgomery, E. G., 1912. Preliminary report on effect of close and broad breeding on productiveness in maize. Nebraska Agr. Exp. Sta., 25th Annual Report, pp. 181–192.

Morrow, G. E., and Gardener, F. D., 1893. Field experiments with corn. Illinois Agr. Exp. Sta. Bull. 25, pp. 173–203.

1894. Experiments with corn. Illinois Agr. Exp. Sta. Bull. 31, pp. 359–360.

Muller, H. J., 1916. The mechanism of crossing-over III. Am. Nat. **50**: 350–366.

1917. An Oenothera-like case in Drosophila. Proc. Am. Acad. of Sciences **3**: 619–626.

Naudin, C., 1865. Nouvelles recherches sur l'hybridité dans les végétaux. Nouvelles Archives du Museum d'Histoire Naturelle de Paris. **1**: 25–174.

Pearl, R., 1915. Modes of research in genetics. pp. vi+182. New York: Macmillan.

Roberts, H. F., 1912. First generation hybrids of American and Chinese corn. Report Am. Breeder's Assoc. **8**: 367–384.

Riley, E. H., 1910. A new zebra hybrid. Am. Breeder's Magazine **1**: 107–110.

Ritzema Bos, (J.), 1894. Unterschungen über die Folgen der Zucht in engster Blutsverwandtschaft. Die Biologisches Centrallblatt **14**: 75–81

Sageret, A., 1826. Considérations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacées en particulier. Annales des Sciences Naturelles **8**: 294–314.

(Sargent), C. S., 1894. A hybrid walnut tree. Garden and Forest **7**: 434–436.

Shull, G. H., 1908. The composition of a field of maize. Report Am. Breeder's Assoc. **4**: 296–301.

1909. A pure line method of corn breeding. Same **5**: 51–59.

1910. Hybridization methods in corn breeding. Am. Breeder's Magazine 1:98–107.

1911. The genotypes of maize. Am. Nat. **45**: 234–252.

1914. Duplicate genes for capsule form in *Bursa bursa-pastoris*. Zeitschr. f. ind. Abst. u. Vererb. 12:97–149.

Shull, A. F., 1912a. The influence of inbreeding on vigor in *Hydatina Senta*. Biol. Bull. **24**: 1–13.

1912b. Studies in the life cycle of *Hydatina Senta* III. Jour. Exp. Zool. **12**: 283–317.

Spillman, W. J., 1909. Application of some of the principles of heredity to plant breeding. U. S. Dept. of Agr., Bur. of P. I. Bull. 165, pp. 74.

Stout, A. B., 1916. Self- and cross-pollinations in *Chichorium intybus* with reference to sterility. Mem. N. Y. Bot. Gard. **6**: 333–454.

Swingle, W. T., and Webber, H. J., 1897. Hybrids and their utilization in plant breeding. Yearbook, U. S. Dept. of Agr. for 1897, pp. 383–420.

Tupper, W. W., and Bartlett, H. H., 1916. A comparison of the wood structure of *Oenothera stenemeres* and its tetraploid mutation *gigas*. Genetics **1**: 177-184.

Van Mons, J. B., 1836. Arbres fruitiers ou pomologie Belge Expérimentale et Raisonnée. Vol ii. Louvain.

Weismann, A., 1904. The evolution theory. 2 Vols. (Translated by J. A. Thomson and M. R. Thomson) London: Arnold.

Wellington, R., 1912. Influence of crossing in increasing the yield of the tomato. New York Agr. Exp. Sta. Bull. 346, pp. 57–76.

Weston, W. H., 1918. The downy mildews of maize, their origin and distribution. Notes of the 123d regular meeting of the Botanical Society of Washington by H. N. Vinall. Jour. Wash. Acad. of Sciences **8**: 43.

Whitney, D. D., 1912a. Reinvigoration produced by cross-fertilization in *Hydatina Senta*. Jour. Exp. Zool. **12**: 337–362.

1912b. "Strains" in *Hydatina*. Biol. Bull. **22**: 205-218.

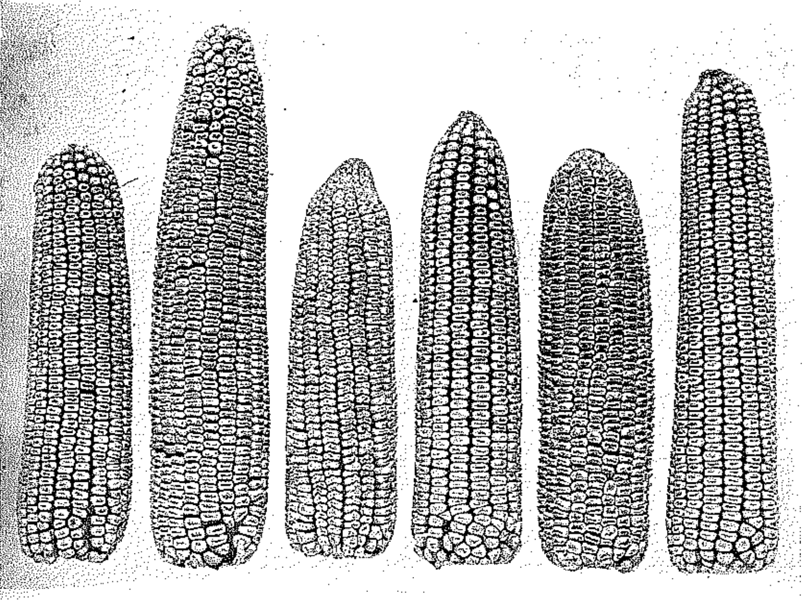
1912c. Weak parthenogenetic races of *Hydatina Senta* subjected to a varied environment. Biol. Bull. **23**:321–330.

Wichura, M., 1865. Die Bastardbefruchtung im Pflanzenreich erläutert an den Bastarden der Weiden. pp. iv+95. Breslau: Morganstern.

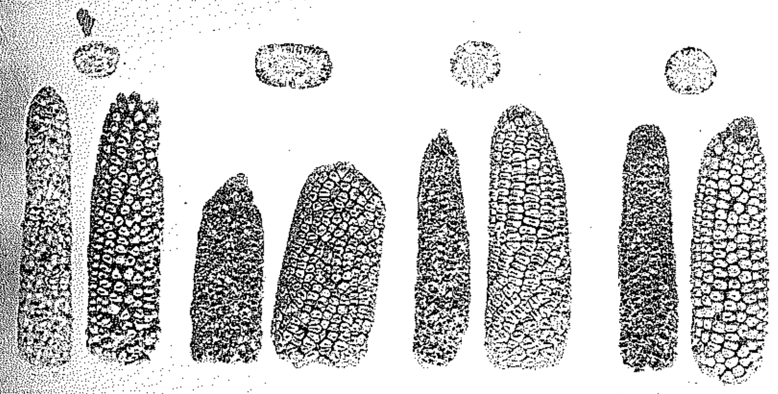
Wiegmann, A. F., 1828. Ueber die Bastarderzeugung im Pflanzenreich. pp. 40. Braunschweig.

Woodruff, L. L., 1911. Two thousand generations of Paramoecia. Archiv. f. Protistenkunde **21**: 263–266.

Wolfe, T. K., 1915. Further evidence of the immediate effect of crossing varieties of corn on the size of seed produced. Jour. Am. Soc. of Agr. **7**: 265–272.

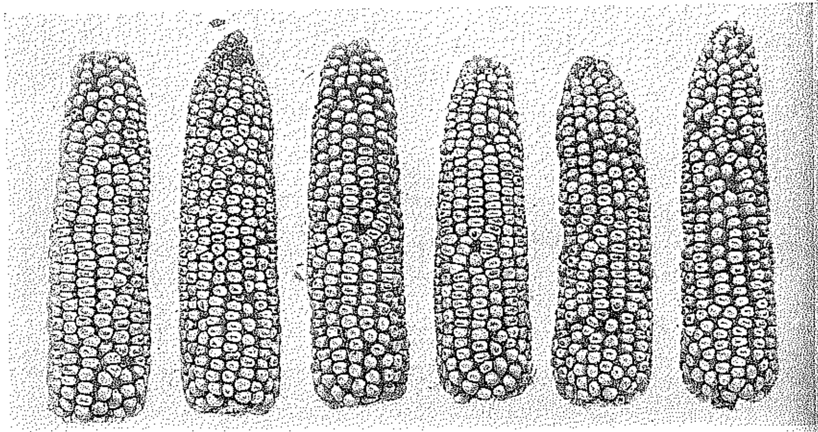


a. A non-inbred variety of Leaming dent corn.

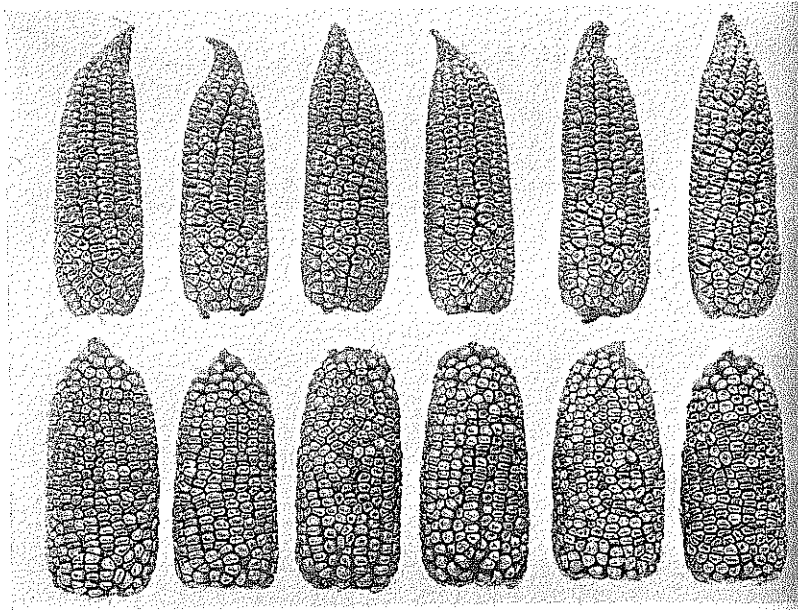


b. Four inbred strains derived from the Leaming variety after nine generations of self-fertilization showing an ear, a cob and a cross-section of a cob of each.

PLATE II.

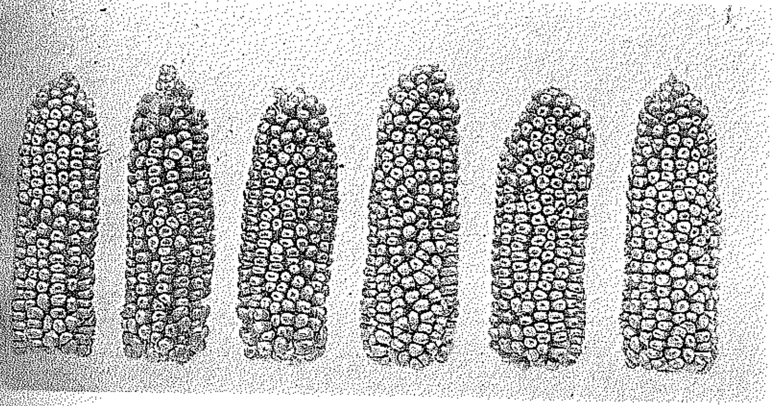


a. Representative ears of inbred strain No. 1-6-1-3, etc.

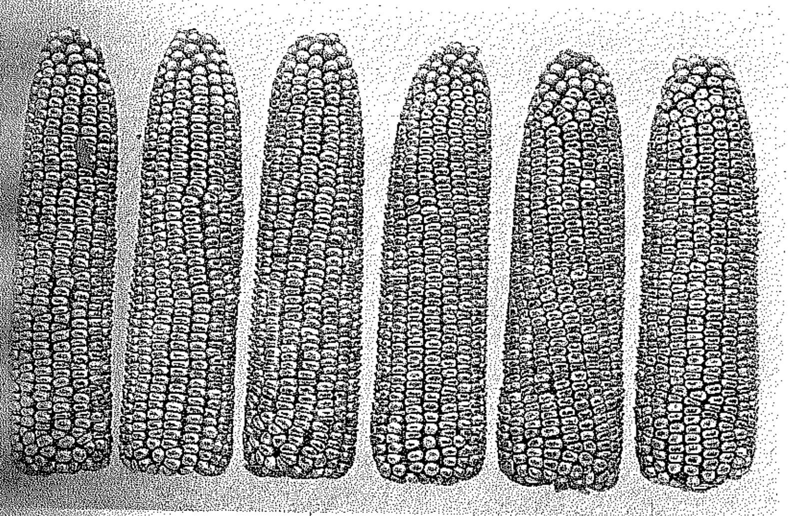


b. Representative ears of inbred strain No. 1-9-1-2, etc., above and No
1-7-1-1, etc., below.

PLATE III.

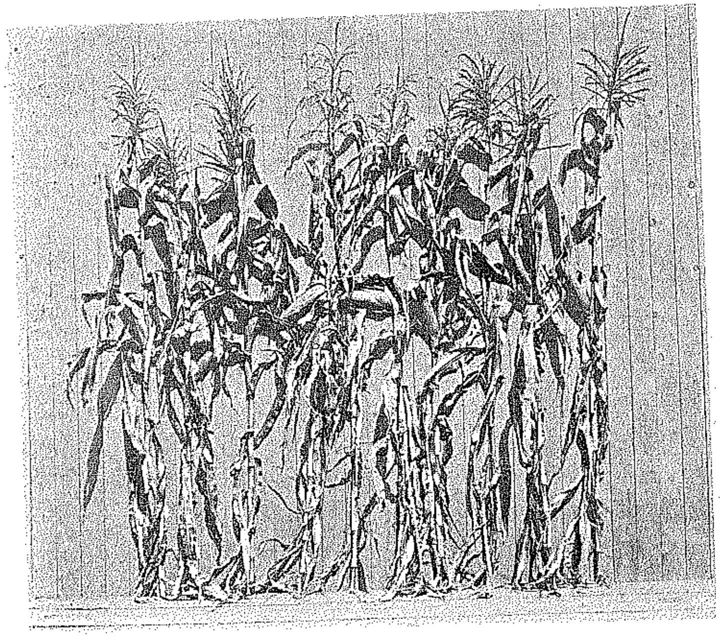


a. Representative ears of inbred strain No. 1-7-1-2, etc.

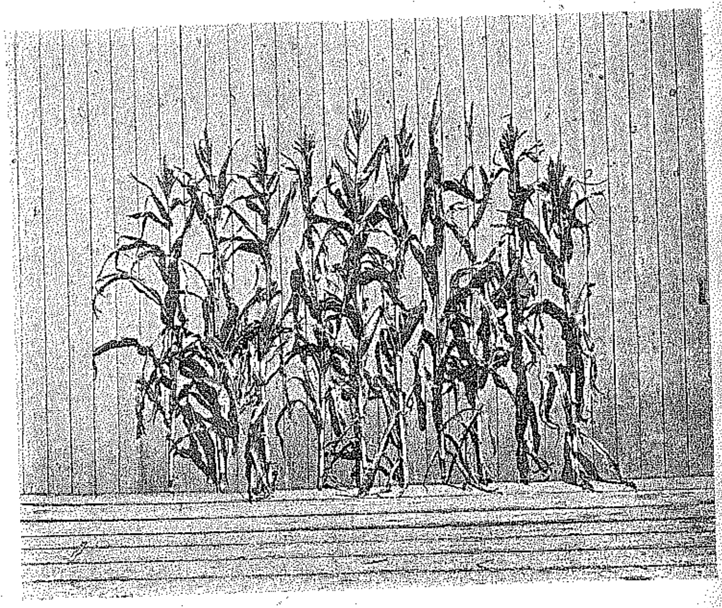


b. The first generation cross of inbred strain No. 1-6-1-3 by 1-7-1-2.

(Plates I to III inclusive, with the exception of Ib, are on the same scale). The plants which produced these ears were all grown on the same field and the non-inbred variety and the first generation cross were grown in adjoining rows. The ears of these latter two represent the best ears produced by 60 plants of each.

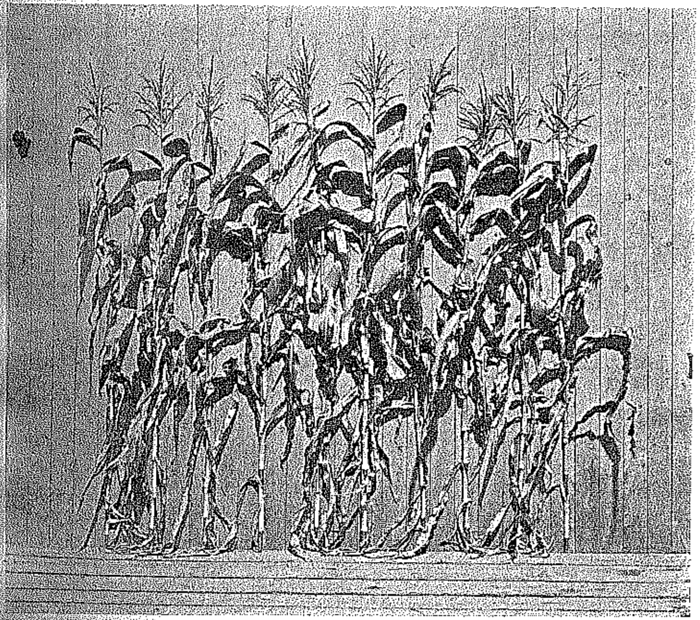


a. Representative plants of the original, non-inbred Leaming variety.



b. Representative plants of the inbred strain No. 1-6-1-3, etc.

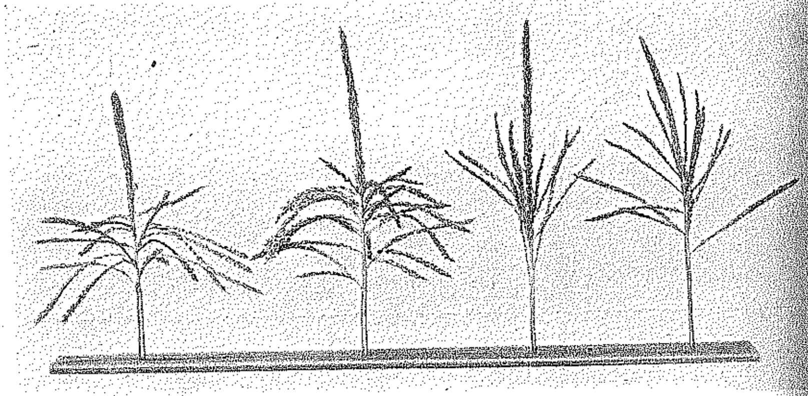
a. Representative plants of the inbred strain No. 1-7-1-2, etc.



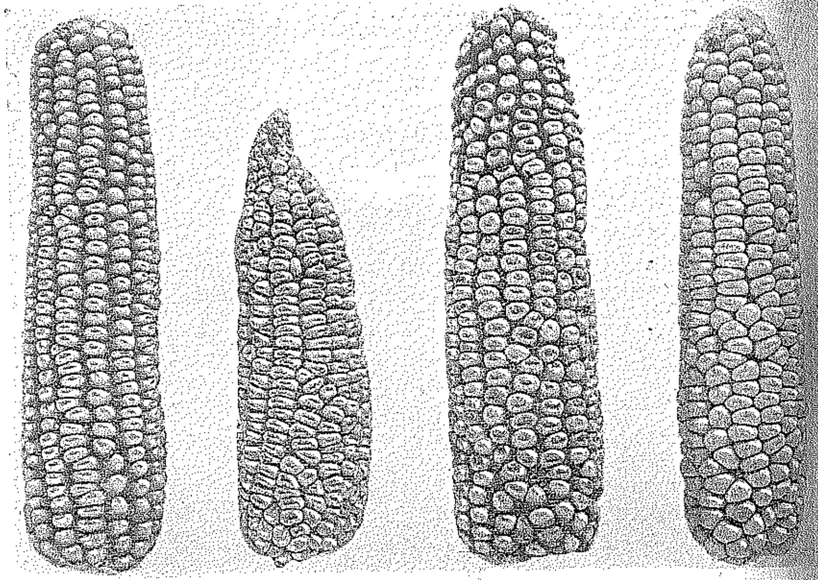
b. Representative plants of the first generation cross of inbred strain No. 1-6-1-3 by 1-7-1-2.

(Plates IV and V are on the same scale.)

PLATE VI.

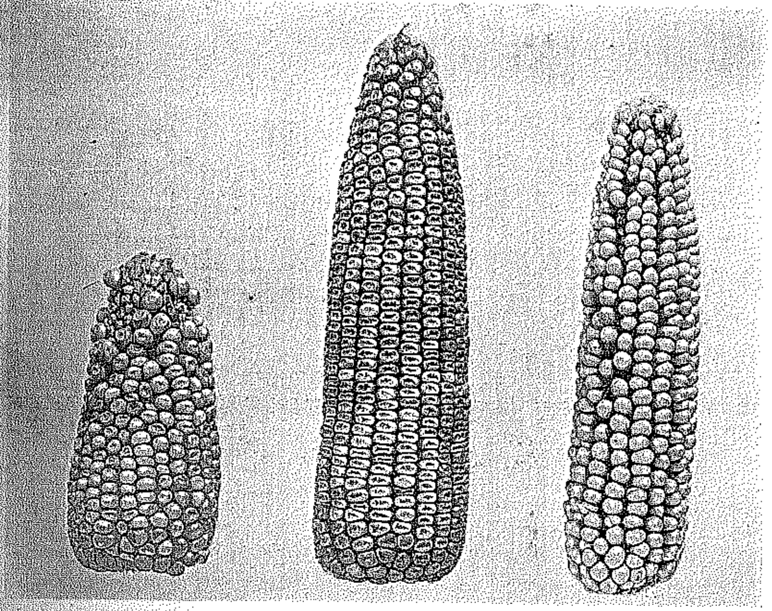


a. Two fully developed tassels on the left and two partially sterile tassels on the right characteristic of four different inbred strains of maize. From left to right they are, 20A-8-5-10; 1-9-1-2; 1-6-1-3; 21-3-13-9.

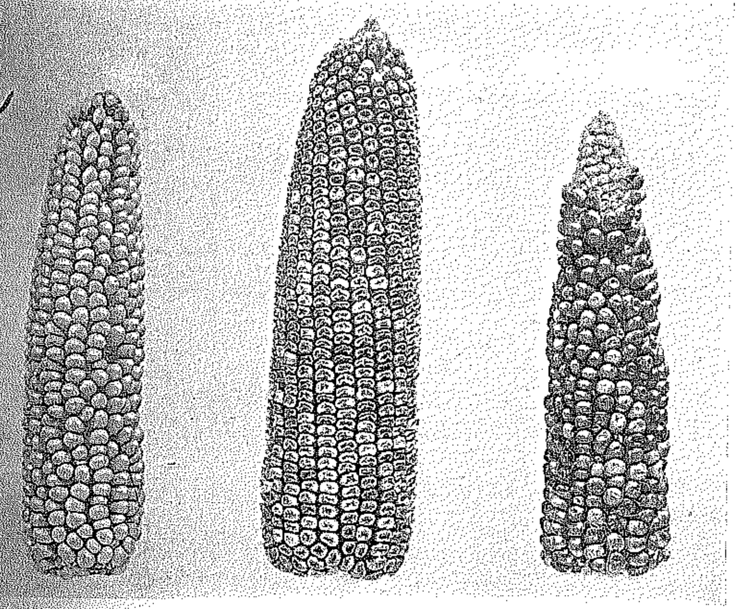


b. Representative ears from the corresponding strains shown in the illustration above. The first strain on the left produces fully developed tassels and moderately developed ears. The second produces the best developed tassels and the poorest ears. The other two have poorly developed tassels and moderately well developed ears.

PLATE VII.

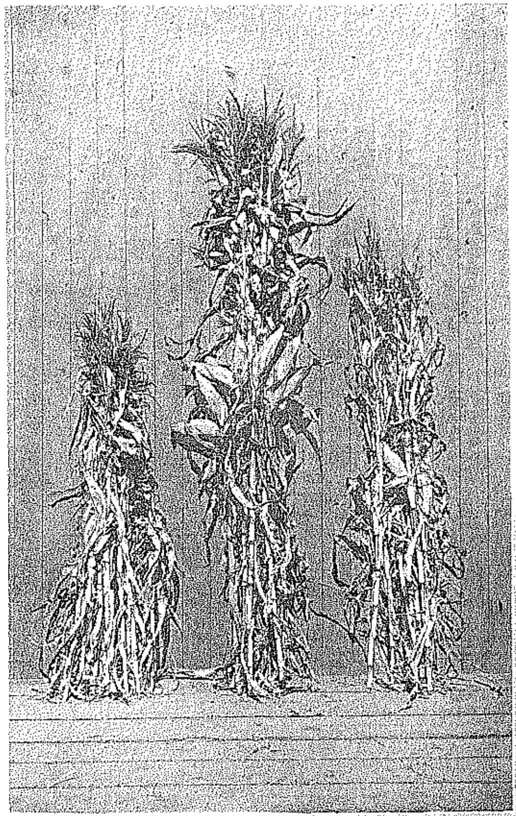


a. Two inbred strains of dent corn, No. 1-6-1-3 at the right and No. 1-7-1-1 at the left and the first generation cross in the center. The three ears were grown under equal conditions and gathered on the same day to show differences in maturity.

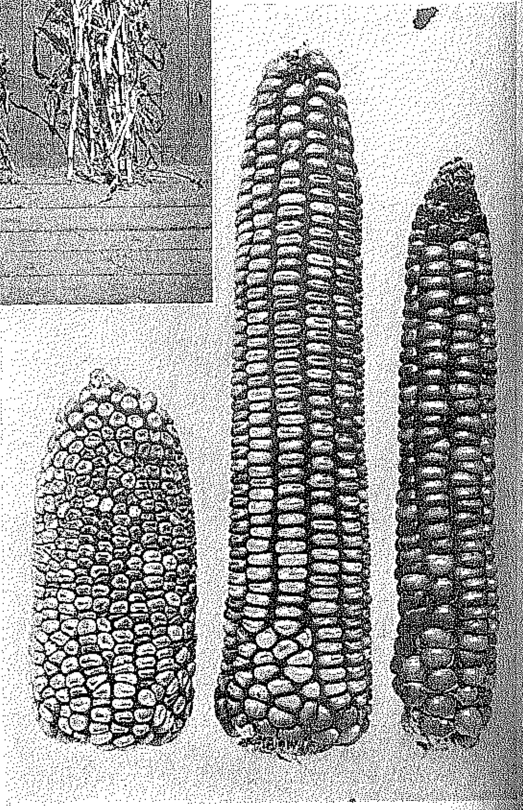


b. Two inbred strains of dent corn, No. 1-7-1-2 at the right and No. 1-6-1-3 at the left and the first generation cross in the center showing the differences in maturity.

PLATE VIII.

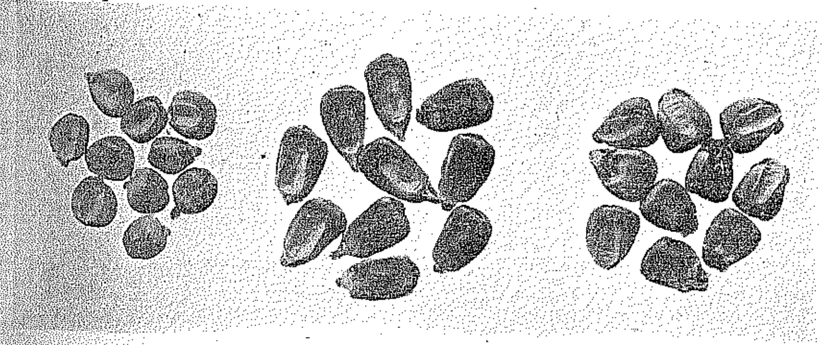


a. Two inbred strains of dent corn, No. 1-6-1-3 at the right and No. 1-7-1-2 at the left, and their first generation cross.

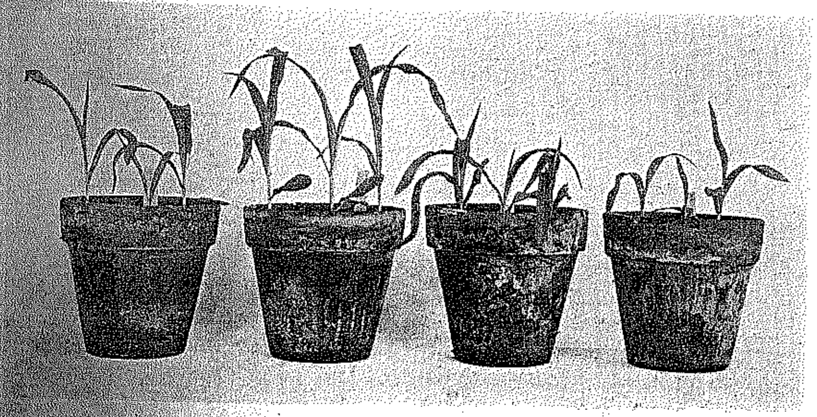


b. An inbred flint and an inbred dent corn compared with the first generation cross.

PLATE IX.



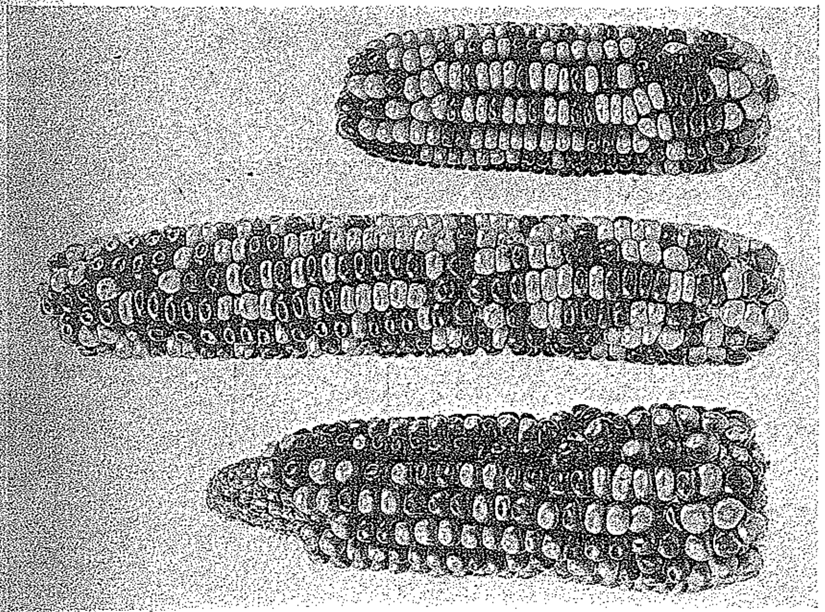
a. Seeds of two inbred strains of corn and the seeds produced upon the first generation hybrid plant in the center. The second generation plants grown from these large seeds have an advantage over either the parents or the first generation hybrid.



b. Two inbred strains and their first and second generation hybrids. From right to left they are: inbred strain No. 1-9-1-2, No. 1-7-1-1, (1-9 x 1-7), F_1 and F_1.

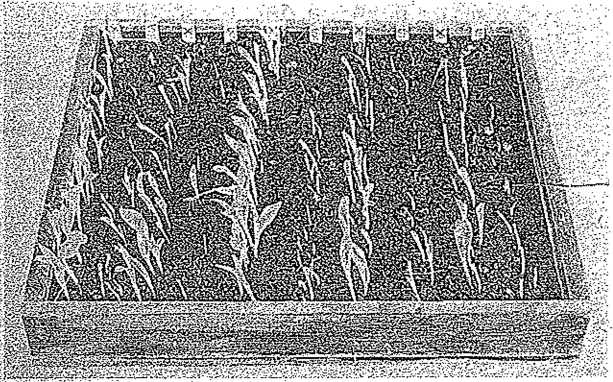
a. The same two inbred strains and their first and second generation hybrids as in IX b. From right to left they are: inbred strain No. 1-9-1-2, No. 1-7-1-1, (1-9 x 1-7) F_2 and F_1.

b. Same as above—ten plants of each.



a. Selfed, reciprocally crossed and out-crossed seeds obtained by pollinating plants of three different strains with a mixture of yellow and white-carrying pollen from the plants which bore the two ears shown below, showing the ratio and distribution of the two different kinds of seeds produced on each ear.

(The seeds resulting from the "yellow" pollen were colored by hand on all three ears.)



b. Seedlings showing the rate of growth and the amount of germination of selfed and crossed seeds from the same ears from five different plants.

PLATE XII.

a. The first generation cross of an inbred strain which lacks brace roots but has the habit of branching freely from the base of the plant (shown at the right) with an inbred strain (shown at the left) which has well developed brace roots but does not branch at the base. The three lots of plants have resulted from three seeds each.

b. A closer view of the roots of the plants shown in the above illustration.

Connecticut Agricultural Experiment Station

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Insects Attacking the Potato Crop in Connecticut

By W. E. BRITTON.

CONTENTS

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