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G. T. Sprague

GEORGE FREDERICK SPRAGUE

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BY ARNEL R. HALLAUER

GEORGE F. SPRAGUE conducted research in the genetics and breeding of corn for nearly seventy years. His career spanned the interval from the initial studies on the potential of the inbred-hybrid concept for the development of inbred lines to produce hybrids in the 1920s to the potential of molecular genetics for the improvement of lines and hybrids in the 1990s. Throughout his seventy-year career, he always had an active research program. Sprague was a dedicated biologist who had an interest in all facets of maize genetics and breeding. He was trained in classical genetics, but he also made significant contributions to understanding the inheritance of quantitative traits; experimental methods for evaluation of lines for use in hybrids; relative efficiency of evaluating hybrids over locations and years; development and improvement of germplasm resources for the extraction of lines for use in hybrids; types of genetic effects important for the expression of heterosis; and identification of transposable elements that contributed to genetic variation.

Sprague was primarily interested in basic research, but he always emphasized that the applied aspect of research needed to be integrated with the basic research. Based on

his experience and the successful development of the inbred-hybrid concept for providing hybrids to producers, Sprague had great foresight in the future direction of corn research during the last half of the twentieth century. He recognized there would be a rapid transition from the prominence of publicly supported breeding programs before World War II to the rapid expansion of the commercial hybrid-seed-corn industry after World War II. He encouraged and supported the publicly supported agencies to emphasize high-risk long-term research agendas; the applied aspects of line and hybrid development would be the main focus of the commercial seed industry.

Sprague also realized that development and improvement of germplasm resources would be necessary to maintain the genetic improvement of lines and hybrids. He was a strong proponent of the recurrent selection methods developed in the 1940s for genetic improvement of maize germplasm. He developed synthetic cultivars during the 1930s and 1940s that were the basis of his selection studies. Continued selection within the synthetic cultivars was conducted and they were integrated with line and hybrid development programs. One of these synthetic cultivars, Iowa Stiff Stalk Synthetic, became an important germplasm source of inbred lines that were, and continue to be, prominent in the pedigrees of hybrids in the U.S. Corn Belt during the last fifty years. It is estimated that 40% to 45% of U.S. hybrids include germplasm whose origin traces to Iowa Stiff Stalk Synthetic.

George F. Sprague is recognized nationally and internationally for his contribution to the successful implementation of the inbred-hybrid concept for developing superior corn hybrids. In the developed areas of the world, hybrid corn is grown on nearly all of the maize-growing area and the percentage of hybrid maize has increased in the lesser

developed areas. Sprague's vision and research contributions have impacted all areas. He was a leader and active supporter of maize research throughout his career. He will always be recognized for his prominent role in the science of corn genetics and breeding during the twentieth century.

PERSONAL HISTORY

George Frederick Sprague was born at Crete, Nebraska, on September 3, 1902, the second youngest of seven children. His parents were Elmer Ellsworth and Lucy Manville Sprague. Both parents were graduates of Doane College at Crete, Nebraska. His father was a minister operating under the Congregational Home Missions Board.

Sprague attended grade school at Thedford and Butte, Nebraska, and graduated from Lincoln High School in Lincoln. Although the economic situation of the family was very poor, the seven children grew up with the expectation they would attend college. After he graduated from high school, Sprague enrolled in the College of Agriculture at the University of Nebraska in Lincoln for the 1920 fall semester. His choice of college was based partly on convenience but also because he was raised in rural and small-town environments. Also, in high school he became very interested in botany because of the influence of his teacher, Miss Rice.

In college, Sprague obtained employment with the Animal Husbandry Department tending experimental feed trials of swine and sheep. During the summers he worked on farms as a hired hand to earn funds to pay the fall semester tuition fees. After his sophomore year, he transferred to the Agronomy Department, where he was a laboratory assistant for both the cereals and forage crops courses. This was a very fortunate move because Sprague came under the influence of Professor F. D. Keim. Professor Keim was an unusual and

perceptive individual who had an impact on many of the undergraduate students at the University of Nebraska. Professor Keim took a keen interest in his students. He had an uncanny ability to evaluate students and suggest various career opportunities. Some students were steered toward Smith-Hughes teaching and county agent work and a few toward research; Sprague was one of the latter. At least four of Professor Keim's students were elected to the National Academy of Sciences.

Sprague's schooling was delayed one semester at the University of Nebraska because of the influenza outbreak of 1918. If not for the delay, he could have graduated mid-year. He continued taking graduate courses that would apply toward a M.S. degree. Sprague graduated from the University of Nebraska in 1924 with a B.S. degree in agriculture. Upon graduation he obtained a position as a junior agronomist with the U. S. Department of Agriculture (USDA) at the North Platte substation in Nebraska. His responsibilities were to initiate a program of cereal improvement. He continued his graduate studies at the University of Nebraska, but the materials for his M.S. thesis problem were grown at North Platte. He fulfilled the requirements for his M.S. degree in agronomy in 1926.

During the course of his M.S. studies, Sprague realized the need for additional training. Accordingly, he applied for a leave of absence from the USDA and for entrance to the Graduate School at Cornell University. Both requests were approved, and he enrolled at Cornell in the fall of 1926. Sprague considered it very fortunate that he was able to obtain Professor R. A. Emerson, a corn geneticist, as his major advisor. Soon after his arrival at Cornell, the bank at North Platte was closed, and funds that he had planned to use for his residency were no longer available. Fortunately, through Professor Emerson's influence, Sprague obtained

a field assistant appointment, which provided adequate funds for him to complete the two-year residency requirement. Sprague completed his preliminary examinations and returned to North Platte in the spring of 1928 as an assistant agronomist in the USDA. In 1929, he was transferred to Arlington Farms, Virginia. His Ph.D. dissertation studies were continued at North Platte and at Arlington Farms. The Ph.D. dissertation was submitted and accepted, and the Ph.D. degree in genetics was granted in 1930 from Cornell University.

Sprague was elected to the National Academy of Sciences in 1968. He was affiliated with its Section 32, Applied Biology, which became Section 62, Plant, Soil, and Microbial Sciences. He was an active member and served on several ad hoc committees. From 1972 to 1975 he served as chair of the section on applied biology. One of his major activities was with the committee on genetic vulnerability of major crops (1970-72). He had a prominent role in the preparation of the monograph *Genetic Vulnerability of Major Crop Plants*, which influenced expansion of germplasm research in the United States.

George F. Sprague died on November 24, 1998, of natural causes at his home in Eugene, Oregon. His memory was lucid, and he maintained an interest in the genetics and breeding of corn up to the time of his death. He is survived by two daughters (Phyllis Lance of Iowa City, Iowa, and Judy Sprague of Eugene, Oregon), two sons (Don of Ames, Iowa, and George of Eugene, Oregon), and two grandchildren.

PROFESSIONAL HISTORY

After the completion of his graduate studies, Sprague continued his professional career as an assistant agronomist with the USDA at Arlington Farms. He collaborated with F. D. Richey, who was the senior agronomist in charge

of corn investigations for the USDA, and initiated studies on the genetics and breeding of corn. This was the start of a forty-eight-year career with the USDA. His associations with prominent geneticists and breeders at Cornell University and Arlington Farms were very influential in the development of his philosophy of the importance of research that included both theoretical and applied aspects. While he was at Arlington Farms, he also selected sixteen inbred lines that were considered to have above average root and stalk strength. He inter-mated the sixteen inbred lines to form a synthetic cultivar, designated as Stiff Stalk Synthetic. Stiff Stalk Synthetic became an important cultivar in his future professional career.

Sprague was transferred to Columbia, Missouri, in 1934 to develop a cooperative USDA-Missouri University corn improvement program. He continued his genetic and breeding studies as an agronomist. He was stationed at Columbia until 1939, when he was transferred to Ames, Iowa, as an agronomist to assume leadership of the cooperative USDA-Iowa State University corn improvement program. His transfer to Ames was influenced by the prominence of the program that had been initiated there by Merle T. Jenkins in 1922. Jenkins and Sprague had a high regard for each other and had similar philosophies and ideas for developing productive research programs. Jenkins emphasized breeding research to identify methods to effectively and efficiently develop superior inbred lines for the U.S. Corn Belt. Sprague continued and strengthened the program during the years 1939-58 with the support and encouragement of Jenkins.

The twenty years that Sprague was stationed at Ames were probably the most satisfying and productive years of his long career with the USDA. He was a collaborator in the Department of Agronomy at Iowa State University and became an active participant in research, teaching, and training of

graduate students with majors in plant breeding. Although he was not obligated to teach while he was a USDA employee at Iowa State, he organized a graduate-level corn-breeding course, which he taught for eighteen years. He had a strong interest in the graduate training of students, and the course became a core component of students with majors in plant breeding. His excellence as a teacher was recognized with a Gamma Sigma Delta Award for teaching at Iowa State. His teaching interests, however, were not restricted to the classroom. He served as major advisor to more than thirty students who completed the requirements for M.S. and Ph.D. degrees with majors in plant breeding. He supplemented classroom instruction with informal discussions that could occur anytime during research activities in the laboratory or field. Sprague maintained an open-door policy; he was always willing to discuss plant breeding with graduate students and faculty.

Sprague developed and conducted a broad research agenda while he was stationed at Ames. It was an active and exciting time in corn research, because the inbred-hybrid concept was becoming a reality, and several of the more widely grown hybrids (e.g., U.S.13, IA939, IA13) included inbred lines developed by the publicly supported breeding programs. In 1936, only 3.1% of the U.S. corn acreage was planted with hybrid seed. The superiority of the hybrids was evident during the drought years of the 1930s, and the use of hybrid seed increased rapidly with all of the corn acreage in Iowa and Illinois planted with hybrid seed by 1950. Sprague initiated a broad range of research projects to strengthen the methods used in developing hybrids and alternative uses of corn (e.g., higher amylose and increased oil content) during World War II.

Sprague was very successful in interrelating basic studies in genetics and quantitative genetics theory with applied

plant breeding. He was at an ideal location to enhance his interests to apply theory to plant breeding because of his interactions and discussions with Joseph O'Mara (geneticist), Jay L. Lush (animal quantitative geneticist), and Oscar Kempthorne (statistician and quantitative genetics theorist). Each had unique talents and interests, but they formed a solid core for advancements made in animal and plant breeding at Ames.

When Sprague transferred to Ames in 1939, he brought seeds of Stiff Stalk Synthetic, a cultivar he had started intermating at Arlington Farms. Hybrid seed corn had become a reality, but Sprague believed that development and improvement of germplasm resources were necessary to ensure consistent, incremental genetic improvement over time. Based on a previous study by Merle T. Jenkins, Sprague initiated selection, based on half-sib families with U.S.13 as a tester, in Stiff Stalk Synthetic in 1939. The source population and selection methods were very effective. From this selection, came the widely known Iowa Stiff Stalk Synthetic. Two inbreds, B14 and B37, were developed from the initial cycle of the selection started in 1939 and were released to the seed industry in 1953 and 1958, respectively. B14 and B37 were used extensively to produce hybrid seed in the United States and in other temperate areas of the world. Continued selection within Iowa Stiff Stalk Synthetic eventually became the source germplasm for inbreds B73, B84, B104, and B110.

Because of the debate on the relative importance of different types of genetic effects in the expression of heterosis observed in corn hybrids, Sprague initiated, in 1949, another selection study that included Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic No. 1, also based on half-sib family selection. Initial response for development of inbred lines was not as rapid as for the program started in 1939. But the program was continued, and inbred lines B89, B94,

B105, and B111 were developed from Iowa Stiff Stalk Synthetic and inbred lines B90, B91, B95, B97, B99, and B112 were developed from Iowa Corn Borer Synthetic No. 1.

The selection programs initiated by Sprague in 1939 and 1949 were based on the concepts of recurrent selection methods. Objectives of the recurrent selection methods were to genetically improve the base cultivars and to maintain genetic variation for continued future selection. Several recurrent selection programs were initiated at different locations throughout the United States during the 1950s to determine response to selection for different types of populations; types of progenies evaluated; and types of genetic effects important in selection. Sprague initiated selection in Krug High I Syn. 3 in 1953 to compare the relative effectiveness of inbred and half-sib family selection for population improvement; selection for specific combining ability in Kolkmeir and Lancaster open-pollinated cultivars was initiated in 1943 to compare the relative importance of dominance and overdominance in yield heterosis; and selection for specific combining ability was initiated in 1949 in the Alph open-pollinated cultivar and the F2 generation of the WF9 x B7 cross to determine the relative importance of dominance and overdominance effects in yield heterosis. In addition to developing improved germplasm through recurrent selection, Sprague designed each selection study to provide information on the relative importance of different types of genetic effects in selection response and yield heterosis. Most of the studies were continued until about 1980. General conclusions were that observed response to selection for increased grain yield was 2% to 6% per cycle, regardless of the population and selection methods used, and additive genetic effects with partial-to-complete dominance were of greater importance than overdominance and epistatic effects.

Sprague's research goals in corn breeding and genetics were primarily long-term and fundamental for development of more effective methods for corn improvement. His contributions to corn research were pervasive and well documented, having ranged from the genetics of scutellum color (1927) and heterofertilization (1932), effects of mutagenic agents (1936), aberrant ratios caused by virus infection (1971), and mutability in the a-ruq, Uq system (1984), to estimates of number of plants required to sample a corn cultivar (1939), relative importance of general and specific combining ability (1942), early testing of inbred lines (1946), inheritance of oil and protein (1949), estimates of rates of mutation (1955), effectiveness of recurrent selection methods (1952, 1961), and cytoplasmic-genic interaction (1983). Probably the most frequently cited paper is the one Sprague and Tatum published in 1942 in which the terms "general" and "specific" combining were introduced and defined. Combining ability of an inbred line was a phrase used to define the potency of an inbred line in hybrids. Sprague and Tatum partitioned the combining ability among diallel crosses of inbred lines into 1) average performance of a line in crosses with all other lines (general combining ability), and 2) performance of the cross of specific pairs of lines relative to their average performance (specific combining ability). The concepts of general and specific combining abilities stimulated theoretical research for the types of genetic effects important for each and a method to evaluate inbred lines in hybrids. The terms "general and specific combining abilities" are commonly used throughout all of plant breeding. Sprague also made lasting contributions to the importance of early testing for the evaluation of inbred lines in hybrids and to the effectiveness of the recurrent selection methods to develop germplasm resources. His stature in the corn research community was evident with

his selection to serve as editor of the corn monograph *Corn and Corn Improvement* published in 1955 (1st ed.), 1977 (2nd ed.), and 1988 (3rd ed.). This monograph became one of the best selling monographs ever published by the American Society of Agronomy.

Sprague's career changed abruptly in 1958. Merle T. Jenkins retired from the USDA, and Sprague was asked to assume leadership of corn and sorghum investigations. The change was from an active participant in an individual research project to largely one of administrator, advisor, and coordinator of the work of several research units distributed throughout the United States. He assumed the new assignment in Beltsville, Maryland, with the same intensity that he had showed in the classroom and laboratory. He wanted to expand research and attract the best possible new scientists into the corn and sorghum research programs of the USDA. He was successful in establishing new positions that emphasized basic research for the improvement of corn and sorghum. Although his primary responsibilities were as an administrator, he continued research on the genetics of corn, which he considered a release valve for the burdens of administration. He continued as investigations leader from 1958 until his retirement in 1972. At his retirement, Sprague had completed forty-eight years of employment with the USDA, starting as a junior agronomist at North Plate, Nebraska, and finishing as the leader of corn and sorghum investigations at Beltsville, Maryland.

Upon retirement, Sprague accepted an appointment as professor of plant breeding and genetics at the University of Illinois, Urbana. He resumed a more active research program and was an active participant in the corn research program. Although he did not have a formal teaching appointment, he was a willing listener and advisor of graduate students. None of the graduate students, however, was

able to either hand plant or hand harvest corn as quickly as Sprague. Sprague continued at the University of Illinois until 1994, and he made positive contributions until his final retirement. Although more than ninety years old, he was always looking to the future to determine what methods, techniques, and germplasm could be used for the genetic improvement of hybrids provided to the producers.

PUBLIC SERVICE

Research and administrative responsibilities were Sprague's primary interests, but he was active in his professional societies: the American Society of Agronomy, Crop Science Society of America, American Genetic Association, and the National Academy of Sciences. In addition to being an active member of several committees of these societies, he served as vice-president and president of the American Society of Agronomy (1960), president of the Crop Science Society of America (1961), and chairman of the section on applied biology (1972-75) of the National Academy of Sciences. He was a charter member of the National Plant Genetics Resources Board, formed in 1975 as an advisory committee on plant germplasm to the U. S. Secretary of Agriculture. Sprague was reappointed twice and served three consecutive terms, the maximum permitted by law. While a member of the board, he strongly advocated that the collection and preservation of germplasm must be accompanied by evaluation and enhancement to realize the full potential of the program. He also served about ten years on the Maize Crops Advisory Committee, a committee to develop and provide guidance for a national plan for corn germplasm enhancement.

FOREIGN SERVICE

Sprague actively assisted with food production in other areas of the world. He was a consultant to the Rockefeller

Foundation for many years. He worked with E. J. Wellhausen on corn-breeding and training programs to assist corn breeders in Latin America. He served on a special mission for the development of hybrid corn-breeding programs in Europe sponsored by the Marshall Plan and assisted the USDA advisement on the hybrid corn program for Yugoslavia. In 1963, he was given the responsibility by the U. S. Agency for International Development to lead and organize an effort for increasing production of major cereal crops in Africa. A research station was established at Kitale, Kenya, to assist Kenya and surrounding countries. He was leader of the joint USAIDAR project from 1963 to 1972. Sprague believed hybrid corn could be used in developing countries, and a program was planned that included germplasm enhancement and development of adapted hybrids. Hybrids were grown in 1964 in Kenya, and with improved production practices, corn production was doubled. Sprague also was a member of the first U.S. delegation of agricultural scientists to be invited to visit China in the early 1970s. Sprague's advice and counsel were widely sought internationally, and he visited all areas of the world where corn was an important crop.

HONORS AND AWARDS

1947 Fellow, American Society of Agronomy
1957 Gamma Sigma Delta Award, Iowa State University
Crop Science Research Award, American Society of Agronomy
1958 Faculty Citation, Iowa State University Alumni Association
Honorary Doctor of Science Award, University of Nebraska
1959 Distinguished Service Award, U. S. Department of Agriculture
1960 Academica Correspondente, Academia Nacionale de Agricoltura, Bologna, Italy
1963 Fellow, American Association Advancement of Science
1965 Superior Service Award, U. S. Department of Agriculture
1968 Fellow, Washington Academy of Sciences
Member, National Academy of Sciences
1972 Crop Breeding Award, National Council of Commercial Plant Breeders
1978 Wolf Prize in Agriculture, Wolf Foundation, Israel
1980 DeKalb Career Award, Crop Science Society of America
1984 Fellow, Crop Science Society of America
1997 Honorary Member, American Society of Agronomy

THREE SOURCES OF information were excellent aids to summarize the long career of George F. Sprague: *Der Züchter-Genetics and Plant Breeding* 37(4):149-50 by H. F. Robinson; *Maydica* 29(4):351-55 by A. R. Hallauer; and *Plant Breeding Reviews* 2:1-11 by W. A. Russell. Personally, I first met George F. Sprague in 1956 when he accepted me as a graduate student in corn breeding. He was my advisor for my M.S. degree and was my supervisor as a USDA employee from 1958 to 1972. His years as my mentor were instructive, positive, and enlightening, and provided me a unique insight to his thinking for my research in corn breeding and genetics.

SELECTED BIBLIOGRAPHY

1927

Heritable characters of maize XXVII colored scutellum. *J. Hered.* XVIII:41-44.

1929

Heterofertilization in maize. *Science* LXIX:526-27.

1931

With F. D. Richey. Experiments on hybrid vigor and convergent improvement in corn. USDA Technical Bulletin 267.

1932

The inheritance of colored scutellum in maize. USDA Technical Bulletin 292.

1934

Experiments on iarovizing corn. *J. Agr. Res.* 48:1113-20.

1936

Hybrid vigor and growth rates in a maize cross and its reciprocal. *J. Agr. Res.* 53:819-30.

1939

An estimation of the number of top-crossed plants required for adequate representation of a corn variety. *J. Am. Soc. Agron.* 31:11-16.

1942

With L. A. Tatum. General vs. specific combining ability in single crosses of corn. *J. Am. Soc. Agron.* 34:923-32.

1943

With B. Brimhall and R. M. Hixon. Some effects of the waxy gene in corn on properties of the endosperm starch. *J. Am. Soc. Agron.* 35:817-22.

1945

With M. L. Kinman. Relation between number of parental lines and theoretical performance of synthetic varieties of corn. *J. Am. Soc. Agron*. 37:341-51.

1946

Early testing of inbred lines of corn. *J. Am. Soc. Agron*. 38:108-17.
The experimental basis for hybrid maize. *Biol. Rev*. 21:101-20.

1947

With W. T. Federer. A comparison of variance components in corn yield trials. 1. Error, tester x line and line components in top cross experiments. *J. Am. Soc. Agron*. 39:453-63.

1949

With B. Brimhall. Quantitative inheritance of oil in the corn kernel. *Agron. J*. 41:30-33.

1950

With B. Brimhall. Relative effectiveness of two systems of selection for oil content of the corn kernel. *Agron. J*. 42:83-88.

1951

With W. T. Federer. A comparison of variance components in corn yield trials. II. Error, year x variety, location x variety and variety components. *Agron. J*. 43:535-41.

1952

Early testing and recurrent selection. In *Heterosis*, ed. J. W. Gowen, pp. 400-417. Ames, Iowa: Iowa State College Press.

1955

With J. F. Schuler. Natural mutations in inbred lines of maize and their heterotic effect. II. Comparison of mother line vs. mutant when outcrossed to unrelated inbreds. *Genetics* 41:281-91.
Corn breeding. In *Corn and Corn Improvement*, ed. G. F. Sprague, pp. 221-92. New York: Academic Press.

1956

With W. A. Russell. Some evidence on type of gene action involved in yield heterosis in maize. In *Proceedings of the International Genetics Symposia,* pp. 522-26. Tokyo: *Cylologia*.

1971

With H. H. McKinney. Further evidence of the behavior of AR in maize. *Genetics* 67:533-43.

1974

Plant breeding, molecular genetics and biology. NAS-NRS Conference on Genetic Improvement of Seed Proteins. Washington, D.C.: National Academy of Sciences.

1976

Plant breeding, molecular genetics and biology. In *Genetic Improvement in Seed Proteins*. Washington, D.C.: National Academy of Sciences/National Research Council.

1980

With D. E. Alexander and J. W. Dudley. Plant breeding and genetic engineering: A perspective. *BioScience* 30:17-21.

Germplasm resources of plants: Their preservation and use. *Annu. Rev. Phytopathol.* 18:147-65.

1983

Heterosis in maize: theory and practice. In *Heterosis: Monographs on Theoretical and Applied Genetics*, ed. R. Frankel, Chapter 2. Berlin: Springer-Verlag.