Special Lecture

GENETIC CONCEPTS UNDERLYING HYBRID MAIZE BREEDING

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Hybrid maize breeding originated directly from studies on heredity by G. H. Shull that were designed initially not to solve a practical problem but rather to gain insight into a theoretical question. Shull was interested in the genetic basis of kernel-row number in *Zea mays*, a quantitatively varying character. The experimental procedures he adopted involved inbreeding maize by continued self-fertilization, and crossbreeding. The observed results of these processes were striking and unexpected. They quite overshadowed the earlier interest of kernel-row number. Shull perceived the significance of his findings for improving the maize plant by a radically new method. He then outlined, in the first decade of this century, with a degree of foresightedness at which we can only marvel today, the essential procedures whereby maize may be bred to previously unattained levels of excellence.

Three broad periods may be recognized during which the biological concepts and techniques underlying hybrid maize were developed. There is, first, the period during which Darwin, Mendel, and Johannsen worked. The publication in 1859 of Darwin's *Origin of Species* ushered in a new era in biology. The results of Darwin's experiments on inbreeding and crossbreeding, which were the most constructive performed up to that time, were brought together in a volume which he entitled *"The Effects of Cross- and Self-fertilization in the Vegetable Kingdom"*, published in 1877. Mendel's epoch-making studies on inheritance in the garden pea, which provided the key to understanding heredity, were reported in 1865. They were long neglected, and came to general attention only in 1900. W. Johannsen, the Danish plant physiologist, published his classical work on pure lines in the common bean, as natural products of continued self-fertilization, in 1903. We may consider the latter date as marking the end of the first period.

The significance for maize breeding of the concepts of heredity and evolution, with whose beginnings the names of Mendel, Darwin, and Johannsen are associated, were demonstrated during the second of the three historical periods I have chosen to recognize. This period was dominated by the experimental work of G. H. Shull and of E. M. East on inbreeding and crossbreeding maize. The critical investigations were carried out between 1905 and 1912.

The third stage in the evolution of hybrid maize was characterized by adaptive research, concerned with numerous and varied technological problems encountered by breeders the answers to which were not forthcoming either from genetic theory or from prior experience in developing open pollinated varieties. This stage began with D. F. Jones' key discovery of the double cross as a practical means of producing commercial seed. Up to the time of Jones' invention there was little basis for thinking that the potential advantages of hybrid maize, clearly foreshadowed by the observations of

Shull and East, could be broadly realized in practice. Both Shull and East eventually had concluded that the production of F_1 hybrid seed directly by crossing two inbred lines would be prohibitively expensive. Jones' double-cross method, of course, removed this block to the extensive use of controlled hybridity in maize. It also marked a turning point in the attitude of agricultural leaders in the United States toward the economic possibilities of hybrid maize. As a result, in the decade that followed, large scale maize breeding programs were funded and developed throughout the United States' Corn Belt. Some of these programs were publicly supported, others were privately financed. They have been abundantly productive.

It should be noted in passing that hybrid maize marks an inflection point in the history of agricultural research. Hybrid corn first gave agricultural research universal public identification in the United States. The significance of the achievement has since been recognized around the earth. A result has been a quickening influence on agricultural research everywhere. This fact is of special significance at the present juncture in human affairs. The earth's exploding population threatens a food famine. Obviously, the population of the earth must be brought under control if a great human catastrophe is to be avoided. The now widespread revolution in agriculture, which received an initial major impetus from hybrid maize breeding, significantly extends the time during which a rational balance between population and the food supply can be attained.

Darwin's Studies on Self- and Cross-fertilization

Darwin was the first to formulate general principles concerning the hereditary effects of inbreeding and crossbreeding. Numerous examples of hybrid vigor had been recorded by horticulturists before Darwin's time. Kölreuter and Knight, for example, noted the phenomenon late in the 18th century. Gärtner, in 1849, showed that hybrid vigor not only was of widespread occurrence among flowering plants but also was pervasive in its effects on the individual. Darwin himself compared the vigor of self- and cross-pollinated plants of several different species. Close inbreeding was observed to decrease vigor and fertility, whereas these qualities often were enhanced in crosses between different stocks. Darwin drew the significant conclusion that the vigor associated with hybridity does not result from the mere union of two distinct individuals but from the fact that the sexual elements united differ from each other. He was wrong in thinking, however, that such differentiation was a direct result of exposure of the ancestral stocks to unlike environmental conditions, as Lamarck previously had argued. Darwin demonstrated that lack of health in a parent was not a condition of vigor in hybrid offspring. Crosses between different healthy individuals often yielded conspicuously vigorous offspring. Darwin was unaware of Mendelian inheritance and so was unable to answer the question whether the ill effects of inbreeding proceeded from inbreeding as such or was a result of the inheritance received. Also he could not determine whether the deleterious effects of self-fertilization levelled off or continued indefinitely through successive generations.

Mendel

Mendel's demonstration that the genetic substance is discrete and particulate was basic, of course, for the elucidation of problems of heredity in general. His work provided a key to the understanding of inbreeding and crossbreeding which Johannsen, Shull, and East eventually were to utilize in interpreting the results of their experimental studies in this field.

Mendel's conclusions regarding the effects of crossbreeding and of inbreeding by self-fertilization are of direct importance for our present subject. Mendel showed that crossing two lines of peas known to differ in specific ways led to hererozygosis in the immediate offspring for the contrasting determinants for these characters. The heterozygotic condition could not be fixed. Mendel demonstrated algebraically that, as a result of the self-fertilization that regularly prevails in the pea, there was an orderly return to homozygosis among the descendants of such heterozygotes. He pointed out that, according to his theory of heredity, the number of heterozygous gene pairs was reduced one-half in each generation by self-fertilization, and that the number of kinds of resulting homozygous genotypes was a simple function of the amount of heterozygosis in the foundation plant.

Mendel directly demonstrated that all the constant combinations possibly by the assortment of the seven differentiating characters he studied were actually obtained in his various experiments. Their numebr was $2^n=128$. Mendel offered this observation as practical proof that "The constant characters which appear in the several varieties of a group of plants may be obtained in all the associations which are possible according to the mathematical laws of combination, by means of artificial fertilization." This statement, published by Mendel in 1866, embodies the key idea in the pure line theory as applied to naturally self-fertilized plants and enunciated by Johannsen in 1903. Also it is the central statistical concept underlying G. H. Shull's 1908 paper on *"The Composition of a Field of Maize"* and his 1909 article entitled *"A Pure Line Method of Corn Breeding"*. Thus Mendel's experiments on the garden pea provided the basis for a rational interpretation of the evidence on inbreeding and crossbreeding available when controlled hybridization was first envisaged as a method of producing superior maize.

Johannsen's Pure Line Theory

Johannsen's work on pure lines in the common bean, published in 1903, was a major step forward in understanding the composition of varieties of cultivated plants. For a half century after Darwin, who was unable to resolve the problem, the effects of selection were widely misunderstood. Darwin believed that any species or variety would be continually changed in the direction of selection if a certain type of individual was chosen for propagation in each generation. This mistaken idea was rectified only after Johannsen had distinguished sharply between genotype and phenotype and had demonstrated that in regularly self-pollinated species, like the common bean, the individuals making up a population were homozygotes. The self-pollinated descendants of each such homozygote he designated a pure line. In a classical set of experiments Johannsen showed that selection within a pure line was wholly ineffective in shifting the type.

The experimental material Johannsen used was a common, brown bean known in the trade as the Princess variety. The character he studied was seed weight. He showed that the Princess variety was genetically heterogeneous for seed weight. The variety consisted, in fact, of a mixture of genotypes conditioning seed weight that could be separated from each other by establishing lineages of plants each based on a single seed.

Mendel had shown that continued self-fertilization leads to homozygosis, and Johannsen experimentally established the fact that an unselected commercial variety of a self-pollinated species consisted of a mixture of homozygous genotypes. We can see that, at this point, it was but one step in theory to the conclusion which Shull drew only five years later that if self-pollination were enforced on a naturally cross-pollinated species like maize, for example, an initially heterogeneous and heterozygous population of plants comprising a cultivated variety also could be transformed into an assemblage of more or less distinctive pure lines.

G. H. Shull and E. M. East, Funders of Hybrid Maize Breeding

We come now to the scientific work which directly initiated hybrid maize breeding. This research was done by G. H. Shull, a staff member at the Station for Experimental Evolution at Cold Spring Harbor on Long Island, New York, and by E. M. East, at the Connecticut Agricultural Experiment Station at New Haven.

Attempts were made by several American investigators previous to the time of Shull and East to utilize systematically the vigor associated with hybridity in the improvement of maize. Most of these attempts trace to the interest which Darwin's publications aroused in the effects of inbreeding and crossbreeding. The first prominent American advocate of Darwin's views on organic evolution was Asa Gray, Professor of Botany at Harvard University. One of Gray's former students, W. J. Beal, a staff member at Michigan Agricultural College, reported in 1878 that a cross between two locally adapted maize varieties gave a 10 per cent increase in yield over the parents. Corroborative evidence was published in 1881 and 1882. Beal advocated the production of hybrid seed by planting two varieties in alternate rows one of which was to be detasseled so that the seed borne by it would have resulted from crossing with the other strain.

Additional attempts to bring hybrid vigor under control for the betterment of maize were made at the University of Illinois previous to 1905, and were fostered especially by Eugene Davenport and P. G. Holden, both of whom had studied under Beal at Michigan. McCluer, a horticulturist at Illinois in 1892, and also Morrow and Gardner in 1893, again showed that certain F_1 varietal hybrids were superior in yield to parental strains. Holden, invited by Davenport to become Professor of Agricultural Physics at Illinois in 1895, began an intensive program of self-fertilization in maize in 1895, and subsequently crossed inbred lines he had produced. He observed that crosses between distinct inbred strains differed widely in yield. Holden left Illinois in 1900. The Illinois maize investigations then took a new direction under the leadership of C. G. Hopkins, who sought to increase protein content of the maize kernel by selection. It is interesting to note that E. M. East, then a graduate student in agriculture at the University of Illinois, began his work with maize as a chemical analyst in Hopkin's laboratory in 1900, and that East's appointment at the Connecticut Agricultural Experiment Station five years later was on Hopkin's recommendation to Director Jenkins who was seeking a man qualified to undertake investigations on improvement of the chemical composition of maize. It was at this stage in his career, however, that East's interest in science came to focus in heredity rather than chemistry.

Two significant developments in theoretical genetics of importance for hybrid maize breeding had occurred by 1905, at which time the research interests of Shull and East turned in this direction. (1) Mendel's work on the mechanism of heredity had been brought to the general attention of biologists, and (2) Johannsen's investigations on pure lines in the bean had provided the first clear insights, in terms of Mendelian heredity, into the composition of populations of naturally self-fertilized plants. The next major step toward hybrid corn was the extension, in effect, of the concepts that Mendel and Johannsen had established to populations of the cross-pollinated species, *Zea mays* itself. The step was effected by Shull in a brilliant series of experiments at Cold Spring Harbor, the results of which East impressively confirmed at New Haven at about the same time.

In a remarkable paper published in 1908 under the title "*The Composition of a Field of Maize*" Shull showed that continued self-fertilization resolved an ordinary strain of maize into a collection of relatively stable biotypes (or elementary species, as he termed them) comparable to the naturally occurring pure lines Johannsen had demonstrated in garden beans.

"The obvious conclusion to be reached", Shull wrote, "is that an ordinary corn field is a series of very complex hybrids produced by the combination of numerous elementary species. Self-fertilization soon eliminates the hybrid elements and reduces the strain to its elementary components. In a comparison between a self-fertilized strain and a cross-fertilized strain of the same origin, we are not dealing, then, with the effects of cross- and self-fertilization *as such,* but of the relative vigor of biotypes and their hybrids. The greater vigor of the cross-fertilized rows is thus immediately brought into harmony with the almost universal observation that hybrids between nearly related forms are more vigorous than either parent."

Shull went on to say that "The fundamental problem in breeding this plant is the development and maintenance of that *hybrid combination* which possesses the greatest vigor."

The next year (1909) Shull formulated a method of breeding maize based upon this point of view. He proposed that many inbred lines be produced, and then crossed with each other. The resulting F_1 hybrids would be tested in yield trials to determine which was the best combination. After the right pair of pure strains was thus identified they would be grown repeatedly in detasseling plots for the production of hybrid seed and for propagation of the two parent lines.

The following year (1910) Shull's experimental work with maize had advanced to the point at which he felt justified in drawing broad conclusions regarding the effects of inbreeding and crossbreeding a crosspollinated plant like maize. In summarizing these conclusions I shall paraphrase the words Shull used in a 1910 article entitled *"Hybridization Methods in Corn Breeding"*.

(1) Self-fertilization invariably results in progeny of reduced size, vigor, and productiveness as compared with the offspring of a cross-bred plant of similar origin. This relation holds true whatever the merit of the parent self-fertilized plant itself. (2) The decrease in size and vigor accompanying self-fertilization is greatest in the first generation and becomes progressively less as the generations advance. (3) Individual inbred lines from a common varietal source differ from each other. (4) Crosses between sibs within an inbred family show only slightly greater vigor than selfs in the family. (5) Crosses between self-fertilized lines usually give progenies comparable in productivity to families which have not been self-fertilized. Pairs of inbred lines occur, however, which when crossed with each other give higher yields than the original cross-bred foundation stock. Yield and quality of the F_1 hybrid crop are functions of the particular inbred lines used as parents, and these qualities remain the same whenever the cross is repeated. (6) Variation from plant to plant increases and yield declines in F_2 as compared with F_1.

East's earliest experimental results on inbreeding and crossbreeding in maize were published in 1908, 1909, and in 1912 (with H. K. Hayes). Later, his views were fully and forcefully developed in the well-known book issued in 1919, with D. F. Jones as coauthor, and entitled *"Inbreeding and Outbreeding"*. East's conclusions were similar to those of Shull, to whom he gives credit for having first formulated the correct explanation of the data on inbreeding and crossbreeding maize.

The experimental work which East began at Connecticut in 1905 was continued by H. K. Hayes after East transferred to Harvard University in 1909, and by D. F. Jones for several decades after 1914 when Hayes moved to the University of Minnesota. The Connecticut investigations thus spanned the entire period from the inception of the idea of hybrid maize to large scale hybrid maize production. It was in the hands of East and his successors, Hayes and Jones, at Connecticut, that Shull's pioneer work on continued self-fertilization and crossbreeding of maize was verified and it was there that hybrid maize was demonstrated by Jones to be a commercial possibility.

Adaptive Research

As pointed out earlier in this article, the commercial utilization of hybrid maize was made possible by D. F. Jones' invention of the double cross method of producing seed. This novel and efficient procedure, marking the beginning of the final historical period I have recognized, made it practicable to apply on a large scale in the improvement of maize the principles of controlled inbreeding and crossbreeding which Shull had first defined. The systematic exploitation of hybrid vigor, however, raised many operating problems that were new in plant breeding experience. It was essential to discover and adapt breeding procedures to the new doctrine by which the genetic improvement of maize was now being guided. The potential gains to be made were high. Adaptive researches were undertaken to realize these new possibilities that were concrete, often novel, ingenious, and vigorously pursued. They ranged over the wide spectrum of field and laboratory problems faced by the maize breeder in his efforts to meet the diverse needs of producers and users of hybrid seed. Such investigations will continue indefinitely as hybrid maize enters new territory and as agricultural conditions change in areas in which the crop already is well established.

It is not proposed to review in this article the large amount of adaptive research that has already been done on hybrid maize, even in outline. Critical summaries of much of it were published in 1958 by R. W. Jugenheimer in *"Hybrid Maize Breeding and Seed Production"* and by H. K. Hayes in 1963 in a book entitled *"A Professor's Story of Hybrid Corn"*. Many members of this audience are presently engaged in studies vital for realization of the potential gains inherent in the controlled use, on a mass basis, of hybridity in maize in their respective geographical areas. A principal purpose of this meeting is to consider together how best to advance these investigations in southeast Asia. My task, however, is more general.

There are two particular topics in this area on which I shall comment, however briefly. One is cytoplasmic male sterility and the other is the genetic basis of heterosis.

Cytoplasmic Male Sterility

A recent triumph in hybrid maize breeding has been elimination of the need for hand detasseling in crossing fields by the use of cytoplasmically determined male sterility. An essential aspect of this genetic system of mating control is the restoration of male fertility, as desired, by utilizing genes that override the effect of the cytoplasmically borne pollen sterility determinants.

Fifteen years ago, before the genetic control of male fertility was widely used, it was estimated that detasseling the female rows in a commercial crossing field cost about $20.00 (U.S.) per acre. Training and supervising the large number of temporary workers employed in detasseling was especially troublesome to seed producers. The hand method of converting the normally monoecious maize plant into a functionally pistillate individual has now been almost entirely replaced in the United States by the use of cytoplasmically determined male sterility, which effects the same change.

An outline of the biological research underlying this industrial application of male sterility will be of interest.

Cytoplasmically controlled male sterility of the type now used in the production of hybrid maize seed was discovered in flax (*Linum usitatissimum*) and was first reported by Bateson and Gairdner in 1921. The main features of the phenomenon subsequently were described in articles by Chittenden, Pellew, and Gairdner, colleagues of Bateson at the John Innes Horticultural Institution, then in London.

The first practical use of this system of genetically controlled male sterility was in the production of hybrid onion (Allium) seed. A single male sterile plant, which was propagated by bulbils, was discovered in the Italian Red onion variety in 1925. Studies by H. A. Jones and A. E. Clarke, published in 1943 and 1947, showed that the Italian Red plant in question carried a special kind of cytoplasm (S), and also was homozygous for a gene designated *ms*. Most commercial onion varieties were found to contain normal (N) cytoplasm which, in combination with either *ms* or a dominant allele, *Ms*, conditioned full fertility. Jones and Clarke showed that the dominant *Ms* factor likewise overrode the male sterilizing effect of (S) cytoplasm. The cytoplasmic male sterile character was transferred by Jones and Clarke to several varieties by backcrossing, thus making possible the production of commercial hybrid onion seed. Hybrid onions were then bred which were outstanding in shape, size, flavor, uniformity of maturity. Jones and Clarke pointed out that this system of controlled mass hybridization could be used with other crop plants also. D. F. Jones and P. C. Mangelsdorf, in 1951, demonstrated applicability of the system, including genic restoration of male fertility in the final cross, to the production of hybrid maize seed, and the method is now widely employed in the United States.

Duvick (1965) states, in a recent review, that the form of cytoplasmically determined male sterility now most widely used in maize breeding was derived from a single plant discovered by Rogers in Texas in 1944 in a variety known as Golden June. At least one other kind of cytoplasmic male sterility determinant occurs in maize (the so-called USDA source), and there may be a few others.

Duvick demonstrated that a single major gene, termed Rf_1, conditioned restoration of male fertility in Texas cytoplasm. Rf_1 is located on chromosome 3, a few crossover units from the centromere, probably on the long arm. Alleles of Rf_1 have been found that cause partial restoration of pollen fertility in Texas cytoplasm. One such partial fertility restorer originally characterized M14, an inbred strain widely used in the production of Corn Belt hybrids.

A second locus, designated Rf_2, possibly on the short arm of chromosome 9, also is involved in pollen fertility restoration in Texas cytoplasm. The recessive allele (rf_2) at this locus, however, which is non-restoring, occurs but rarely in maize inbreds. There is evidence also for genes modifying the effect on pollen fertility of the major factors Rf_1 and Rf_2. Duvick has shown that presence of such modifiers is most readily detected under cool, moist, rather than hot, dry, growth conditions.

No firm evidence has been brought forward for mutability of the determinants of the Texas type of cytoplasmic male sterility. Many instances have been reported of fluctuations in sterility in certain environments, but Duvick considers that in all these cases alleles of Rf_1 are involved which are only partial fertility restorers. Likewise, high energy irradiation and treatment of seed with such chemical mutagens as acriflavine and streptomycin have been ineffective in inducing mutation in pollen sterility determinants.

The cellular basis of cytoplasmically determined male sterility remains obscure. Rhoades showed in 1933 that microsporogenesis in a cytoplasmically determined male sterile maize race originally from Peru, but now lost, was normal. He, and others, have observed that degeneration often begins at about the time of division of the microspore nucleus, or it may occur later. In any case, the cytoplasmically conditioned male sterility is expressed as inability of the microspore to develop into a functional pollen grain.

Neither the light microscope nor the electron microscope has disclosed any cytoplasmic inclusion that is certainly identifiable with pollen sterility. Edwardson's report in 1962 that differences can be seen with the electron microscope between cells in maize plants carrying Texas type as compared with cells possessing normal cytoplasm has not been confirmed.

Heterosis

The genetic basis of hybrid vigor has long been, and continues to be, a subject of scientific interest. The two best known hypotheses advanced to account for the phenomenon have been termed dominance and overdominance.

Davenport called attention in 1908 to the now widely recognized fact that the dominant member of a gene pair usually is advantageous to an organism, whereas the the corresponding recessive, in homozygous conditions, has a weakening effect. He stated that this relation could explain the decline in vigor that usually follows inbreeding. Bruce put forward a similar view in 1910. In the same year, Keeble and Pellew reported that hybrids between two pure breeding varieties of sweet peas were larger than either parent, and showed that the increased vigor resulted from the action of two different dominant factors, one conditioning long internodes and the other increasing internode number.

There were criticisms, however, of the simple dominance hypothesis. First, if vigor is not the direct result of heterozygosity as such then individuals should be obtainable that are homozygous for all the beneficial dominant factors, and hence as vigorous as the hybrids. Secondly, in F_2 of a cross between two inbred strains the distribution should be skewed since dominant and recessive alleles would be distributed according to the terms of the binomial $(\frac{3}{4}+\frac{1}{4})^n$ where n is the number of heterozygous loci.

Jones in 1917 removed the first objection by pointing out that favorable dominants and detrimental recessives often would be closely linked and hence would not be readily separable during inbreeding. Heterozygous combinations, therefore, would be superior to both homozygotes. Collins pointed out in 1921 that with a large number of factor pairs, regardless of linkage, the skewness in a distribution disappears.

It had been shown many times that populations of cross fertilized organisms, including maize, contain large number of detrimental recessives. Some of the observed heterosis following crosses between different inbred maize lines obviously is due to the action of dominant genes in covering up the effects of unfavorable recessive factors.

Both Shull and East, in the course of their early work on inbreeding and crossbreeding maize, had speculated that a stimulus to development was associated with heterozygosis of the individual. East later postulated that each of a series of alleles had a particular positive action and that the effects were additive in the heterozygote. No loci of this sort were known at the time, but Stadler in 1939 pointed out that certain *R* heterozygotes in maize formed anthocyanin in more plant parts than did the parents, and suggested that other genes acting in this way could cause hybrid vigor. Hull, who introduced the term overdominance, based the superiority of heterozygotes on heterozygosity, as such. He pointed out that frequently hybrids between two inbred maize lines yielded more than the sum of the inbreds, and that this result was not possible if dominant genes acted in an additive manner only.

Several examples are now known of loci at which the result of heterozygosity approximates that of the sum of the two corresponding homozygotes. The *R* locus in maize has already been mentioned. Tan described another case in the lady bird beetle, Harmonia, in which mosaic dominance occurred for color pattern in the wing covers. Flor, in 1947, described another instance in flax. He found each inbred flax strain resistant to a certain rust biotype, but a hybrid between such inbreds was resistant to both biotypes. The blood group antigens in mammals show the same relationship. Irwin demonstrated in 1947 that in birds a hybrid has all the red blood cell antigenic properties of its parents. Parallel examples of isozymes in homozygotes and their respective heterozygotes are now being reported.

A classical case of overdominance is afforded by sickle-cell anemia in man. Sickle-cell hemoglobin, due to the Hb^S gene, is rare in most human populations, but occurs with a frequency as high as 10 to 20 percent in a broad belt across central Africa, where individuals carrying the factor have been found to be resistant to malaria. The Hb^S allele is homozygous lethal, or usually so. Individuals homozygous for the much more common Hb^A allele are susceptible to malaria, and so are at a severe disadvantage where the disease is endemic. Allison has shown that $Hb^A Hb^S$ heterozygotes are at a selective advantage in malarial regions over both homozygotes.

The above examples show that both dominance and overdominance of genes are involved in heterosis. It would be premature, however, to conclude that they fully account for hybrid vigor. Present knowledge of the mechanisms regulating gene expression in higher organisms is limited. Is it not a reasonable expectation that, as studies in this still obscure area advance, additional factors important for heterosis will come to light? As a working hypothesis, one might visualize gene regulatory devices of two kinds of significance in this context. One might be widely operative in the genome and the other class might be locus specific, or would affect only particular groups of genes that exert interrelated effects in development. An adequate understanding of the genetic basis of heterosis awaits a fuller knowledge of chromosome organization.

The Continuing Search for Understanding

I wish to make a few remarks in closing about the general significance of the pattern of research that led to hybrid maize. In my judgment, the spectrum of studies underlying hybrid maize provides a model of the kinds of investigations that should be broadly fostered in the interests of agriculture.

Hybrid maize grew out of a mosaic of theoretical and adaptive researches that were eventually translated into a new, exceedingly effective, and widely applied breeding technology. A turning point in the history of the enterprise was Jones' invention in 1918 of the double cross method of using inbred lines. Jones demonstrated that by the use of double crosses controlled heterosis could be used in the production of hybrid seed on a commercial scale. As a result hybrid maize breeding was undertaken at numerous centers in the decade that followed and, by the middle 1930's, hybrids were rapidly replacing open pollinated varieties throughout the United States' Corn Belt.

Invention of the double cross, however, was only the step that started the forward economic march of the new form of maize. The concept and rationale of the product already had emerged from the studies on the genetic effects of inbreeding and cross-breeding originating with Darwin, Mendel and Johannsen, and markedly advanced by Shull and East. Shull and East correctly interpreted the effects of self- and cross-fertilization in a naturally cross-fertilized species in Mendelian terms and also proved, on a nursery basis, applicability of the concept of controlled heterosis to maize breeding. The researches involved thus ranged from inquiries that had no other purpose initially than a fuller understanding of certain natural phenomena for the sake of such understanding to adaptive, utilitarian studies undertaken in response to the needs of breeders, seed producers, and users of hybrid maize.

Theoretical and adaptive research often are interrelated and may constitute a stimulating and mutually efficient feedback system. They tend, however, to be polarized activities in practice, even if encouraged together. The one is undertaken primarily for the sake of extending the boundaries of knowledge, and the other is done in order to adapt theoretical knowledge to a useful end, by improving a technological process or commercial product.

These two broad classes of research usually are pursued by different people who, furthermore, may experience a measure of conflict in their contacts with each other, in terms of attitude toward science and its applications. Such conflict is understandable. The problems confronting theoretical and applied scientists are unlike and the contexts in which they are studied may differ radically.

The applied scientist's problems often are not only intricate in themselves but also may be involved in a complex of practices from which they can not be freely dissociated. The difficulties of solving them effectively may be greatly enhanced, of course, if the suggested action program growing out of the researches is counter to already established economic and social policies and practices. A corresponding breadth of comprehension, aptitudes, skills, patience, and tolerance on the part of the applied scientist is essential to effective work.

Theoretical scientists, on the other hand, tend to choose explicitly definable problems of conceptual interest that may be pursued in detachment from ordinary affairs. They seek experimental systems to which relevant questions of their own choosing may be put and to which, it is hoped, clearcut, meaningful answers will be forthcoming. From the answers to related questions of limited scope the answers to larger questions are built. It is by such experimental reduction, or compartmentalization, of phenomena, followed by integration, that scientific theories are built. A yearning to understand that reaches beyond the desire to control nature motivates the theoretical scientist. Speculative insight, experimental ingenuity, and a feel for unity in the natural order are needed qualities. The objective is to know and to understand; possible use of the findings may be left to others.

All of us here are committed in some measure to practical pursuits; we seek to convert the results of science into new technology. The need for immediately usable results in some instances is urgent, and we proceed to apply existing knowledge accordingly. This is an appropriate occasion nevertheless in which to remind ourselves of the significance for our welfare of science in its own right. Hybrid maize has been brought to wide human use by much ingenious adaptive research and the continuing, creative efforts of numerous skillful breeders. What I wish to emphasize especially is that it is a monumental example also of the values inherent in fundamental biological research and an impressive affirmation of the vital social function of all science. We are the beneficiaries in a very real sense in this instance of man's will to understand. The deepest meanings for the human enterprise of man's desire to investigate and to interpret natural phenomena for the sake of understanding them is well set forth in the following passage by the distinguished physicist, Victor Weisskopf.

> "The value of fundamental research does not lie only in the ideas and results it produces. The spirit that prevails in the basic sciences affects the whole scientific and technological life of a community because it determines its way of thinking and the standards by which its creations are judged. An atmosphere of creativity is established that penetrates to every frontier." (Scientific American 218:

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The literature references following are not inclusive, but are intended as a guide to most of the sources on which I have drawn in preparing the foregoing article.

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