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Corn Breeding

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Abstract
The 100th anniversary of the inbred-hybrid corn concept was celebrated in 2008. It was in 1908 that G. H. Shull first presented the idea that corn could be improved by 1) selfing of plants to develop inbred lines, 2) making crosses (i.e., hybrids) among the inbred lines, 3) testing the hybrids in replicated trials to determine which hybrid has the best yield, and 4) reproducing the best hybrid and making seed available to the farmer. In the early part of the 20th century there was a rapid expansion in the interest and use of corn as a livestock feed in what we today call the "U.S. Corn Belt." Acreages for producing corn increased, but one of the major obstacles was the relatively low yield of the open-pollinated varieties being grown at the time. From 1865 to 1935 (70 years), the average U.S. corn yields exceeded 30 bushels/acre in only four years. Hence, the question was: How can we increase corn yields? The information that G. H. Shull presented at the American Breeders Meetings in Omaha, NE in 1908, 1909, and 1910 was to have a profound affect on the type of corn grown in the 20th century. The inbred-hybrid corn concept of Shull often has been called the greatest plant breeding achievement of the 20th century.

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Introduction

The 100th anniversary of the inbred-hybrid corn concept was celebrated in 2008. It was in 1908 that G. H. Shull first presented the idea that corn could be improved by 1) selfing of plants to develop inbred lines, 2) making crosses (i.e., hybrids) among the inbred lines, 3) testing the hybrids in replicated trials to determine which hybrid has the best yield, and 4) reproducing the best hybrid and making seed available to the farmer. In the early part of the 20th century there was a rapid expansion in the interest and use of corn as a livestock feed in what we today call the "U.S. Corn Belt." Acreages for producing corn increased, but one of the major obstacles was the relatively low yield of the open-pollinated varieties being grown at the time. From 1865 to 1935 (70 years), the average U.S. corn yields exceeded 30 bushels/acre in only four years. Hence, the question was: How can we increase corn yields? The information that G. H. Shull presented at the American Breeders Meetings in Omaha, NE in 1908, 1909, and 1910 was to have a profound affect on the type of corn grown in the 20th century. The inbred-hybrid corn concept of Shull often has been called the greatest plant breeding achievement of the 20th century.

Initially, Shull's idea received limited interest. Because the inbred lines developed by self-pollination had very poor vigor, had very poor seed yield, were very susceptible to the pests of corn, and were overwhelmed by weeds (there were no pesticides in those days), the costs of producing the hybrid seed corn would be prohibitive for the farmer. But the idea was very intriguing. For the next 10 years a few scientists continued to work on the inbred-hybrid concept to try and find a method to make the concept practical and useful. The first breakthrough came in 1919 when D. F. Jones, working in Connecticut, suggested that two of the single-cross hybrids, suggested by G. H. Shull, be used to produce double-cross hybrids. This suggestion reduced the problem of producing hybrid seed corn at a cost that would be acceptable to the farmer. The year 1922 was the turning point because a national effort by the State Agriculture Experiment Stations and the U. S. Department of Agriculture was initiated to make the inbred-hybrid concept feasible to increase corn yields. The Iowa State breeding program was started in 1922, and was to be a major contributor for improving corn to the present.

Iowa Work

The Iowa corn breeding program has been a cooperative effort between the USDA-ARS and the Iowa Agriculture Experiment Station, located at Ames. Two of the most prominent researchers for increasing the effectiveness and efficiency of the inbred-hybrid concept were M. T. Jenkins and G. F. Sprague who were the leaders of the Iowa corn breeding program from 1922 to 1958. Both were unique in that they made significant contributions to both the theoretical and empirical aspects of corn breeding. Jenkins determined the relation between inbred line and their hybrids (note: he found no relation); he suggested use of a tester to determine the combining ability of new inbred lines in hybrids; he developed prediction methods for double-cross hybrid performance based on single-cross and/or testcross data; and he determined the value of early testing to reduce the number of progenies for hand pollination in breeding nurseries. Sprague conducted further studies on the value of early testing; he determined the relative importance of general and specific combining for previously tested and untested inbred lines; he expanded testing programs and used statistical methods to determine the most efficient distribution of resources; he initiated recurrent selection programs for the genetic improvement of germplasm resources; and he initiated and conducted genetic studies to gain an understanding of the genetic basis (what are the causes) of heterosis expressed in corn hybrids.

The conclusions and recommendations that Jenkins and Sprague reported rapidly became accepted as standard breeding methods to enhance the development and evaluation of inbred lines for use in hybrids. By 1935, some double-cross hybrid seed was being provided for use by farmers. Farmers could rapidly see that the hybrids were superior to the open-pollinated varieties. By 1945 nearly 100% of the Iowa corn acreage was planted to double-cross hybrids. Because of the improvements made in developing more vigorous inbred lines and the availability of herbicides to control weeds, single-cross hybrids started to be produced and made available to farmers in the early 1960s. Today, nearly 100% of the corn hybrids offered for sale to the farmers are single crosses, which is what Shull had originally suggested.

Jenkins and Sprague, however, firmly believed that the information and ideas generated from their basic research would be enhanced if they also developed inbred lines and hybrids that would contribute to corn production by the Iowa farmer. Both were equally successful in developing widely used inbred lines and hybrids. Jenkins developed inbred lines that were used as parents of the first widely distributed double-cross hybrids. IA939 was one of the most widely grown double-cross hybrids in Iowa and included four lines all developed by Jenkins. IA13 included only Jenkins lines. At the national level U.S.13 double-cross was widely grown and included one line from Jenkins. Several of Jenkins' inbred lines would continue to be used in breeding nurseries until about 1960.

G. F. Sprague would have even greater impact than M. T. Jenkins. One of the most evident problems in growing open-pollinated varieties was poor root and stalk strength, which caused extensive lodging. During the 1930s, Sprague developed a synthetic variety by intermating 16 inbred lines that he considered to possess above average stalk strength (i.e., to reduce stalk lodging). Sprague designated the synthetic as Iowa Stiff Stalk Synthetic (ISSS). He initiated recurrent selection programs in ISSS in 1939 and 1949; both programs are still being continued in 2009. Iowa Stiff Stalk Synthetic became the greatest source of useful inbred lines than any other germplasm used by corn breeders. Prior to 1960, the heterotic groups recognized by corn breeders to produce inbred lines that consistently produced the best hybrids were from Reid Yellow Dent and Lancaster Sure Crop, which was called the Reid Yellow Dent-Lancaster heterotic pattern. Today, in the U.S. Corn Belt and other temperate corn production areas of the world, the heterotic groups are recognized as ISSS (for female parents) and non-ISSS (for male parents). Why did Iowa Stiff Stalk Synthetic become such a good source of germplasm for useful and high performance inbred lines in commercial hybrids? Sprague was a great believer that good germplasm was the basic ingredient for ultimate success. He initiated cyclical (designated as recurrent selection) selection techniques that permitted incremental genetic improvement for favorable genes. There are no time periods because, to be successful, the cyclical selection methods must be conducted continuously and without interruption.

The success of these selection programs was clearly demonstrated by Mikel in 2006. He surveyed the pedigree records (germplasm source) of 908 proprietary corn inbred lines that had been submitted to the U.S. Patent Office for either patents or plant variety protection (PVPs) by the commercial corn breeders and their organizations. Mikel concluded that 63% of all the inbred lines submitted included some portion of their germplasm derived from ISSS. Inbred lines such as B14, B37, B64, B68, B73, and B84 have had a prominent role in commercial hybrids either directly or indirectly to produce modified versions of the originally released inbred lines. The inbred lines were released freely to any breeder, public or private, to use as they desired without any restrictions.

Sprague left Ames in 1958 to assume leadership of the corn and sorghum programs for the U. S. Department of Agriculture stationed at Beltsville, MD. I was hired to fill his vacancy at Ames. (Note: I filled, not replaced.) Rapid changes were occurring in the hybrid seed corn industry during the 1950s. Public breeding programs, such as the one at Ames, were rapidly being downsized, discontinued, or changed the types of research they conducted. Conversely, commercial breeding programs were rapidly increasing in size, scope, and number, which continues today. Previously, the public breeding programs had been the major contributors for developing inbred lines, testing of hybrids, and recommending hybrids the farmers should grow. These activities were assumed by the commercial breeders because they had the production and marketing skills to provide good quality hybrid seed for farmers. The hybrid seed corn industry became a very competitive business and each organization wanted to acquire and maintain their market share of the hybrids they marketed. Hence, they desired to retain ownership of the lines used to produce hybrids.

One of the last instructions Sprague gave me as he left Ames for Beltsville was "Do not try to compete with commercial companies in applied research but conduct more basic, high-risk types of research to garner additional information on the genetic and breeding methods to increase the effectiveness and efficiency of developing superior inbred lines and hybrids. Also, continue the cyclical breeding methods to develop improved germplasm sources for commercial breeding programs." During the past 50 years I clearly remember his parting words, and I desired to retain the status of the corn breeding research conducted by Jenkins and Sprague.

The cooperative state-federal corn breeding program has been productive during the past 50 years conducting basic research on selection and breeding methods; adapting tropical germplasm sources to temperate environments (U.S. corn breeders use less than 3 percent of the corn germplasm available in the world); conducting genetic studies to determine the types of genetic effects important in selection and heterosis; and, lastly, continuing cyclical selection methods to improve our germplasm resources. Two additional goals of the breeding program have been the training of graduate students in corn breeding (nearly 200 students completed M.S. and Ph.D. degrees during past 50 years) and continued development of inbred lines and their evaluation in hybrids, which has been 10 to 15 percent of our total efforts. The continuation of inbred line development and their hybrids was done primarily to give credence to our basic research studies. This approach has been validated because inbred lines were released, based on their hybrid performance, and made available to the commercial breeders. Although it seems we ignored Sprague's wisdom of inbred line development, he was very supportive and appreciative of our efforts because nearly all the newly released inbred lines were derived from the cyclical selection programs: i.e., we developed original lines rather than recycled lines from previously released inbred lines; we left that phase of breeding to the commercial breeders.

The Future

What is the future of public breeding programs? They continue to be either downsized or eliminated to the point that public corn breeding programs are nearly irrelevant in the broad spectrum of corn breeding today. About 20 years ago, the potential of molecular genetics was emphasized and resources in the public sector were reallocated to the newer science-molecular genetics. During the past 20 years molecular biology has made spectacular advances, as witnessed by the insertion of genetic factors of Bt and glyphosate resistance by molecular means. But what of the future? Who will train and educate the future plant breeders; introduce, evaluate, and adapt new sources of germplasm; conduct long-term cyclical programs to improve our germplasm resources; and conduct other high-risk research programs? The commercial hybrid seed corn industry is as competitive today as ever and the bottom line determines who stays in business. The molecular genetics contributions have been very important in reducing the factors that can inhibit hybrid performance, which is good.

The corn breeding methods stimulated by Shull in 1908 have been effective. Average U.S. corn yields were stagnant from 1865 to 1935 (usually less than 30 bushels/acre). With the introduction of hybrids in 1935 to 1970, average U.S. corn yields more than doubled to 72.5 bushels/acre. Since the introduction of single-cross hybrids in the 1960s, we have seen nearly a linear increase of about 2 bushels/acre per year. In the 21st century (2001-2008), U.S. average corn yields have averaged 146.5 bushels/acre, double the yield of 1970. Average yields in Iowa have ranged from 146 bushels/acre (2001) to 181 bushels/acre (2004) for an average yield of 166 bushels/acre. A few are predicting that within 20 years U.S. corn production will be in the 300 bushels/acre range, which is double the average yield of the first eight years of the 21st century. To achieve this level we would need about 7.5 bushels/acre per year increase in grain yield, which is more than double the rate in the past 20 years. The prediction of 300 bushels/acre yield is predicted on the information gleaned from molecular genetic studies. The corn genome has been sequenced and the molecular genetics will identify important genes for yield, pest tolerance, heat and drought tolerance, and genes important in the expression of heterosis in hybrids. Based on the past, great strides have been made in corn improvement, and it is a given that continued progress will be made. The prediction of 300 bushels/acre seems optimistic, but the author has been surprised, to some extent, with the progress made during the past 50 years. These are exciting times in corn breeding. The author is ignorant of the molecular tools that are available, and how all the information generated at the molecular level is translated to the phenotype of corn in the field. It is certainly more complex than my previous experiences in corn breeding. I support the newer techniques used to manipulate the more than 50,000 genes in the corn genome to produce better inbred lines to produce better hybrids. I wish them all continued success.