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PERSPECTIVES

Hybrid corn beyond heterosis: reading George Shull's hybrid corn articles (1908–1909)

JEAN-PIERRE BERLAN*

Institut National de la Recherche Agronomique, 2 Place Pierre Viala, 34000 Montpellier, France
*E-mail: jpe.berlan@gmail.com.

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The theoretical conclusion of Shull's first article 'The composition of a field of maize'—the breeder's task is 'the development and maintenance of that hybrid combination which possesses the greatest vigor'—has, for all practical matters, nothing to do with his breeding proposal to make 'as many self-fertilization as practicable… Then all possible crosses are to be made among these different pure strains', namely extending the small grain isolation method to maize. This conclusion should have been clear for an unprejudiced biologist as soon as Shull's second article (January 1909), and was inevitable after his third one (December 1909). This article highlights Shull's skillful rhetoric and semantic that shaped the prejudice blinding biologists for more than a century and their neglect of Shull's stated goals of crop uniformity and breeders' property rights.

Introduction

In a period of two years from January 2008 to December 2009, George Shull presented three talks at the annual meeting of the young American Breeders' Association, published in the Association's journal. These articles determined the course of breeding and led to the present monopolistic seed industry. 'The composition of a field of maize' (28–30 January 1908) reduced a field of maize to crosses of depressed pure lines and alluded to a new breeding method, 'continuous hybridization' derived from biological assumptions concerning maize inbreeding depression and heterosis. The second (6–8 January 1909a) revealed his method under the title 'A pure line method in corn breeding'. The third (8–10 December 1909b) reviewed 'Hybridization methods in corn breeding' and added the results of eight other pure-line crosses that confirmed the value of his hybridization method (Shull 1909b).

The theoretical bent of 'The composition…' has attracted much attention at the expense of the practical fabric of the two following articles. Thus, the distinguished population geneticist James Crow expressed the unanimous view of the genetic and agronomic community when he celebrated in a 1998 essay, the 90th anniversary of George Shull's Composition: hybrid corn 'marked the beginning of the exploitation of heterosis in plant breeding, surely one of genetics' greatest triumphs' (Crow 1998, p. 923). According to the radiation geneticist Lewis Stadler, the 'increase in yield (according to Stadler hybrid corn increased yield by 25%) costs nothing except the added costs of producing the special kind of seed and the added costs of harvesting a larger crop' (quoted by Shull 1948, p. 550). This huge yield surge stemmed from Shull's Composition theoretical insight: because of heterosis, 'the fundamental problem (…) is the development and maintenance of that hybrid combination which possesses the greatest vigor' (Shull 1908, p. 300). Hybrid corn and the exploitation of heterosis are now the paradigm of agricultural genetics and breeding as shown by the important 1997 Cimmyt international symposium,

This article is dedicated to Diane Paul.

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Heterosis in Crops. Heterosis would contribute to 'Food security; poverty alleviation; natural resource protection' (Director General of CIMMYT 1998, p. 2).

However, a careful reading of the second and third articles do not confirm the unanimous belief that heterosis has, for all practical matters, anything to do with hybrid corn nor that its exploitation brought about a yield increase other than unique and marginal. I will consider the three articles as a whole and dissect their rhetoric and semantic. Before I do so, it is necessary to have a clear understanding of their chronology.

The chronology

Replying to geneticist Edward East, who had requested on 5 February 1908 a 'copy of your interesting paper on maize (The composition… NDA) (…) to study your results before planting', Shull wrote on 3 March 1908:

> I am glad that your extensive experiments in corn breeding might have led you to the same conclusion as that at which I have arrived (…). There is little doubt in my mind that if I had held on to my idea of the composition of a corn field until I could have worked out some of the subsidiary problems, I could have raised a monument to myself which would be worthy to stand with the best biological work of recent times. But the matter seemed to me of too great importance in view of the value of our maize crop to selfishly keep it to myself longer than was necessary to assure myself of its correctness (in Jones 1944).

'The subsidiary problems' were key: would the cross of his depressed 'nearly pure lines' (the first 'hybrid') recover its vigour as he had inferred from his Mendelian reduction of heterozygous maize plants to crosses of homozygous depressed pure lines? In January 1908, he had not yet performed this crucial experiment. But Shull did not 'hold on to his idea' and announced, albeit allusively, his revolutionary 'continuous hybridization'. At harvest time in the fall 1908, his cross had recovered its vigor and in January 1909 he could reveal his 'Pure line method …'.

However, once again, he anticipated the results of his future experiment with eight 'hybrids'. Would the yield variation among his small sample of crosses be large enough to make it worthwhile to replace the original natural variety by the best 'hybrid' from the sample? In December 1909, the eight bushels yield gain brought about by the best cross (Shull 1909b, p. 69) was promising enough provided that 'experiment stations (…) undertake the solution to these fundamental problems' (Shull 1908, p. 301), a euphemism, as we will see, for the intractable practical difficulties ahead.

The 'composition' solved the corn breeder's problems in an industrial capitalist society: crop uniformity and breeders' property rights.

The 'development and maintenance of that hybrid combination which possesses the greatest vigor' (Shull 1908, p. 300) solved the problem of crop uniformity, normalization, standardization required by the emerging industrial system of mass production.

As to breeders' rights:

> The problem of getting the seed corn that shall produce the record crop, or which shall have any specific desirable characteristic combined with the greatest vigor, may possibly find a solution, at least in certain cases, similar to that reached by Mr. Q. I. Simpson in the breeding of hogs by the combination of two strains which are only at their highest quality in the first generation, thus making it necessary to go back each year to the original combination, instead of selecting from among the hybrid offspring the stock for continued breeding (Shull 1908, p. 300).

In this light, the yield increase could be limited to whatever was necessary to convince farmers to adopt the revolutionary 'hybrid' corn. These features of Shull's articles, property rights and crop uniformity, have been neglected, while attention was focussed on the corn yield gains of exploiting heterosis.

Briefly stated, from the very beginning Shull knew that his method solved the corn breeders' problems of achieving plant uniformity and breeders' property rights while a yield gain appeared possible. It was matter of experiments to confirm his theoretical discovery of a revolutionary breeding method.

But is 'The composition …' of January 1908 the very beginning?

Inconsistencies

In January 1909, Shull announced that his first 'nearly pure line' cross had recovered its vigour. Sown in the spring of 1908, it had been harvested in the fall. He then had made the cross in July 1907. Nowhere this date appears. Quite the contrary: 'The continuation of these studies during the past year (…) has given unexpected suggestion for a new method of corn breeding' (Shull 1909a, p. 52). Only 42 years later in 1950, when he was an icon of genetics, did he remember and mention the date correctly (Shull 1952, p. 28).

The true beginning of 'hybrid corn' is not 'The composition…' in January 1908 but July 1907. Shull, then, did not want to draw attention to what had prompted this 'unexpected suggestion': he had discovered the 1836 La Gasca/Le Couteur's isolation method in Hugo de Vries' book *Plant breeding* published in the first part of 1907 (de Vries 1907, pp. 34–35). Empirically implemented in England since the early 19th century, it consists in replacing a variety or population by 'copies' of a better plant—a (quasi) clone. For instance, 'Patrick Shirreff in Scotland developed his wheat

Mungoswell from a plant that had survived the severe 1813 winter exceptionally well' (Evershed 1884). It exploits the natural variation of populations or varieties and requires individually reproducible, namely clonable plants.

His Mendelian work on maize heredity begun in earnest in 1905 had prepared Shull to understand immediately why the isolation/cloning method worked for autogamous individually reproducible small grain cereals such as wheat, why it did not work for the cross pollinated maize contrary to breeders' expectations, and how it could work for maize: crossing random homozygous individually reproducible pure lines obtained by a series of self-fertilizations would give individually reproducible (by the breeder only) heterozygous *ordinary* maize plants misnamed 'hybrid'. But Shull focussed on heterosis and kept silent about his true achievements: his early understanding of the consequences of Mendelism for breeders and the possible extension to maize of the small grain isolation/cloning method.

How such individually reproducible ordinary plants are to be made? This is the object of his second article. Shull unfolds his method in three steps.

(i) He first recalls the observation running from the opening sentence to the conclusion of 'The composition…': because of heterosis, uniformity can only be attained at the expense of decreased yield:

> '… efforts at the attainment of homogeneity by the method now in use tend to lessen physiological vigor, and therefore lessen the yield, owing to the fact that such homogeneity in the offspring is to be attained only through homozygosis in respect to all those characteristics which affect the form and size of the ear, width, depth, shape and composition of the grain, and any other feature in which homogeneity may be desired. This is doubtless, the explanation of the interesting experience related by Mr Joseph I. Wing at the meeting of the American Breeders' Association two years ago. His father had selected a very fine deep-grained variety of corn in which great uniformity had been attained, but only at the expense of decreased yield (Shull 1909a, pp. 56–57).

(ii) He explains the principle of his method to solve the problem:

> (…) the vigor of the entire crop should be equal to the best plants produced by the method now in use. This would seem to result necessarily *in a larger yield* (my italics) than can be produced by the present method. But not only will all the plants in the field have the same degree of complexity, but will all be made up of the same combination of hereditary elements, and consequently there must result *such uniformity as is at present unknown in corn* (my italics) (Shull 1909a, p. 57).

Replacing an 'entire crop' by the most heterozygous, i.e. the best plant, would 'result necessarily in a larger yield' and insure 'an uniformity so far unknown in corn'. This implies that this best plant replacing the variety should be 'individually reproducible or clonable', terms that Shull carefully avoided.

(iii) Last, he moves to the last step: making such *individually reproducible plants*:
'The process may be considered under two heads: (1) finding the best pure-lines; and (2) the practical use of the pure-lines in the production of seed-corn.

> (1) In finding the best pure-lines, it will be necessary to make as many self-fertilization as practicable, and to continue these year after year until the homozygous state is nearly or quite attained. Then all possible crosses are to be made among these different pure strains and the F_1 plants coming from each cross are to be grown (…) and then studied as to yield and the possession of other desirable qualities (…).
> (2) After having found the right pair of pure strains (…)' (Shull 1909a, p. 57).

Experimental evidences supported Shull's construction—there is inbreeding depression, vigour goes with hybridity or heterozygosity, crossing depressed pure lines restores vigour etc. His method, then, appeared to follow from his biological considerations on heterosis. But Shull's skillful rhetoric and semantic are a delusion: the correlation between vigour and hybridity or heterozygosity is not causality as his rival Edward East (who had his own version 'continuous hybridization') rightly pointed out (East 1909, p. 174); and in any case, Shull applied the general logical principle of the isolation method to maize: there is always a gain to replacing a variety of 'anythings' by 'copies' of a better 'anything'. Heterosis is, for all practical matters, irrelevant. All that is needed is a variety made up of 'individually reproducible elements' to exploit its variations, namely to apply the Le Couteur/LaGasca small grain isolation/cloning method.

Nowhere is the delusion clearer than in Shull's overlooked concluding article. He selected the best 'hybrid', i.e. an individually reproducible plant, 'a result of the particular hybrid combination' (Shull 1909b, p. 68) out of a random sample of eight to replace the original cross-bred variety. His success paradoxically convinced everyone of the value of his 'hybrid' corn method of exploiting heterosis, although it demonstrated that it exploited the natural variation of a corn population by the isolation method.

Finding the best pure lines meant, in fact, finding the best pure line cross. Shull had noticed this circularity in 'The composition…' 'In the present state of our knowledge, it is impossible to predict from the study of two pure strains what will be the relative vigour of their hybrid offspring' (Shull 1908, p. 300). He expected the problem to be solved, in vain since heterosis is unpredictable. So breeders have to inbreed

maize plants for a number of generations, thus producing an extremely large number of pure-lines that must be crossed two by two to identify the best cross, that is the best lines. '… simply finding the best combination of parents and then repeating the combination year after year' (Shull 1909a, p. 69) was an extravagant and unfeasible task. The only possibility was to randomly extract a small sample of individually reproducible plants from a corn population, meaning that only a small gain could be expected. And it could be expected *only once*: repeating the random process with the same population would yield approximately the same best cross. Further gain could only come from populations improved by mass selection. Hybrid corn then never exploited heterosis, it could only exploit once a small fraction of variation of corn populations and it could hardly increase yield.

Had biologists devoted the same attention to Shull's second and third articles, namely on what Shull 'did (and on what they were invited to do)', this conclusion would have been clear as early as January 1909, and in December 1909, it was inevitable.

Exploiting natural variations of corn populations by the isolation/cloning method was an extravagant proposal, so extravagant that Shull hid it behind the scientific justification (Shull 1908, p. 301) of the imperious heterosis. Moreover, acknowledging his debt to Le Couteur, LaGasca and de Vries would have reduced his monument to, at best, a small stone memorial. Thus, he chose another course: exploiting the 'magic of heterosis' (an expression found in the genetic/breeding literature). I have highlighted Shull's skillful rhetoric to persuade his readers that his hybrid corn breeding method was a logical consequence of his theoretical heterosis developments and to divert their attention away from the reality of the Le Couteur/LaGasca isolation/cloning method. It implied the use of a misleading vocabulary: hybrid, hybridity, hybridization, heterosis etc. rather than, exact words or expression that could have revealed the truth such as individually reproducible plants. For with the isolation/cloning technique of the early Industrial Revolution, breeding became cloning: homozygous (quasi) clones and whenever feasible in 20th century, proprietary heterozygous (quasi) clones—and Dolly in the 21st.

Briefly stated, the inordinately celebrated huge gains of the exploitation of heterosis by 'hybrid corn' never existed.

Conclusion

'The composition …' did not mark 'the beginning of the exploitation of heterosis'. Yet, it set the stage for all further developments. The opening sentences reads:

> While most of the newer scientific results show the theoretical importance of isolation methods, and practical breeders have demonstrated the value of the same in the improvement of many varieties, the attempt to employ them in the breeding of Indian corn has met with peculiar difficulties, owing to the fact that self-fertilization, or even inbreeding between much wider than individual limits, result in deterioration.

So, Shull began implementing the isolation method in July 1907 because 'isolation methods' did not work for maize…

Shull went on:

> The cause of such a result is wholly unknown at present' (Shull 1908, p. 296).

As with Edgar Allen Poe's Purloined letter, which was hidden in plain sight in a wrinkled envelope, Shull's maize isolation method was in full view, enveloped in the plural of isolation methods. He bet that competent and seasoned biologists would act like the detectives of the prefect of police and probe endlessly the still 'wholly unknown' mysteries of heterosis while ignoring what they actually did: implementing the isolation/cloning method.

Shull's 'Composition of a field of maize' is a masterpiece: it sent generations of biologists astray chasing the mysteries of heterosis; it established Shull's priority on the exploitation of the elusive heterosis (the worldwide paradigm of breeding), and on its implementation with his revolutionary breeding technique, 'hybrid corn'. It turned reality upside down: his breeding technique appeared as a consequence of his theory of heterosis although his theory was actually an *ad hoc* construction to justify his extending the early nineteenth century isolation/cloning method to maize; it hid the extravagance of his breeding method and its inability to increase yield behind the 'magic of heterosis'; it highlighted isolation method**s** to stamp out the isolation/cloning method; it solved the twin overdominant problems of an industrial capitalist agriculture, industrial uniformity and breeders' property rights, and created the present monopolistic seed industry; and last, it insured that Shull would not have to share his 'monument' with anyone.

In his 1907 book, *Plant breeding,* Hugo de Vries made a perceptive observation about the social forces influencing the course of genetics and breeding:

> This assertion [according to which varieties would deteriorate in the farmer's field] has a distinct and deep significance *in agricultural practice*, and *has also gained a great deal of influence in discussions of theoretical questions* [my italics]. (…) It is easy to see that the gain made by the breeder of the new variety depends in large part on the acceptance of this proposition. In the varieties produced by Le Couteur and Shirreff, all seed is of equal value provided the lines are kept pure and free from admixture. Anyone may multiply them with the same success as the original breeder. However, based on Hallett's principle, all profits from the

production of reliable seed grain accrue to whoever kept the original pedigree (De Vries 1907, p. 43).

Mutatis mutandis…

Notes and acknowledgments

I stuck to the unfortunate habit of conflating hybrid vigour (a *phenomenon*) with a particular *theory* accounting for it (East's 1909 'physiological stimulation due to heterozygosity'). Shull's heterosis (1914, in Shull 1948) inaugurated this confusion that added a non-Mendelian mystery to the whole matter. How and why the conflation took place is a story in itself. Readers will find it in 'Hybrid corn and the unsettled question of heterosis', *J. Genet.* 2018, **97**, 5, pp. 1075-1082. My book *La planète des clones,* La Lenteur: Vaour 2019, deals with the endless 'anomalies' (Thomas Kuhn) arising from the discordance between theory (exploiting the elusive heterosis) and practice (exploiting variation of populations) and offers a political economy overview of breeding since the Industrial Revolution to the so-called Gmos and Dolly. Last, these views are the result of a collective work. Richard Lewontin invited me, an economist, to develop what were mere intuitions about hybrid corn in his intellectually ebullient population genetics laboratory where even technical issues were cast in their proper philosophical, historical, epistemological and political economy context. There Diane Paul, historian of sciences, introduced me to her field and was supportive intellectually and morally, particularly during the discouraging last years when I realized how difficult it was to publish views running against the ongoing paradigm or dogma in countries where 'hybrid corn' is the iconic triumph of the genetic and agronomic establishment. Anything worthwhile I wrote is common and any mistake is mine.

References

Berlan J.-P. 2018 Hybrid corn and the unsettled question of heterosis. *J. Genet.* **97**, 1075–1082.

CIMMYT 1998 Book of abstracts. The genetics and exploitation of heterosis in crops. An international Symposium (ed. CIMMYT), Mexico.

Crow J. F. 1998 90 years ago: the beginning of hybrid maize. *Genetics* **148**, 923–928.

De Vries H. 1907 *Plant-breeding, comments on the experiments of Nilsson and Burbank*. The Open Court Publishing, Chicago.

East E. M. 1909 The distinction between development and heredity in inbreeding. *Am. Nat.* **43**, 173–181.

Evershed H. 1884 Improvement of the plants of the farm. *J. Roy. Ag. Soc.* **23**, 371–381.

Jones D. F. 1944 Biographical memoir of Edward Murray East (1879–1938). *Biog. Memoirs Natl. Acad. Sci.* (Washington DC, USA, **XXXIII**). 217–242.

Shull G. H. 1908 The composition of a field of maize. *Am. Breed. Assoc. Rept. IV*, 296–301.

Shull G. H. 1909 A pure-line method in corn breeding. *Am. Breed. Assoc. Rept.* **V**, 51–59.

Shull G. H. 1909 Hybridization methods in corn breeding. *Am. Breed. Assoc. Rept. VI*, 63–72.

Shull G. H. 1948 What is "Heterosis"? *Genetics* **33**, 439–446.

Shull G. H. 1952 Beginnings of the heterosis concept. In *Heterosis, a record of researches directed toward explaining and utilizing the vigor of hybrids* (ed. J. Gowen), Iowa State College Press, Ames, pp. 14–48.

Corresponding editor: Durgadas P. Kasbekar