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Chapter 1

Early Ideas on Inbreeding and Crossbreeding

In tracing the historical background of a great scientific advance or discovery, the historian nearly always has the opportunity of showing that the scientists who receive the credit for the work are really late-comers to the field, and that all the basic principles and facts were known much earlier. Finding these earlier records is always something of a pleasure; comparable, perhaps, to the pleasure a systematist experiences in extending the range of some well known species.

The historian may be tempted, in consequence, to emphasize these earlier contributions a little too strongly and to re-assign the credits for the scientific advances which have been made. In the present state of the history of science, it requires only a little searching of the records to discover contributions which have been overlooked and which are very pertinent to the advance in question. This wealth of data, which accumulates almost automatically, seems to deserve emphasis. But great steps forward generally are made not by the discovery of new facts, important as they are, or by new ideas, brilliant as they may be, but by the organization of existing data in such a way that hitherto unperceived relationships are revealed, and by incorporating the pertinent data into the general body of knowledge so that new, basic principles emerge.

For example, even so monumental a work as Darwin's *Origin of Species* contains few facts, observations or even ideas which had not been known for a long time. The work of many pre-Darwinians now appears important, especially after Darwin's synthesis had shown its significance. Of course, this does not belittle Darwin in the slightest. It only illustrates the way science grows.

The emergence of the scientific basis of heterosis or hybrid vigor is no exception. Practically all of its factual background was reported before Mendel's great contribution was discovered. Even workable methods for utilizing hybrid vigor in crop production were known, but it was not until the classic post-Mendelian investigations of Shull, East, and Jones were completed, that heterosis took its proper place in genetics. The following discussion of the importance of heterosis will be confined to its pre-Mendelian background.

Heterosis can be described as a special instance of the general principles involved in inbreeding and outbreeding. To fit it into its proper niche, we will trace first the evolution of our ideas on the effects of these two contrasting types of mating. Since our earliest breeding records seem limited to those of human beings and primitive deities, we will start with the breeding records of these two forms.

Hybrid vigor has been recognized in a great many plants during the last two hundred years. We will therefore describe briefly what was known of its influence on these plants. Because heterosis has reached its greatest development in *Zea mays*, we will trace briefly the pre-Mendelian genetics of this plant, and show how the facts were discovered which have been of such great scientific and economic importance.

The ill effects of too-close inbreeding have been known for a long time. Indeed, Charles Darwin (1868) believed that natural selection had produced in us an instinct against incest, and was effective in developing this instinct because of the greater survival value of the more vigorous offspring of exogamous matings. One of his contemporaries, Tylor (1865), noted that many savage tribes had tabooed the marriage of near relatives, and he assumed that they had done so because they had noticed the ill effects of inbreeding. The Greeks looked upon certain marriages between near relatives as crimes. This has been known almost universally ever since Freud popularized the tragedy of King Oedipus. At present, we outlaw close inbreeding in man, and our custom is scientifically sound.

We are apt to be mistaken, however, if we read into the standards of our distant preceptors the factual knowledge which we have today. The intellectual ancestors of European civilization approved of inbreeding and actually practiced it on supposedly eugenic grounds. The fact that their genetics was unsound and their eugenic notions impractical is irrelevant. They had their ideals, they were conscientious and they did their duties. The Pharaohs married their own sisters when possible so that their godlike blood would not be diluted. Marriage between half brother and sister was common in other royal families of the period. Actually, as we shall see, the two great pillars of European thought, Hebrew morality and Greek philosophy, endorsed inbreeding as a matter-of-course.

The Hebrews, who derived mankind from a single pair, were compelled to assume that the first men born had to marry their sisters—as there were then no other women on the earth. Indeed Adam and Eve themselves were not entirely unrelated. The marrying of a sister was obviously respectable, and it seems to have occurred routinely among the Hebrews and their ancestors for several thousand years. Abraham's wife, Sarah, was also his sister. At times even closer inbreeding took place. Abraham's nephew, Lot, impregnated his own two daughters. The latter instances occurred, however, under exceptional circumstances—and Lot was drunk. But as late as the time of King David, brother-sister marriages took place. The imbroglio between David's children, Tamar, Ammon, and Absalom, shows that a legal marriage between half-brother and sister would then have been a routine occurrence.

The Greeks also could hardly have had scruples against inbreeding, as evinced by the pedigrees they invented for their gods. Their theogony shows many instances of the closest inbreeding possible for either animals or gods in which the sexes are separate. Zeus, the great father of the gods, married his sister, Hera. Their parents, Kronos and Rhea, also were brother and sister, and were in turn descended from Ouranos and Gaea, again brother and sister. Thus the legitimate offspring of Zeus—Hebe, Ares, and Hephaestus—were the products of three generations of brother-sister mating. Moreover, the pedigrees of the Greek heroes show an amount of inbreeding comparable to that in our modern stud books for race horses. They were all related in one way or another and related to the gods in many ways. A single example will be cited. Zeus was the father of Herakles and also his great-great-grandfather on his mother's side. Herakles' great-great-grandmother, Danaë, who had found such favor in the eyes of Zeus, was herself descended from Zeus through two different lines. With immortals, backcrossing offered no real problems.

East and Jones (1919) have pointed out that close inbreeding was common among the Athenians even at the height of their civilization. These scientists were of the opinion that most of the freemen in Attica were rather closely related to each other. Marriage between half brother and sister was permitted, and marriage between uncle and niece fairly common. A Grecian heiress was nearly always taken as a wife by one of her kinsmen so that her property would not be lost to the family. Common as inbreeding was during the flowering of Greek culture, it was as nothing compared with the inbreeding which occurred in the period after the Trojan War and before the true historical period. In this intervening time, Greece was divided into innumerable independent political units, many of them minute. One island six miles long and two miles wide contained three separate kingdoms. Political boundaries as well as bays, mountains, and seas were functional, isolating mechanisms; and the Greeks were separated into many small breeding units for fifteen to twenty generations. Isolation was never complete, however, and there were enough wandering heroes to supply some genic migration. There were also some mass migrations and amalgamations of different tribes. The general situation was startlingly close to the conditions which Sewall Wright (1931) describes as the optimum for rapid evolution.

We may be tempted to explain as cause and effect what may be only an accidental relationship in time; and, while recognizing that it is far fetched, to ascribe the sudden appearance of what Galton called the ablest race in history to the ideal conditions for evolution which their ancestors had. We would also like to consider, as the necessary preliminary to the hybrid vigor, that period of inbreeding which preceded the flowering of Grecian culture. This hybrid vigor we would like to recognize as an important factor in the production of the great geniuses who flourished in the later, larger city states of Greece.

So much for the classical attitude toward endogamy. It slowly changed, and exogamy which had always existed became the exclusive custom. At the time of Sophocles, all forms of inbreeding were not considered ethical and pleasing to the gods. The sin of Oedipus lay in his having made a forbidden backcross rather than in mere inbreeding which was lawful. We do not find any records of degeneracy appearing in his children—indeed his daughter Antigone was a model of feminine virtue. It seems that close human inbreeding came to an end without its ill effects ever having been recognized.

The Nordics also were unaware of any degeneracy inherent in inbreeding. Their great god Wotan included a bit of inbreeding in his plan for creating a fearless hero who could save even the gods themselves from their impending fate. Wotan started the chain reaction by begetting Siegmund and Sieglinde, twin brother and sister. The twins were separated in infancy. They met again as adults and, recognizing their relationship, had an illegitimate affair—begetting the hero Siegfried. Although Siegfried was not exactly an intellectual type, he was certainly not a degenerate—representing rather the ideal male of a somewhat primitive culture.

As the centuries passed, incest was extended to cover brother-sister mating, even when the parties involved were unaware of their relationship. There is no need to cite here the many examples of the later tragedies based upon this plot. It soon became an almost universally accepted standard in literature, from epics to novels. The luckless Finnish hero, Kullervo (*The Kalevala*, Rune XXXV), thus brought disaster to his family by seducing his sister unknowingly. Defoe's long suffering heroine *Moll Flanders* (1722) had to abandon an apparently successful marriage when she discovered that her husband was her brother. On the other hand, as late as 1819, Lord Byron defended brother-sister marriage passionately in his drama *Cain*—but this was a scandalous exception to the rule. The marriage of kin nearer than first cousins had become legally and morally taboo. Perhaps we may follow Westermarck in assuming that endogamy became passé, not because its biological ill effects were recognized, but because men knew their kinswomen too well to marry one of them if they could possibly get a wife elsewhere.

It is possible that we have thus far paid too much attention to inbreeding and outbreeding in man. Our excuse is that there are almost no other records of inbreeding from classical times. There are no plant records, of course, for sex in plants was not understood in spite of the general practices of caprification and hand pollination of the date palm. Records of inbreeding and outcrossing in domestic animals are almost completely lacking even in the copious agricultural literature of the Romans. Aristotle's History of Animals. 576a15 (Thompson 1910) does state that horses will cover both their mothers and their daughters ". . . and, indeed, a troup of horses is only considered perfect when such promiscuity of intercourse occurs"—but he seems to be almost alone in referring to the subject. Later on in the same book (630b30) he cited a happening which we quote.

The male camel declines intercourse with its mother; if his keeper tries compulsion, he evinces disinclination. On one occasion, when intercourse was being declined by the young male, the keeper covered over the mother and put the young male to her; but, when after the intercourse the wrapping had been removed, though the operation was completed and could not be revoked, still by and by he bit his keeper to death. A story goes that the king of Scythia had a highly-bred mare, and that all her foals were splendid; that wishing to mate the best of the young males with the mother, he had him brought to the stall for the purpose; that the young horse declined; that, after the mother's head had been concealed in a wrapper he, in ignorance, had intercourse; and that, when immediately afterwards the wrapper was removed and the head of the mare was rendered visible, the young horse ran away and hurled himself down a precipice.

This behavior of the stallion was considered so remarkable that it was described by Aelian, Antigonus, Heirocles, Oppian, Pliny, and Varro. Varro confused the tradition and made the horse bite his keeper to death.

It is fairly safe for us to assume that in both classical and medieval times the flocks and herds were greatly inbred. Transportation difficulties would have insured inbreeding unless its evil effects were realized, and we have at least negative evidence that they were not. Varro, who gave many detailed directions for the breeding of all domestic animals, does not even mention the question of kinship between sire and dam. We do have an interesting literary allusion by Ovid, however, to the routine inbreeding of domestic animals in his account of the incest of Myrrha in the tenth book of the *Metamorphoses*. The affair between Myrrha and her father Cinyras was like that of Oedipus and his mother Jocasta. The fates had decreed that Myrrha should become the mistress of her father. Torn by her unholy desires she debates the matter with her conscience. Her better nature argues (From the metrical translation of Brookes More, 1922):

But what more could be asked for, by the most
Depraved? Think of the many sacred ties
And loved names, you are dragging to the mire;
The rival of your mother, will you be
The mistress of your father, and be named
The sister of your son, and make yourself
The mother of your brother?

In stating the other side of the case Myrrha describes the "natural" inbreeding of animals.

A crime so great—If it indeed is crime.
I am not sure it is—I have not heard
That any God or written law condemns
The union of a parent and his child.
All animals will mate as they desire—
A heifer may endure her sire, and who
Condemns it? And the happy stud is not
Refused by his mare-daughters: the he-goat
Consorts unthought-of with the flock of which
He is the father; and the birds conceive
Of those from whom they were themselves begot.
Happy are they who have such privilege!
Malignant men have given spiteful laws;
And what is right to Nature is decreed
Unnatural, by jealous laws of men.
But it is said there are some tribes today,
In which the mother marries her own son;
The daughter takes her father; and by this,
The love kind nature gives them is increased
Into a double bond.—Ah wretched me!

The debate ends as we would expect, and in due course Myrrha is delivered of an infant boy who certainly showed none of the ill effects of the inbreeding which produced him. He grew up to be quite an Adonis. In fact he *was* Adonis.

We can profitably skip to the late eighteenth century before we pursue further the matter of inbreeding. This was the period when Bakewell was emphasizing the importance of breeding in improving farm animals, when the various purebreds were beginning to emerge, and when the efficacy of artificial selection was beginning to be understood.

By the beginning of the nineteenth century, practical attempts to improve the different breeds of cattle led to intensive inbreeding. A prize bull would be bred to his own daughters and granddaughters. At first, the breeders seemed to believe that a selection of the very best individuals followed by intensive inbreeding was the quickest method for improving the stock. On theoretical grounds this seemed to be the case, and great advances were actually made by this method—but sooner or later something always happened. The inbred stock seemed to grow sterile, but vigor could be reestablished by outcrossing. The actual cause of degeneracy in the inbreds was not understood until Mendelian inheritance was discovered, but the remedial procedures of the practical breeders could hardly have been improved on. We owe to them the basis of our finest stocks. They inbred to add up and concentrate desirable qualities and then crossbred to prevent degeneration, then inbred again and crossed again, all the time selecting their breeding stocks most carefully. Charles Darwin (1868) described this process most accurately and listed the pertinent publications.

There was a striking divergence in this work between theory and practice, which is just as well, as the only theories available at the time were inadequate. Those breeders who held that inbreeding was the *summum bonum* did not hesitate to crossbreed when the occasion demanded, and those who emphasized the virtues of hybridization inbred whenever inbreeding gave them the opportunity of adding up desirable qualities. Darwin, himself, stated, "Although free crossing is a danger on the one side which everyone can see, too close inbreeding is a hidden danger on the other." We await the twentieth century for a real improvement in breeding methods.

The first plant hybrid was described as such in 1716, and during the next forty-five years many descriptions of hybrid plants were published. Some attempts were even made to produce new varieties, but in retrospect the work seems somewhat dilettante.

From 1761 to 1766, Josef Gottlieb Koelreuter (1766) published the several parts of his well-known classic, and plant hybridization was put upon a different and more scientific basis. His investigation of hybridization was intensive, systematic, and scientific. He described, among other things, hybrid vigor in interspecific crosses in Nicotiana, Dianthus, Verbascum, Mirabilis, Datura, and other genera (East and Jones, 1919). He also observed floral mechanisms which insured cross pollination and assumed in consequence that nature had designed plants to benefit from crossbreeding. It is worth emphasizing that hybrid vigor in plants was first described by the person who first investigated plant hybrids in detail. Koelreuter continued to publish papers on plant hybrids until the early nineteenth century.

Meanwhile other contributions had been made to our knowledge of the effects of outcrossing and the mechanism for securing it. In 1793, Sprengel depicted the structure of flowers in great and accurate detail, and showed how self pollination was generally avoided. In 1799, Thomas Andrew Knight described hybrid vigor as a normal consequence of crossing varieties and developed from this his principle of anti-inbreeding. Other hybridizers noted the exceptional vigor of many of their creations. Indeed, hybrid vigor in plants was becoming a commonplace. Among the botanists who recorded this vigor were: Mauz (1825), Sageret (1826), Berthollet (1827), Wiegmann (1828), Herbert (1837), and Lecoq (1845). Gärtner (1849) was especially struck by the vegetative luxuriance, root development, height, number of flowers and hardiness of many of his hybrids.

Naudin (1865) found hybrid vigor in twenty-four species crosses out of the thirty-five which he made within eleven genera. In Datura his results were spectacular. In reciprocal crosses between *D. Stramonium* and *D. Tatula* the offspring were twice the height of the parents. Knowledge of plant hybridization was increasing more rapidly at this time than the biologists knew, for this was the year in which Mendel's (1865) paper *Versuche über Pflanzen-Hybriden* appeared. Mendel discovered hybrid vigor in his pea hybrids and described it as follows:

> 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 the plants when stems of very different lengths are crossed. Thus, for instance, in repeated experiments, stems of 1 ft. and 6 ft. in length yielded without exception hybrids which varied in length between 6 ft. and 7½ ft.

We shall cite but one more scientist who wrote on the general subject of hybrid vigor in plants. This is Charles Darwin, whose *Cross and Self Fertilization in the Vegetable Kingdom* appeared in 1876. This was a book of great importance and influence, but no attempt will be made here to summarize this work of nearly five hundred pages. At the beginning of his concluding chapter, Darwin stated:

> The first and most important conclusion which may be drawn from the observations given in this volume, is that cross-fertilization is generally beneficial and self-fertilization injurious.

There is a special reason why this book of Darwin's is of such great importance for any historical background to heterosis. Darwin worked carefully and quantitatively with many genera, including *Zea mays*. He measured accurately the amount of hybrid vigor he could induce, and he published his data in full. His work stands in the direct ancestral line to the twentieth century research on the subject, and the great advances made from 1908 to 1919 are based solidly on this work. There are no great gaps in the steady progress and no gaps in the literature.

Zea mays was brought to Europe in 1493 by Columbus on his homeward voyage. This was sometime before the great herbals were written, so our first descriptions of the new grain are to be found in the books of the travelers and explorers. Later, Indian corn appeared under various names in the early herbals, and it was described in detail in the famous *Krautebuch* of Tabernaemontanus, first published in 1588. The author obviously yielded to his enthusiasm in devoting five and a half folio pages to corn and including thirteen illustrations in his treatment. He was the first to describe the results of xenia—the occurrence of different colored grains on the same ear—but his explanation of the phenomenon has nothing to do with cross pollination. He ascribed it directly to God Almighty.

And one sees an especially great and wonderful mystery in these spikes, *Gott der Herr*, through the medium of nature which must serve everyone, disports himself and performs wonders in his works and so notably in the case of this plant that we must rightly be amazed and should learn to know the One True Eternal God even from his creatures alone. For some of the spikes of this plant, together with their fruit, are quite white, brown and blue intermixed. Thus, some rows are half white, a second series brown and the third blue; and some grains, accordingly are mixed with each other and transposed. Again, sometimes one, two, or three rows are white, the next rows blue, then again white and after that chestnut-brown; that is, they are interchanged on one row and run straight through on another. Some spikes and their grains are entirely yellow, others entirely brown, some are white, brown, and blue, others violet, white, black, and brown: of these the white and blue are prettily sprinkled with small dots, as if they had been artistically colored in this way by a painter. Some are red, black, and brown, with sometimes one color next to the other, while at other times two, three, even four colors, more or less, are found one next to another in this way.

During the next century and a half, many other descriptions of the occurrence of different colored grains on a single ear were published. I have found about forty of them and there are doubtless many more. The earliest correct interpretation of this phenomenon had to await the eighteenth century and is contained in a letter written by Cotton Mather in 1716. Here the different colored grains occurring together on an ear are ascribed to a wind-born intermixture of varieties. This letter is the first record we have of plant hybridization, and antedates Fairchild's description of a Dianthus hybrid by one year. In 1724, Paul Dudley also described hybridization in maize, and he was able to eliminate one of the hypotheses which had been used to explain the mixture. As a broad ditch of water lay between the mixing varieties, he could show that the mixed colors were not due to the rootlets of different strains fusing underground, a view held at the time by many New Englanders, both white and red.

Hybridization in maize was described again in 1745 by Benjamin Cooke, in 1750 by the great Swedish traveler and naturalist, Pehr Kalm, and in 1751 by William Douglass. By the early nineteenth century, knowledge of plant hybrids was widespread. Plant hybridization was becoming a routine practice, and there is little doubt that different varieties of maize were crossed many times by American farmers who did not record their breeding experiments in writing.

Brown and Anderson (1947, 1948) have recently shown that the modern races now grown in the corn belt are derived from both the northern flint and the southern dent varieties. Hybridization in corn was easy to perform and the results were easy to recognize. The intermixtures of colors were so spectacular that they were frequently described, by Gallesio (1806), Burger (1808), Sageret (1826), Gärtner (1827), and others.

We detour briefly here into some of the technical aspects of xenia. Double fertilization and the mixed nature of the endosperm were discovered by Nawaschin in 1899. In 1881, Focke introduced the term *xenia* but he used it to include what we now call *metaxenia.* Focke collected from the literature many supposed instances where the pollen influenced directly the color and form of the flowers, the flavor and shape of the fruits, and the color and content of the seeds. How many of these cases were really due to Mendelian segregation we will probably never know, since the investigators did not know enough to take proper precautions.

We can, however, divide the history of true xenia into three periods: first, when its visible effect was considered a *lusus naturae* (1588); second, when it was known to be caused by foreign pollen (1716); and third, when the embryo and endosperm were recognized as two different structures and when the influence of the pollen upon the latter was recorded specifically. In the paragraph on *Zea* in the section on xenia, Focke cites the work of Vilmorin (1867), Hildebrand (1868), and Körnicke (1876), who described the effect of pollen on the endosperm.

We should note a brief comment on the subject which has been overlooked and is earlier than the papers cited by Focke. In 1858, Asa Gray described xenia in maize. He reported starchy grains in ears of sweet corn and many different kinds and colors of grains on the same ear. He had two explanations for this occurrence: (1) cross pollination of the previous year and (2) direct action of the pollen on the ovules of the present year. It is obvious that by *ovules* he did not mean *embryos*. This may be the earliest authentic recognition of the real problem of xenia.

In reviewing the nineteenth century records of hybrid vigor in *Zea mays*, we start with those of Charles Darwin (1876). Darwin planned his experiments most carefully. He crossed and selfed plants from the same stock, and raised fifteen plants from each of the two types of seed he had obtained. He planted the seed from both the selfed and crossed plants in the same pots, from six to ten plants per pot. When the plants were between one and two feet in height, he measured them and found that the average height of the plants from the selfed seed was 17.57 inches, while that from the crossed seed was 20.19 inches or a ratio of 81 to 100. When mature, the two lots averaged 61.59 inches and 66.51 inches, respectively, a ratio of 93 to 100. In another experiment when the corn was planted in the ground, the ratio of the selfed to the crossed was 80 to 100. Darwin called in his cousin, Francis Galton, to check his results and Galton judged them to be very good after he had studied the curves that he drew.

The direct connection between Darwin's work and our present hybrid corn is shown by Darwin's influence on W. J. Beal who was the real leader in the American research designed to improve maize. Beal reviewed Darwin's book in 1878, and even wrote an article which was little more than a paraphrase of what Darwin had published. Beal's own contributions appeared a little later.

In 1880, Beal described how he had increased the yield of corn on a large scale. Two stocks of the same type of corn which had been grown a hundred miles apart for a number of years were planted together in alternate rows. All of one stock grown in this field was detasseled and thus it could not be self fertilized but could produce only hybrid seed. The tasseled stalks of the other lot would still be pure bred as there was no foreign pollen to contaminate their ears and they could again serve as a parent to a hybrid. A small amount of the first parental stock which furnished the detasseled stalks was grown apart for future hybridization. The hybrid seed was planted, and produced the main crop. Beal increased his yield by this method by as much as 151 exceeds 100. This method and these results, it should be emphasized, were published in 1880.

E. Lewis Sturtevant, the first director of the New York Agricultural Experiment Station, made a number of studies of corn hybrids starting in 1882. His findings are interesting and important but not directly applicable to heterosis. Singleton (1935) has called attention to this work and to the excellent genetic research which the western corn breeders were carrying on at this time—such geneticists as W. A. Kellerman, W. T. Swingle, and Willet M. Hays. They anticipated many of Mendel's findings and described dominance, the reappearance of recessives (atavisms), and even Mendelian ratios such as 1 to 1 and 3 to 1. They were all concerned with practical results. Hays (1889), in particular, tried to synthesize superior breeds of corn by hybridizing controlled varieties.

Sanborn (1890) confirmed Beal's results and reported that his own hybrid corn yielded in the ratio of 131 to 100 for his inbred. He also followed Beal's method of planting his parental stocks in alternate rows and of detasseling one of them. He made an additional observation which we know now is important:

> It is this outcrossed seed which will give the great crops for the next year. It will be noted that I gained twelve bushels per acre by using crossed seed. The operation is simple and almost costless and will pay one hundred fold for the cost involved. *The cross must be made every year using new seed, the product of the outcross of two pure seed.* (Italics C. Z.)

If our farmers had known of this discovery reported in 1890 they might not have tried to use their own hybrid corn as seed.

Singleton (1941) also called attention to a pre-Mendelian interpretation of hybrid vigor by Johnson (1891) which, in the light of our present knowledge, deserves more than passing notice. We can state it in Johnson's own words:

> That crossing commonly gives better offspring than in-and-in breeding is due to the fact that in the latter both parents are likely to possess by inheritance the same imperfections which are thus intensified in the progeny, while in cross breeding the parents more usually have different imperfections, which often, more or less, compensate each other in the immediate descendants.

We come next to a publication of G. W. McClure (1892). This paper is deservedly famous, and its many contributions are incorporated into our modern genetics literature. Here we shall cite only the observations which pertain to heterosis. McClure noted (1) that sterility and deformity often follow selfing, (2) that crossing imparts vigor, (3) that it is impossible to tell in advance what varieties will produce corn of increased size when crossed, (4) that what appears to be the best ear does not always produce the largest crops, and (5) nearly all of the hybrid corn grown a second year is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties.

McClure also called attention to the fact that our fine varieties of fruits have to be propagated vegetatively, and hinted that the deteriorations of the seedlings from fruit trees was not unrelated to a like deterioration which occurred in the seedlings grown from hybrid corn.

The year following McClure's publication, Morrow and Gardiner (1893) recorded some very pertinent facts they had discovered as a result of their field experiments with corn. They reported that, "In every instance the yield from the cross is greater than the average from the parent varieties: the average increase per acre from the five crosses [they had made] being nine and a half bushels." They noted further in a paper published later the same year that, "It seems that cross bred corn gives larger yields at least for the first and second years after crossing than an average of the parent varieties, but how long this greater fruitfulness will last is undetermined." Gardiner continued the work and in 1895 published the data he obtained by repeating the experiments. He found that in four of six cases the yield was greater in the cross, the average being twelve bushels per acre.

We now come to the great corn breeding research project which was undertaken at the University of Illinois in 1895 by Eugene Davenport and P. G. Holden. Both of these scientists had been students of Beal and were interested in his work on inbreeding and cross breeding maize. We are indebted to Professor Holden for an account of this work which he printed privately in 1948. This account gives us valuable historic data not to be found elsewhere, as most of the University of Illinois records were destroyed by fire.

An intensive series of inbreeding experiments was undertaken by Holden, and later on the inbred lines were crossed. Hybrid vigor was noted, and it was found in addition that the crosses between different inbred lines differed widely in their yield and in their general desirability. The main purpose of the experiments was to find out how to use controlled crossing early and effectively. After Holden left Illinois in 1900, the project was taken over by C. G. Hopkins, a chemist, who was interested in increasing the protein content of maize. He hired as his assistant in 1900 a young chemist named Edward Murray East, whom we shall hear about later.

Our account of the background of heterosis is coming to an end as the beginning of the twentieth century makes a logical stopping point. We should mention, however, the great hybrid vigor discovered by Webber (1900) when he crossed a Peruvian corn, Cuzco, with a native variety, Hickory

King. The average height of the parental stocks was 8 feet 3 inches while the cross averaged 12 feet 4 inches, an increase of 4 feet 1 inch.

The next year Webber (1901) called attention to the marked loss of vigor in corn from inbreeding. From 100 stalks of selfed corn he obtained 46 ears weighing 9.33 pounds, while from 100 stalks obtained from crossing different seedlings he obtained 82 ears weighing 27.5 pounds. When he attempted to "fix" his Cuzco-Hickory King hybrid by selfing he got a great loss of vigor and almost complete sterility, but when he crossed the different seedlings there was little loss of vigor. He concluded that to fix hybrids one should not self the plants.

In 1900, the discovery of Mendel's long-forgotten paper was announced. Both Hugo de Vries and C. Correns, two of the three discoverers of Mendel, published papers on *Zea mays* and all future work on Indian Corn was on a somewhat different level.

SUMMARY OF KNOWLEDGE OF HYBRID VIGOR AT BEGINNING OF 20th CENTURY

1. Inbreeding reduces vigor and produces many defective and sterile individuals which automatically discard themselves.
2. Cross breeding greatly increases vigor both in interspecific and intervarietal hybrids. Crossing two inbred stocks restores the lost vigor and frequently produces more vigor than the stocks had originally.
3. All inbred stocks do not produce the same amount of vigor when crossed. Certain crosses are far more effective than others.
4. The simplest method of hybridizing *Zea* on a large scale is to plant two stocks in alternate rows and to detassel one stock. The hybrid corn grown from the detasseled stock produces the great yields.
5. Hybridization must be secured each generation if the yield is to be kept up, although a second generation of open pollinated corn may still be better than the original parental stocks.
6. In inbreeding, both parents are apt to have the same defects which are intensified in the offspring. The cause of hybrid vigor is that in crosses the parents usually have different defects which tend to compensate for each other in the immediate progeny.
7. The fact that hybrid vigor in *Zea* is not permanent but decreases if the hybrids are open-pollinated, seems to be related to the fact that fruit trees, whose desirable qualities are preserved by vegetative propagation, produce seedlings which are inferior.