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90 Years Ago: The Beginning of Hybrid Maize

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IN early 1908, George Harrison Shull, then at the Cold Spring Harbor Laboratory, published a paper with the unimposing title, "The composition of a field of maize." This marked the beginning of the exploitation of heterosis in plant breeding, surely one of genetics' greatest triumphs. It is appropriate, on this 90th anniversary, to look once again at Shull's great contribution and its sequelae.

The increased size and vigor of hybrids between plant varieties and species had been known for centuries. A well-known example of hybrid luxuriance was found in crosses between two species of Jimson weed, *Datura stramonium* and *D. tatula*, in which the hybrids were twice as tall as either parent. The most spectacular example that I know of is the radish-cabbage hybrid; a single plant filled a greenhouse and grew out the roof (East and Jones 1919, p. 192). It was sterile, however, and only in this century were fertile derivatives obtained by polyploidization. A time-honored showpiece of hybrid vigor is the mule, also sterile, but known for 4000 years for its hardiness and longevity. Even in ancient times it was widely known that inbreeding leads to weakness and small size. The avoidance of incest was practiced by many human societies, and there was speculation about such behavior in animals. Zirkle (Gowen 1952, p. 5) quotes a fanciful mixture of science and myth from none other than Aristotle.

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.

The literature of the nineteenth century is full of examples, mostly from plants. As usual, Charles Darwin got in the act. In his words, "Nature thus tells us, in the most emphatic manner, that she abhors perpetual self-fertilization." And, as we have come to expect, his

treatment was thorough, careful, and thoughtful. His book, *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*, was published in 1876. Its 490 pages include myriad examples, with the overall conclusion that inbreeding is generally deleterious and cross-fertilization generally beneficial (Darwin 1876). As pure description, his writings could hardly be improved upon, but an interpretation had to await the rediscovery of Mendel's laws in 1900.

The development of hybrid maize: In his 1908 paper, Shull reported that inbred lines of maize showed general deterioration in yield and vigor, but that hybrids between two inbreds immediately and completely recovered (Shull 1908); in many cases their yield exceeded that of the varieties from which the inbreds were derived. Furthermore, they had a highly desirable uniformity. In a subsequent paper in 1909, he outlined the procedures that later became standard in corn-breeding programs (Shull 1909).

At the same time, E. M. East did similar experiments at Connecticut State College. He also recognized the deleterious effects of inbreeding, but didn't realize the value of crossing inbred lines. Breeding weak parents held no appeal for him until he heard Shull's report in January 1908. In February, he wrote a letter to Shull, saying: "Since studying your paper, I agree entirely with your conclusion, and wonder why I have been so stupid as not to see the fact myself." His report (East 1908) was characteristically generous to Shull, and he added considerable corroborating evidence (Gowen 1952, p. 17).

Nevertheless, East was not convinced of the usefulness of the idea, because the puny inbred lines produced such small quantities of seed. The great cost of seed, he thought, negated any increased yield of the hybrids. This led to a strong disagreement with Shull, but in 1910 they agreed not to let this become an open debate nor to let personalities intrude. They remained true to their word.

The limitation of poor seed production from inbred lines was overcome by an idea from D. F. Jones (1918, 1922), who, while still a graduate student, advocated



G. H. Shull in 1932.

using four-way, or double-cross hybrids. This involved crossing two inbred lines and crossing that hybrid with the hybrid of two other inbred lines. The seed-producing strain was thus a heterozygous single-cross, and four-way hybrids yielded about as much as two-way. The abundant seed immediately made the program practical. The four-way crosses were slightly more variable than two-way hybrids, but much less so than randomly mated (“open-pollinated”) varieties. East and Jones and their role in the history of genetics has been the subject of an earlier Perspectives article (Nelson 1993).

The word “heterosis” was introduced by Shull (1914) as shorthand for such awkward expressions as “stimulation of heterozygosis.” He emphasized that the word was not intended to imply any particular explanation, but was purely descriptive (see also Shull 1948). The photo above shows Shull at the time of the 1932 International Genetics Congress.

Hybrid maize invades the Midwest: Meanwhile back in the corn belt, selection for improved yield in open-pollinated varieties was proving to be ineffective. Although qualitative traits could be readily improved by selection, yield was not very responsive. Shull’s idea of crossing inbred lines spread rapidly through the agricul-

tural experiment stations in the 1920s, stimulated especially by Jones’ idea of four-way crosses. In 1924, Henry A. Wallace, later to be Secretary of Agriculture, Vice President, and in 1948, the Progressive Party’s candidate for President, sold a few bushels of seed from his recently developed hybrid crosses, the first commercial sale of hybrid seed (Crabb 1947). Several companies appeared in the next decade. In some regions the inbred lines and crosses were performed by companies who sold the seed each year to farmers. In other areas—Wisconsin was an example—strains were developed at the University Experiment Station and seed was distributed to breeders and farmers.

The transition from open-pollinated to hybrid maize was astonishingly rapid. In Iowa, the proportion of hybrid corn grew from less than 10% in 1935 to well over 90% 4 years later. The transition in other corn-belt states was almost as fast, although somewhat slower in other parts of the United States. But by the 1950s, the great bulk of maize throughout the United States was hybrid. Why was this acceptance so rapid, especially in the corn belt? Substantially better yield is one reason, of course, but how obvious was this to the individual grower? The greater uniformity of hybrids was useful for machine harvesting, and this was undoubtedly a factor. Furthermore, a field of corn in which all the plants are alike, each with a single ear at the same height, is aesthetically pleasing, and this appealed to many corn growers. The hybrids could also incorporate favorable qualitative traits and be adapted to different habitats, especially length of growing season. Another possible reason was the practice of having leading growers demonstrate the robust hybrid plants to their neighbors. Yet another reason for the rapid spread, possibly the most important one, was that 1934–36 was in the dust-bowl period, and the hybrid strains were strikingly more resistant to drought than the open-pollinated varieties then in use (Crabb 1947).

Selection for high-performing hybrids was a vast undertaking involving an enormous number of tests. Inbreds were poor predictors of hybrid performance, and two-way crosses, of four-way yields. Testing of a large number of four-way crosses was a tremendous job, since there were six possible single crosses among the four strains used to produce a double cross. One useful device was due to M. T. Jenkins (Crabb 1947). He suggested predicting four-way yields by the average of the four crosses other than the two used to produce the single crosses. On the average, these mimicked a four-way cross and permitted a considerable saving of testing time and expense. This was only one of many important contributions of this pioneer researcher.

The next major change came with the increasing practicality of single cross hybrids. This was partly indirect: increasingly, breeders used very closely related strains to produce the single crosses, so that the four-way crosses were almost the equivalent of two-way. Eventually, in

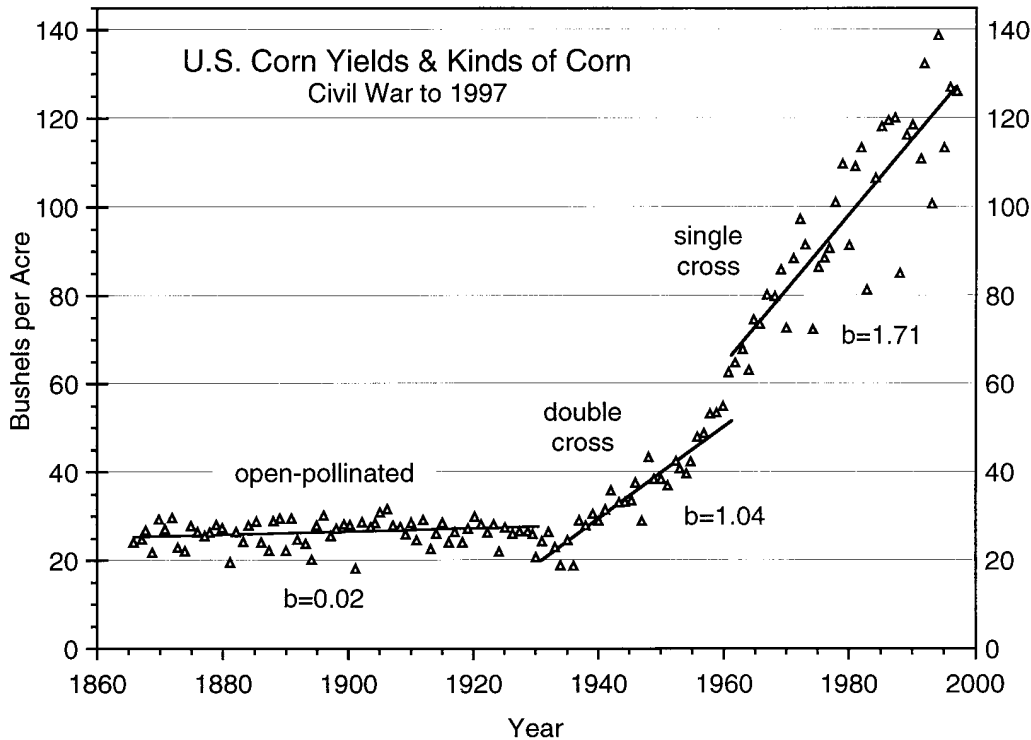


Figure 1.—Maize yield in bushels per acre in the United States. The periods dominated by open-pollinated, four-way crosses, and two-way crosses are indicated, along with regression coefficients (bushel/acre). Redrawn with permission from A. Forrest Troyer. Data compiled by the United States Department of Agriculture.

the 1960s, single crosses began replacing double crosses. Selection for higher yield in inbred lines had produced inbreds with yields high enough that they could be used as seed producers. In fact, the inbred lines were as high-yielding as the hybrids of an earlier period. But the single-cross hybrids were better still, and the gap between inbreds and hybrids remained. Not only were the single crosses higher yielding than double crosses, but they were even more uniform.

With the coming of single crosses, not only did the yield show a sudden increase, but the rate of increase improved. Before the introduction of hybrids in the 1930s, there was almost no increase. In the double-cross era, the rate of increase was about 1 bushel per acre per year. After single-crosses predominated, the annual increase was almost 2 bushels per acre. Current yields are some five times what they were in the prehybrid days. Furthermore, there appears to be no reduction in the rate of increase, so there is no reason to expect that the yield will plateau in the foreseeable future (see Figure 1).

But are we giving the hybrid breeding system too much credit? Farm practice did not stand still during this period. Increasing use of fertilizer, greater density of plants, and herbicides all contributed to greater yield. In addition, better machinery made it possible to time the field operations better, thus enhancing efficiency of the operation and reducing waste. Can we separate these effects from those of better genetic strains? Russell (1974) made a serious attempt to do this. Using hybrid seed preserved from 1930 to 1970 and growing the plants under the same environments, he found a

uniform increase in yield from the newer strains. He concluded that 60% or more of the increased performance was genetic. Similar results were reported by Duvick (1977).

We must not forget that the spread of hybrid maize coincided with the wider use of efficient experimental designs, involving randomization, replication, and better statistical methods, all introduced by R. A. Fisher. Fisher's book, *Statistical Methods for Research Workers*, first appeared in 1925 and went through 14 editions before his death in 1962 (Fisher [1925] 1970). His *The Design of Experiments* first appeared in 1935, and there were 8 editions (Fisher [1935] 1966). In the early 1930s, Fisher spent some time at Iowa State University and exerted a great influence on American agricultural research. Clearly, world agriculture in general and maize in particular owe an enormous debt to Fisher's genius. These better methods increased the rate of improvement of both genetic quality (by more efficient selection) and agronomic practice (by better discrimination among alternative practices). How much of the increase in agricultural productivity should be credited to Fisher, I don't know. But my guess is considerable.

Field techniques have become very sophisticated. Anyone traveling through the corn belt has seen fields in which a few rows of seed-producing plants with pollen-producing tassels removed alternate with one or two rows of pollen-producing plants with tassels intact. Detasseling of those plants that were intended to produce seed uncontaminated by their own pollen was effective, but inconvenient and expensive. This labor-intensive process was replaced by use of cytoplasmic male sterility,

particularly Texas cytoplasm (*cms-T*), along with judiciously used fertility-restoring genes. This saved a great deal of hand labor, and by 1970 more than 85% of U.S. maize carried *cms-T*. But strains with Texas cytoplasm turned out to be susceptible to leaf blight (*Helminthosporium maydis*), which spread through much of the corn belt in a single year (Laughnan and Gabby-Laughnan 1983). The ensuing epidemic was a disaster, especially in humid areas, and the 1970 corn yield dropped from 84 to 72 bushels per acre. By the next year a continuation of the epidemic was avoided, but the maize community had to revert to hand-detasseling. And the message was clear: genetic uniformity has its price.

Why is inbreeding and hybridization so effective?

R. A. Fisher (1949, pp. 116–120) stated the issues clearly. The whole process takes place in three stages: (1) foundation individuals chosen to start the process; (2) inbreeding to near homozygosity; (3) crossing chosen lines. If the individuals at each stage are chosen randomly without selection, the hybrids are essentially a random sample of the original population. Actually, of course, selection takes place in all three stages. Selection at the first stage can do little more than has been accomplished in the past by mass selection. Selection during inbreeding is rendered ineffective by the rapid fixation when heterozygosity decreases 50% each generation. So Fisher placed greatest emphasis on the third stage. If there is a great multiplicity of inbred lines, those that combine to produce the best hybrids can be chosen, and in distinction from ordinary breeding methods, those superior genotypes can be reproduced at will. This is the equivalent of choosing the best individual from a large segregating population—best because of a happy combination of genes and their interactions—and doing the equivalent of reproducing it asexually. He emphasized “deliberately planned multiplicity,” which is indeed what maize breeders were practicing with their thousands of inbred lines.

The genetic basis of heterosis: Since the early days there have been two alternative, though not mutually exclusive hypotheses of heterosis. The *dominance* hypothesis attributes the greater yield of hybrids to the suppression of deleterious recessives from one parent by dominant alleles from the other. The *overdominance* hypothesis assumes that at key loci the heterozygote is superior to either homozygote. Either hypothesis explains qualitatively the decline of performance with inbreeding and its recovery in hybrids, including the possibility that the better hybrids exceed the average of the original populations before inbreeding.

Shull believed that there was something about different germ plasms that led to a stimulus; it need not be Mendelian. East had similar views, but he increasingly emphasized Mendelian loci in which the heterozygote was superior to either homozygote. Convincing examples of such loci did not exist (instances of interallelic complementation came much later), but nevertheless

East (1936) argued for their existence. The alternative dominance hypothesis was also advocated early (Keeble and Pellew 1910; Bruce 1910). There were two early objections to the dominance hypothesis. One was the failure of selection to produce high-yielding inbreds; if all deleterious recessives could be purged, the inbreds should equal the hybrids. Second, the F_2 distribution was not skewed, as would be expected from the expansion of $(3/4 + 1/4)^n$. But it is clear that with linkage (Jones 1917) and a large number of factors (Collins 1921), neither objection holds. On the other hand, overdominance demanded a form of allelic interaction that was rare at best.

The dominance hypothesis held sway until the 1940s. It was clear that it was sufficient to explain the decline with inbreeding and the subsequent recovery when inbred lines were crossed (Crow 1948). It was less clear that this was sufficient to explain the increased performance of hybrids above that of the open-pollinated varieties from which the inbreds were derived. It was argued that purging of deleterious recessives during inbreeding could increase the yield only by an amount equal to the genomic mutation rate (Crow 1948; Fisher 1949, pp. 118–119). Prevailing estimates of mutation rates would place this increase at about 5% or less, not the observed 15–20%. Despite the absence of good examples—sickle-cell hemoglobin was badly overworked—overdominance seemed a possible alternative since a small minority of such loci could suffice.

In the summer of 1950, Iowa State College (as it was then called) held a 5-week conference on heterosis, and the proceedings were published 2 years later (Gowen 1952). By this time a number of people were interested in overdominance. For many years, Fred Hull had been the leading advocate and presented his views at the meeting. Among other arguments, he emphasized the failure of inbreds ever to equal hybrids and the poor results of mass selection. Comstock and Robinson presented a statistical estimate of dominance that was well within the overdominant range. Others (*e.g.*, Dickerson) suggested breeding schemes that would exploit overdominance (for these and other papers, see Gowen 1952). Overdominance was in the air, and this conference had a strong influence on both plant and animal breeders.

Within a few years, doubts appeared. More realistic—and higher—estimates of the total mutation rate reduced the force of the mutation rate argument. The Comstock and Robinson mating scheme permitted an opportunity for recombination between successive crossing generations, and the dominance estimates dropped from the overdominance to the partial dominance range; seeming overdominance had turned out to be pseudo-overdominance caused by linkage of yield-increasing dominants with deleterious recessives (Gardner 1963; Moll *et al.* 1964). Identification of quantitative trait loci (Stuber *et al.* 1992) suggested overdominance, but a

more detailed analysis (Cockerham and Zeng 1996) was more consistent with pseudo-overdominance.

G. F. Sprague suggested a particularly simple experiment. Two maize populations were each selected for improved performance of hybrids from crosses with an inbred tester. With overdominance, the two strains should become similar to each other, since each would incorporate alleles that complement those of the inbred tester. A hybrid between them should show decreased yield. In contrast, with additive and dominance effects these hybrids should show increased yield. The experiments were slow, since each generation of selection involved a 3-year cycle, but preliminary results argued against overdominance (Sprague and Russell 1956) and eventually the results were clear (see Sprague 1983). Hybrids between the two selected strains improved over the course of the experiment. In addition, the two selected populations produced increased yields in hybrids with other testers. These offer strong evidence for the sufficiency of additive and dominant effects. Several workers, including me, have changed from preferring overdominance to accepting dominance as sufficient. From the beginning, Sprague has emphasized experimental evidence, and, from the present viewpoint, his early conclusions are correct. In addition, he has made numerous practical and theoretical contributions and is one of the chief architects of modern maize breeding.

The current view, then, is that the dominance hypothesis is the major explanation of inbreeding decline and the high yield of hybrids. There is little statistical evidence for contributions from overdominance and epistasis. But whether the best hybrids are getting an extra boost from overdominance or favorable epistatic contributions remains an open question. The happy side of this story is that, despite ignorance and changing views of this fundamental issue, maize yields have continued to increase, with no sign that the rate of increase is diminishing.

A change of emphasis: In the summer of 1997, a second heterosis conference was held, 47 years after the Iowa State conference. This was sponsored by the International Maize and Wheat Improvement Center (CIMMYT) and took place in Mexico City. The two conferences contrasted in a number of significant ways.

The 1950 conference emphasized mainly maize, along with some discussion of swine and poultry. The 1997 conference included discussions of sorghum, millets, rape seed, sunflowers, wheat, rice, and cotton, along with a number of trees and vegetable crops. There was a major contrast in emphasis. In 1950, the papers were all biological and the emphasis was on getting the highest yields in good environments. The 1997 conference had much more concern for problems in the developing areas. There was more emphasis on ecology: How can we increase food production and at the same time do as little harm to the environment as possible, leaving non-agricultural areas undisturbed? Greater yield per hect-

are leaves more hectares that can be left in pristine condition. A second difference was the current emphasis on varieties that grow well under less favorable conditions, especially drought and poor nutrition. A third difference was greater attention to economic problems—how can there be sufficient capital and appropriate infrastructure for developing better crops for the tropics?

Not always is the maize paradigm the best. For some crops—sunflower appears to be one—crossing inbred lines has produced large increases in yield. For others, this is not true. Even for maize, it may be that open-pollinated varieties are the best in some areas. This may be true, especially in the earlier stages and when locally adapted varieties are already available. Throughout the conference there was an emphasis on empiricism: do what is best for the particular climate, soil, agricultural practice, social structure, and economy.

Back to Shull 1: G. H. Shull 1 was born April 15, 1874, one of eight children in a sharecropping family. His was a remarkable sibship, for all seven survivors became leading citizens and four were listed in *Who's Who*. The hand-to-mouth farm existence meant that Shull 1 had little chance to go to school and was largely an autodidact. He eventually worked his way through high school and taught in country schools for 2 years. After accumulating the necessary funds, he went to Antioch College, where he served as a janitor while becoming the leading student in his class, graduating at the age of 27. After completing graduate work at the University of Chicago he moved to Cold Spring Harbor in 1904. There he joined C. B. Davenport, a former Chicago faculty member who had been appointed director of the Cold Spring Harbor Laboratory. Since Chicago days, the two had shared an interest in biometrics. In 1915, Shull 1 moved to Princeton University, where he remained. For details of his life and work, see Mangelsdorf (1955).

Shull 1 had wide research interests and worked on a number of plants, especially shepherd's purse and evening primrose. His interest in inbreeding and hybridization started early. At the Iowa State conference, he said that his first personal contact with hybrid vigor was with sunflowers. The hybrids between Western and Russian parents, each 5–6 feet tall, produced hybrids averaging more than twice this height. The tallest plant was more than 14 feet, and he showed a picture of himself in the midst of the hybrids, teetering atop a 6-foot stepladder (Gowen 1952, p. 47). Shull 1 also had an interest in self-incompatibility genes in several plants. Being interested in heterosis, he was attracted to translocations and balanced-lethals in *Oenothera* as a way of maintaining heterozygosity.

Of special interest to readers of this journal, Shull 1 was the founding editor of *Genetics* (Mangelsdorf 1955; Crow 1991). He personally arranged for a publisher and assembled an editorial board, and the journal got under way in 1916. He remained editor for 10 years, when he was succeeded by another important figure in

maize breeding, D. F. Jones. Shull did the detailed editing work himself, and the reduction in his output of published papers attests to the amount of time this took. After he ceased to be editor, he retained a strong paternal interest in the journal. Years later, in the 1950s, he apparently was still reading every issue, for the current editors could count on hearing from him if anything did not fit his high editorial standards. He personally contributed the money for the "Galton and Mendel" fund. This was used to defray expenses for extensive tables or illustrations. When this money was used, this fact was to be footnoted with an asterisk and, furthermore, the asterisk was not to be used for anything else. A lapse in following this rule brought an immediate letter from Shull.

I look back with happy nostalgia to hearing him recount the history of his discovery at the 1950 Heterosis Conference (Gowen 1952, pp. 14–48). True to his 1910 promise, he was generous to his rival, East. He had lived to see his idea blossom into a world-wide agricultural revolution. A genial patriarch, he was 76 at the time and clearly enjoyed the well-deserved adulation he received. He died 4 years later, on September 28, 1954.

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