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PERSPECTIVES

Hybrid corn and the unsettled question of heterosis

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Abstract. George Shull's 1908 seminal article 'The composition of a field of maize' marked the 'exploitation of heterosis in plant breeding, surely one of genetics' greatest triumphs'. Hybrid corn became a 'symbol of American agriculture' and 'the paradigm for all developments of F_1 hybrid crop varieties and more generally breeding. But there is still no consensus on the definition of heterosis while its biological basis, causal factors and genetic mechanisms remain 'unknown', or at best 'poorly understood'. It is thus logical to reverse the usual approach from the exploitation of a mysterious heterosis to the triumph of hybrid corn and focus on what breeders and geneticists do rather than on the theoretical reasons for their success. This factual approach produces surprising results: (i) hybrid corn extends the isolation technique of autogamous cereals to the allogamous maize; (ii) a 'hybrid' is an ordinary corn plant made reproducible by the breeder and only the breeder. It is proprietary rather than 'hybrid'; (iii) for all practical purposes, heterosis is irrelevant; (iv) Shull justified his 'hybrid' breeding method by the *ad hoc* argument of maize 'hybrid vigour' which in 1914, he conflated under the name of heterosis with Edward East's concept of physiological stimulation due to heterozygosity; (v) hybrid corn can increase yield only once and by a small margin and (vi) the huge yield gains of the last 80 years came from mass selection, a process inconsistent with the theory of heterosis. In conclusion, the enduring success of 'hybrid' corn was achieved at the expense of farmers, common welfare and biodiversity and dovetails with the industrial agriculture requirements of crop uniformity and breeder monopoly over reproduction. This critical understanding of the paradigm of plant breeding could have important implications for breeders and geneticists.

Keywords. isolation technique; hybrid corn; hybrid vigour; heterosis; Shull's composition of a field of maize.

> *History is the most fundamental science, for there is no human knowledge which cannot lose its scientific character when men forget the conditions under which it originated, the questions which it answered, and the functions it was created to serve. A great part of the mysticism and superstition of educated men consists of knowledge which has broken loose from its historical moorings (Erwin Schrödinger).*

Introduction

It is common wisdom that George Shull's 1908 article 'The composition of a field of maize' 'marked the beginning of the exploitation of heterosis in plant breeding, surely one of genetics' greatest triumphs' (Crow 1998). After its conquest of the Corn Belt in the late 1930s and early 1940s, hybrid maize became a 'symbol of American agriculture' (Welch 1961) and 'the paradigm for all developments of F_1 hybrid crop varieties' (Pickett and Galvey 1997) and more generally for agricultural genetics as shown by the efforts to turn many crops, such as wheat, rice and soybeans, into hybrids. In the immense literature devoted to heterosis, two publications stand out. *Heterosis, a record of researches directed toward explaining and utilizing the vigor of hybrids* (Gowen John W. ed.), published in 1952 was followed almost 50 years later by *The genetics and exploitations of heterosis in crops;* An International Symposium (CIMMYT 1997).

In 1952, Paul Mangelsdorf observed: 'The term heterosis remains ambiguous in spite of many attempts to define it. It continues to have different meanings for different workers' (1952, p. 329). There is still no agreement on a definition of heterosis (quantitative genetics heterosis, better parent heterosis, heterobeltiosis, economic heterosis, heterosis qua hybrid vigour, heterosis qua reverse of inbreeding depression, even negative heterosis). And the biological basis, causal factors and genetic mechanisms of heterosis appear 'virtually as obscure' (CIMMYT symposium announcement) or 'as obscure as they were at the time of the Conference on Heterosis held in 1950' (Stuber 1997, p. 108), 'poorly understood' (Goldman 1997, p. 5), 'largely unknown' (Coors 1997, p. 170), 'unknown' (Tsafaris *et al.* 1997, p. 112) and even might 'never be known and understood' (Hallauer 1997, p. 346).

Thus heterosis remains without an agreed-upon definition and defies explanation. How could an undefined and unknown phenomenon have had such a 'dramatic impact on the development of breeding methods'? 'Hybrid maize', writes Donald Duvick, 'was one of the first examples of genetic theory successfully applied to food production. When first introduced, it seemed almost miraculous (...). Strangely, the genetic basis of heterosis (hybrid vigour) was and still is unknown' (Duvick 2001). What function was heterosis created to serve?

Since heterosis rests on shifting theoretical sands, it is logical to focus on what breeders actually do rather than on the theoretical justification for their actions. This emphasis on practice and facts forms the entire article. The first part will show that Shull justified his revolutionary 'hybrid' breeding method with the ad hoc explanation of 'hybrid vigour'. The second part will study how the hybrid breeding paradigm, namely the set of assumptions, concepts, beliefs and practices that guides the work of agricultural scientists, became entrenched. The concluding part will show how 'hybrid breeders' managed to overcome the contradictions of an impractical technique founded on an irrelevant theory.

The foundation of a myth: Shull's composition of a field of maize (1908)

Shull and the isolation technique

At the beginning of the 19th century, British gentlemen farmers observed that their cereals—wheat, barley and oats—'breed true to type'; i.e., plants retain their individual characters from one generation to the next. This observation led to the 'isolation method' implemented in England from the beginning of the 19th century and codified in 1836 by John Le Couteur on the suggestion of Mariano La Gasca for 'true breeding' plants, wheat, barley and oats (Le Couteur 1836, pp. 42–44). It consists of replacing a variety or population by 'copies' of its best element.

In May 1904, George Shull began his research on heredity within a Mendelian framework at the Cold Spring Harbor Laboratory in New York. He began selfing corn plants from several families to study the inheritance of the number of rows of the ears. From his theoretical researches, Shull gained a clear understanding of Mendelism. He met de Hugo de Vries in California 'probably in 1906' according to a photograph published by Crow in *Genetics* in 2001 (Crow 2001).

Early in 1907, Hugo de Vries published his book, *Plant breeding, comments on the experiments of Burbank and Nilsson*, where he described the isolation method. De Vries' book (and/or Shull's meeting with him) was the spark that triggered Shull's 'unexpected suggestion for a new method of corn breeding' (Shull 1909a, p. 52), namely to extend the isolation method to corn.

Shull's 'continuous hybridization' (Shull 1908, p. 301) or 'pure line method of corn breeding' (Shull 1909a, pp. 51–59) consists of: 'making as many self-fertilizations as practical, and to continue these year after year until the homozygous state is nearly or quite attained. Then all possible crosses are to be made (...) and to be grown (...) and studied as to yield and the possession of other desirable qualities' (Shull 1909a, p. 57). In short, his Mendelian strategy was to build a random scale population of 'reproducible' corn plants to implement the isolation method.

In a single stroke, Shull solved the political economy problems of plant breeding for an industrial society: the creation of crop uniformity (1909a, p. 57; 1909b, p. 71; 1946, p. 548) and of breeders' property rights (1908, p. 300; 1946, p. 549) since only breeders possess the hybrid parental lines, problems that were so far intractable. A 'hybrid' is proprietary. Shull expected a yield gain high enough to offset the cost of his revolutionary proposal provided experiment station breeders implemented it (Shull 1909a, pp. 55–56).

At this point, readers begin to realize that the words and expressions we commonly use may be misleading. Appendix section clarifies our vocabulary.

The isolation method rests on an indisputable logical principle: there is always a gain in replacing a variety or diversity of 'anythings' by copies of the best 'anything' extracted from the variety (biologically, it is another matter). Thus, any attempt to justify it by hybrid vigour or heterosis is irrelevant. Moreover, once the best 'anything' has been extracted and copied, repeating the process with the same variety cannot bring about further gains.

In this light, the failure of the so-called second and third cycle hybrids in the early 1940s (Hull 1952, p. 453; Comstock 1964) could have been predicted from the beginning. To escape the impasse, geneticists and breeders turned to the new developments of quantitative genetics to work out an innovative mass selection scheme, reciprocal recurrent selection (Comstock *et al.* 1949; Comstock 1964) a form of mass selection that was not proven successful until the late 1950s (Sprague 1955, p. 262). All gains then for the last 65 years have come from mass selection and none from heterosis. 'Inbred yields have increased over the years at nearly the same rate as the yields of their F_1 hybrids, therefore heterosis has not increased, in fact it has decreased if calculated as a per cent advantage of hybrid over parents' (Duvick 1997, p. 6). Duvick characteristically turns reality upside down: hybrid yields have increased at the same rate

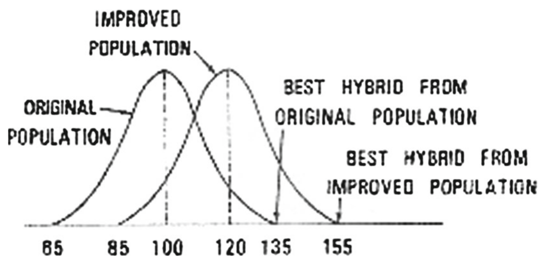

Figure 1. An expected distribution for a finite number of single crosses from the original and an improved population.

as the yield of their inbreds since better inbreds extracted from the improved population give better hybrids.

In 1977, a figure in the chapter Corn breeding from *Corn and corn improvement*, the authoritative reference for maize of the American Society of Agronomy belatedly highlighted this last point (Sprague and Eberhart 1977, p. 342). The figure disappeared from the 1988 edition although Sprague was again one of the editors (figure 1).

It pictures the isolation method for maize and shows that the best 'hybrid' is extracted from a 'finite' population of single crosses, namely from a random scale model of the natural variety made up of 'clonable' plants. This is because the self-fertilization phase generates zillions of pure lines while no selection is possible because 'heterosis' is unpredictable. These clonable plants are distributed equally around the average of the random model (which is also the average of the natural variety), a pictorial evidence that heterosis has nothing to do with Shull's pure lines crossing technique. The standard bell curve does not give any indication as to the actual distribution. If the latter is skewed, small gains are to be expected. The laborious success of the first 'hybrids' (which were double crosses) shows that it is likely to have been the case. Last, a better 'best hybrid' can be expected from increasing the number of random single crosses.

Shull thought his proposal was epoch-making: 'There is little doubt in my mind', he wrote to East on March 3, 1908, 'that if I had held on to my idea of the composition of a field of corn until I could have worked out some subsidiary problems, I could have raised a monument to myself which would be worthy to stand with the best biological work of recent times' (Shull to East, in Jones 1944, p. 224).

In July 1907 then, Shull laid the foundations of his 'monument to himself': he crossed his only two 'nearly pure' lines (in fact, 'hardly pure' since his lines had gone through three generations of selfing) to make the first 'hybrid'. In January 1908, he rushed to the annual meeting of the American Breeders Association to establish his priority although he had no data to support his 'continuous hybridization'. Presumably, he feared that de Vries had come to the same idea. The 'Composition ...' alluded to a method of 'continuous hybridization' (Shull 1908, p. 301). The 'subsidiary problems' that delayed his announcement were the key: the seeds of the first 'hybrid' were ready for the spring planting. Would this cross of his two 'nearly pure' lines recover its vigour as he had inferred from his mastery of Mendelism?

It did. In January 1909, he could announce his success and unveil his 'continuous hybridization' which became 'A pure line method in corn breeding' (the title of his second article). In December 1909, he had eight other (nearly) pure-line clones. Their average yield was almost exactly the same as the yield of the cross bred families, but the best clone yielded 10% more than the cross bred variety. 'From all the results reported ... it may be safely concluded that the production of the highest yield requires simply the finding of the best combination of parents and then repeating this combination year after year' (Shull 1909b, p. 69).

In July 1907, Shull extended the powerful and simple principle of the isolation method to maize. Why it worked for small grain cereals, why it could not work for corn contrary to what corn breeders believed and how it could, at last, work for maize became clear. Finally, breeders and agronomists would achieve the perfect uniformity of corn crops that they had aimed at in vain.

Shull saw the problem of economically producing seed on a deteriorated 'pure line'. In 1912, his double cross experiment started in 1910 failed, but he did not reveal it until 1950. Given his biological and logical acumen, he probably also saw that the isolation technique was an impasse. But he kept silent.

Paraphrasing Shull's opening sentence of 'The composition ...' an account of these first class achievements would be:

> The newer Mendelian scientific results show that the theoretical importance of the isolation method consisted of replacing a variety or diversity of plants by copies of the best plant extracted from the variety. Practical breeders have also demonstrated the value of the same in the improvement of many varieties of true breeding species such as small grain cereals. However, breeders' attempts to extend this method to Indian corn under the name of line breeding were doomed to fail because corn, being a cross-pollinated plant, does not 'breed true to type'. However, Mendelism offers a way to overcome this difficulty. Here is how.

The triumph of 'hybrid' corn in the late 1930 made these seminal for the young science of genetics. Commentators have been rightly flabbergasted by Shull's brilliant Mendelian insight and foresight (see, for instance, the eulogy of Shull in *Genetics* (Mangelsdorf 1955, pp. 1–4).

Shull and hybrid vigour

But Shull took another course. The opening sentence of 'The composition...' argues that isolation methods do not work for maize because of inbreeding deterioration although 6 months earlier, he had begun implementing the isolation method. With the plural, he avoided explaining the isolation method and could swiftly move to esoteric considerations on inbreeding deterioration, hybrid vigour and the like. After this sleight-of-hand, 'The composition ...' advanced from theoretical considerations on hybrid vigour to the 'continuous hybridization' in its last sentence.

The isolation technique for true breeding species requires no justification. But in the case of maize, breeders must first randomly build a variety of clonable maize plants, a task so daunting that Shull thought later it would never work. It ran against the basic principles of agricultural selection: 'breed from the best', 'like engenders like'. How could the cross of two weak plants produce a thriving offspring? Further, it required manipulating an astronomical number of plants.

An irresistible scientific argument to convince experiment station breeders to implement his scheme was necessary. As a theoretician, Shull did not intend to do the work himself. Their success would be his, their failure theirs. 'I hope...that the technique of corn breeding will find a basis in scientific knowledge quite different from the present more or less blind conflict between empirical selection and the little understood injurious effects of inbreeding' (Shull 1908, p. 301). Because of hybrid vigour, Shull argued, the corn breeder's task was to 'develop and maintain the best hybrid combination'. Rather than clonable variations, 'hybrid vigour' became the 'primum movens' of Shull's 'hybridization'—pure lines crossing. This metamorphosis would hold as long as no one realized that it was the isolation method for maize. Three hardly noticeable clues confirm this view.

'The continuation of these studies, wrote Shull in his January 1909 article, *during the past year* (italics mine) (...), besides has given unexpected suggestion for a new method of corn breeding (...)' (1909, p. 52).

'The unexpected suggestion' dates to the first part of 1907 and was triggered by de Vries's book. Some 42 years later, after 'hybrid' corn had triumphed, Shull remembered that he had made the first 'hybrid cross' in *July 1907* (Shull 1952, p. 28). Or consider the adjective 'little' (1908, p. 301) qualifying de Vries's *Plant Breeding*. It cannot apply to a 384 page long book. It qualifies its content—not worth reading. And, last, since he could not avoid citing the famous de Vries, he associated him with the relatively obscure East for an idea that was becoming commonplace (1908, p. 301) and not for the relevant reason, the isolation method.

The entrenchment of the 'hybrid' corn paradigm

From Shull's hybrid vigour to East's 'physiological stimulation due to heterozygosity'

In January 1908, East read Shull's 'Composition ...'. A first round of skirmishes shows that both were treading almost the same path and were at the same point. East 'expected more data upon the subject this summer in connection with some corn experiments' (in Jones 1944, p. 224) while Shull was waiting until spring to check if his first 'nearly pure lines' cross had recovered its vigour.

The battle started in January 1909, when Shull announced his revolutionary technique. East was all the more dashed that during his visit in the summer 1908 Shull had led him to believe that he did not pursue his work.

In his article in the *American Naturalist* of March 1909, East rightly pointed out that 'he (Shull) had not treated the theoretical aspect of the question' (East 1909, p. 180), meaning that Shull's correlation between heterozygosity and vigour was insufficient to justify his pure line hybridization.

East had a causal theory: '(...) we must believe that amphimixis has two functions, the one a recombination of hereditary characters, and the other a stimulation to development. If we postulate that there is an increase in this stimulation when two strains differing in gametic structure are combined, we satisfy all observed conditions'.

He suggested mechanisms through which such stimulation may take place. (...) There may be chemical compounds found in different strains that react when brought together (East 1909, p. 178, East was a chemist) (...) 'differences in gametic constitution setting up a biological "action" analogous to ionization' (ibid.).

Since corn breeders tend towards inbreeding in search of uniformity, East became a 'convert to the first method (i.e. Shull's) in a modified form' (East 1909, pp. 180–181). The corn grower 'should purchase from the line breeder two strains of seed each year, and grow the F_1 generation of the cross between them' (ibid.).

East's theory was crucial as shown by a simple model of a population carrying two alleles A and a (frequency p and q, with $p + q = 1$) with 'physiological stimulation due to heterozygosity'. After selection of the most vigorous plants Aa, the percentage of Aa will rise to 0.5 and will not change. The only solution is to find the pure lines AA and aa and to cross them so that the percentage of the favourable heterozygous Aa plants reaches 100%. This model can be generalized to many genes. East's theory—the superiority of the heterozygous for any reason, to be known later as overdominance—was crucial to convince Experiment Station breeders to implement Shull's pure line hybridization. 'If overdominance (...) predominates (...) the highest yielding genotypes must be heterozygous' (Sprague and Eberhart 1977, p. 325).

East demanded recognition for his theoretical contribution. Shull had neglected it because he knew that his 'hybrid vigour' justification of the isolation method was irrelevant. He could not deride East's postulate and his 'must believe' attitude because it would have destroyed his justification. In reply to East, he claimed: '... I care very little for the question of priority. What we are most concerned in is the *triumph* of the *truth* and especially of *useful* truth (...) (italics Shull's). And in his third article, he quietly annexed East's 'physiological stimulation' as if he had the very same idea from the very beginning (Shull 1909).

From East's physiological stimulation due to heterozygosity to Shull's heterosis

In 1910 a surprisingly sudden truce occurred. In 1942, four years after East's death and 32 years after their agreement, Shull revealed it:

> 'He (East) and I (Shull) had agreed between us that we would not enter into any personal controversy about priority, in order not to impede the hybrid corn program. Now that nothing can stop that program, there can be no further justification for preventing historical truth and accuracy from prevailing' (Shull to Prof. Cunningham in Crabb 1947, p. 50).

'Unus testis, nullus testis'. Shull's craving for a 'monument to himself' and what we know of the ferocity of scientific quarrels, casts doubt on his account of his belated disclosure of their 1910 'gentleman's agreement' (ibid, p. 50).

I can venture a more precise date: between November 4 and the end of December 1910.

In November 1910, two articles by British scientists showed theoretically on the basis of mathematical considerations (Bruce, *Science*, 4 November 1910) and experimentally in the first issue of the *Journal of Genetics* (Keeble and Pellew, November 1910) that Mendelism could account for hybrid vigour. No maize being grown in England, it was a purely scientific matter. For Shull and East, it meant that their disputed 'monument' would not go past the first stone. So at the very end of 1910 at the famous Cornell conference on *The genotype hypothesis and hybridization* (28–29 December 1910), Shull first recognized East's priority for the 'physiological stimulation due to heterozygosity' (it 'may be analysed to that of ionization' (Shull 1910, p. 244), and spent half of his article defending it against 'M. A. B. Bruce' without giving the reference to' Bruce's letter. Shull's objections to Bruce's theory were soon proven to be invalid.

A 'gentleman's agreement' was, in any case, the logical outcome of their quarrel. No experiment station would have implemented a technique based on controversial views. It is likely that Shull took the initiative in November or early December 1910. For whatever its value, East's theory was clearly formulated and his 'invented a new' method of varietal crosses had been shown to work while the success of Shull's pure line hybridization was only a remote possibility.

In 1914, Shull coined the term 'heterosis'. It conflated the phenomenon of hybrid vigour with a particular theory, 'a possibly non-Mendelian physiological stimulation due to heterozygosity' (Shull 1948, p. 441), adding another layer of scientific mystery to East's 'physiological stimulation due to heterozygosity'. 'Hybrid vigour and heterosis became synonymous', contradicting his assertion that 'I (Shull) offered the word 'heterosis' to cover the real, observable phenomena' (*ibid*). All other explanations–the British ones, in particular–were rendered trivial.

Shull and East were among the founders of *Genetics* and Shull was its editor for the first 10 years. They (and Shull particularly) had the scientific power and prestige to quell dissenting views on the North American scene. As to East, his role will again be essential later: the most influential geneticists/breeders of the 20th century—Hayes, Jones, Mangelsdorf, Emerson, Sprague (himself a student of Emerson)—were directly or indirectly East's students, trained in the mysteries of his 'physiological stimulation'. With the success of 'hybrid corn'—proprietary clones—in the late 1930s in the United States and the extravagant propaganda surrounding it, hybrid corn became, thanks to FAO (Juggenheimer 1958), the worldwide paradigm of plant breeding and genetics. It is not exaggerated to speak of an Eastian heterosis school of plant breeding.

Table 1 summarizes the succeeding metamorphoses of reality that led to 'hybrid corn'. The geneticists and breeders' research programme for decades to come was to find cases of such heterosis/hybrid vigour or to use the scientific word, overdominance. Overdominance for corn yield was not found as documented by the careful 1964 experiments of Moll, Lindsey and Robinson (Lewontin and Berlan 1990, pp. 620–621).

Table 1. From clonable variation to heterosis: the shifting bases of the 'hybrid corn' paradigm of agricultural genetics from 1908 to 1914.

Isolation method Le Couteur/La Gasca Beginning 19th century	Continuous 'pure line hybridization' Shull (1908–1909)	Continuous 'line Hybridization' East (1909)	'Hybrid' corn East and Shull End (1910)	'Hybrid' corn Shull (1914)
Clonable variations	Hybrid vigor	Physiological stimulation due to heterozygosity	Physiological stimulation due to heterozygosity	Possibly nonMendelian physiological stimulation due to heterozygosity = Hybrid vigor

East did believe in it as shown by his article published in 1936, two years before his death (East 1936). Shull did not. But it was necessary to convince experiment station workers to build his 'monument' (table 1).

Conclusion

How 'hybrid breeders' led to success an impractical technique based on an irrelevant theory

In February 1922, on the suggestion of his son Henry Agard (the future Secretary of Agriculture during the New Deal and founder in 1926 of Pioneer, still the largest seed company founded in 1926 with 7600 dollars, it was bought by DuPont in 2000 for 10 billion dollars), the Secretary of Agriculture Henry Cantwell Wallace fired Hartley, the head of USDA corn breeding, who did not believe in hybridization (Crabb 1947, pp. 99 and 190) and replaced him with Frederick Richey, who did.

The Wallaces' political intervention in scientific matter, usually anathema 'in a free society where truth is sought for its own sake' (Mangelsdorf 1951, p. 45), was depicted as the victory of genetic enlightenment over prescientific corn breeding. The State threw considerable weight of its agricultural research behind 'hybrid' corn. Scores of 'hybrid corn breeders' raised on the principle of heterosis were recruited to 'work on a cooperative basis' to increase 'hybrid corn' yield and induce farmers to adopt the costly revolutionary 'mule corn' (as they rightly dubbed it). Corn breeding became 'hybrid corn' breeding. Efficient (yield wise) mass selection was abandoned, a sine qua non condition for the success of Shull's inefficient (yield wise) method. Theoretical discussions or dissenting views were ruled out. Far from finding 'a basis in scientific knowledge' as Shull claimed, 'hybrid' corn from 1922 to the early 1940s was an entirely empirical enterprise as Hull observed (1952, p. 452).

The 'hybrid' breeders' task was daunting. No help could come from the theory of heterosis except that no selection was possible, while by the late 1920s the flood of pure lines coming from the inbreeding programmes was threatening to drown them. In Hayes words: 'A catch phrase at these meetings (of 'hybrid breeders') was frequently discussed. It was as follows, 'now that we have got them, what are we going to do with them?' referring to the rather large group of inbred lines available...' (Hayes 1963, p. 33 and again 49).

'In the preliminary phases of hybrid maize development, inbred lines were tested for productivity and combining ability by crossing all inbreds in all possible combinations. It was soon realized that for a few hundred inbred lines, a single diallel cross was virtually impossible because of the large number of crosses required' (McLean *et al.*, CIMMYT 1997).

Why 'virtually'? Let us run the numbers, keeping in mind that heterosis is unpredictable, so that any 'inbred line which could be maintained was a potentially valuable line' (Sprague 1955, p. 243). Starting the inbreeding process with 100-seed grains and supposing that at each generation of selfing each seed grain gives an ear of only 100 grains, at the end of six generations of selfing, we have 10^{14} pure lines. That gives $\sim 10^{28}$ clones that we have to test individually for several years and in several locations to extract the best. 'The earlier concept that inbred line which could be maintained, observed Sprague, was a potentially valuable line has been discarded' (Sprague 1955, p. 243). But Sprague did not pursue this line of thought.

Among the problems raised by Shull's proposal was the impossibility of economically producing clone seeds on depressed pure lines. Shull's 1910 double cross attempted to solve the problem. Seed production would take place on a 'hybrid' (i.e. a clonable maize plant that could be selected for its yield). In 1912, this failed. He revealed his failure in 1952 but 'sought no credit for the fact that I made these four-way crosses some years prior to the similar combination made by Dr Jones' (Shull 1952, p. 44).

In 1916, Jones tried the same technique, but contrary to theoretical expectations, his 1918 double cross 'hybrids' were more productive than the parental single crosses (Jones 1918). His success was immediately advertised (*Scientific American* 1919a, *The Breeder's Gazette* 1919b). The mystery of heterosis thickened.

Yet, Jones's solution to the problem of seed production increased enormously the difficulties of extending the isolation method to maize. With only 100 lines, the breeder had 4950 clones to test. This number is multiplied 2500 times in the case of double crosses. Fisher's 'deliberately planned multiplicity' (Fisher 1949) could not go very far since the costs of increasing the size of the scale model increase with the fourth power of the number of inbred lines, while the expected gains from an increased size of the scale model grow slowly. 'Hybrid breeders' had no choice but to select, but select what?

Finally, they escaped the esoterism of heterosis, and stuck to common sense biology and breeding. They selected 'vigorous inbred lines, free from abnormalities, (...) that have good pollen and ear development, desirable seed characters, ability to withstand lodging (usually correlated with root development) and that have as great as possible resistance to diseases and insect pests' (Hayes 1963, p. 66). They invented and studied all sorts of empirical methods to avoid drowning described by Hayes (1963), Sprague (1955) and others.

At the end of the 1920s, they understood why Jones succeeded: he had combined two complementary gene pools. 'Jones might have had to work for most of a lifetime to find a combination that blended as perfectly as did his first cross of the Burr and Leaming single crosses. The flipped coin had come down and stood on its thin edge' (Crabb 1947, p. 86).

It amounted to extracting double crosses from a population or variety first improved by a varietal cross. Varietal crosses had been pioneered by William Beal in the late 1870s. Working alone, Beal was able to obtain a yield gain of 12% (Beal 1876, 1880). By the mid-1890s, Morrow and Gardner obtained such significant gains at the University of Illinois that they proposed varietal crosses to farmers. It is hardly surprising that by the mid-1930s, scores of 'hybrid breeders' heavily selecting inbred lines, implementing reliable experimental designs based on the new advances of statistical methods (Fisher 1925) and using systematically the genetic diversity of Corn Belt varieties managed to obtain a 15% yield superiority (as overestimated by the Iowa corn yield contest and in part due to the better physical quality of industrially processed seeds (Hayes 1963, p. 168) of proprietary clones over unselected farmers' varieties.

The success of Shull's pure line crossing method was, in fact, due to East's Bealian varietal crosses. The 'hybrid breeders' task proved extraordinarily difficult. By the mid-1930s, they managed to extract superior clones from Corn Belt varieties not because of East and Shull, but in spite of them. But, ironically, the yield gains achieved by the heroic *selection* work of the Richey (1884–1954), Jenkins (1913–1974), Hayes (1884–1972), Sprague (1902–1998) and Baker (1906–1999) and experiment station breeders were credited to heterosis and to its theoreticians Shull and East. Accepting this fact, however unpalatable, will hopefully open a new course for breeders.

Acknowledgements

What were mere intuitions about 'hybrid' corn took shape in the intellectually ebullient atmosphere of Richard Lewontin's laboratory where I learned that even technical genetic issues should be cast in their proper social, epistemological, historical and political framework and where Diane Paul introduced me to the field of history of science. Her sharp mind was decisive from the early stages to the completion of this article. Both declined to coauthor it although it is also theirs. I am grateful to the reviewers of the *Journal of Genetics* for their suggestions.

Appendix

Vocabulary matters

The word 'hybrid' (from Latin *ibridus*, of mixed blood and Greek *hubris*, exuberance, excess) implies a positive effect of crossing on vigour. The 19th century biologists made the distinction between hybridization and crossing. The mule mixing the 'blood' and strength of the horse with the blood and rusticity of the ass is a hybrid.

'In a broad sense, wrote Paul Mangelsdorf in *Scientific American* (1951, p. 39) all corn is hybrid for this plant is a cross-pollinated species in which hybridization between varieties and between races occur constantly. (...)'

A 'hybrid', then, is an ordinary corn plant. Mangelsdorf evades the issue with the claim:

'But the hybrid corn with which we shall deal here is a planned exploitation of this natural tendency on a scale far beyond that possible in nature.'

He then goes on: 'The biological basis of hybrid corn is a genetic phenomenon known as 'hybrid vigour.

No! The biological basis of 'hybrid' corn is natural variations made reproducible by crossing pure lines. The incantatory use of 'hybrid', 'hybridization', 'natural tendency (to hybridize)' misleads users and readers.

Moreover, 'hybrid' conflates the process of making 'hybrids' ('hybridizing' – crossing!) pure lines with the biological result: heterozygous quasi clone or to simplify heterozygous clone if we deal with the biological aspect, or proprietary clone if we focus on the anthropological dimension of turning life into a commodity. James Crow's observation derived from Ronald Fisher (1949) that hybridization is the 'equivalent of reproducing *asexually* (my italics) the best individual of a segregating population', i.e. *cloning*, legitimates extending the term 'clone' (Crow 1998) to the legally 'homogeneous and stable' crops of industrial agriculture.

Dolly extended cloning to mammals. Cloning reflects the two century long drive for uniformity, standardization and normalization required by the mass production of an industrial society. It also reflects the secular struggle against the free reproduction of living organisms. No property rights over varieties are possible because they are heterogeneous and changing while clones, being 'fixed', can be protected and patented. Modern industrial clones contrast with peasant land races or varieties (which have the character of being varied, the opposite of uniformity) produced by mass selection that has created since the beginnings of agriculture the immense wealth of cultivated biodiversity that is now in jeopardy.

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