NATIONAL ACADEMY OF SCIENCES

DONALD FORSHA JONES

1890—1963

A Biographical Memoir by

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April 16, 1890–June 19, 1963

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IF THERE were a Nobel prize in agriculture as there is in medicine, it would undoubtedly have been awarded many years ago to Donald F. Jones for his part in the development of hybrid corn.* This is an achievement in applied genetics that has sparked an agricultural revolution in the United States. It has affected agricultural production in many other parts of the world as well, including the countries of Latin America, where corn is the principal source of food, and those of southern Europe, where corn is an important crop. To this monumental achievement Dr. Jones made four distinct contributions.

Jones's most practical contribution was the invention in 1917 of the double-cross method of hybrid seed production. George H. Shull had shown previously that self-pollination in corn, a naturally cross-pollinated plant, resulted in the isolation of inbred strains that were uniform and true breeding. Following Johanssen, he called these "pure lines." They were much less vigorous than the open-pollinated varieties from which they had been derived. However, when two such lines were crossed, the F_1 hybrids were uniform, like their inbred parents, but much more vigorous and in some cases more productive than

* Since this was written, a notable contribution to agriculture has been recognized by the award in 1970 of the Nobel Peace Prize to Dr. Norman E. Borlaug for his work on the breeding of highly productive new dwarf varieties of wheat for the underdeveloped regions of the globe.

the original open-pollinated varieties. Shull recognized that he had discovered a revolutionary new method of corn breeding, and he made determined efforts to persuade agronomists to adopt and practice it, but with little success. Shull's method of crossing two inbred strains had one serious shortcoming: The hybrid seed was borne on the weak, unproductive plants of the inbred strains used as the female parents. Since production was low, the hybrid seed was costly—too expensive for the average farmer to afford. Edward M. East, who independently of Shull, had observed the effects of inbreeding and crossbreeding in corn, doubted that the crossing of inbred strains to produce hybrid seed would ever become practical.

East, who had participated for several years in the famous experiments at the University of Illinois on selection for chemical composition of corn, initiated a corn-breeding program at the Connecticut Agricultural Experiment Station in New Haven in 1905. When East moved to the Bussey Institution of Harvard as a professor in 1909 he was succeeded by Herbert K. Hayes, who had been his assistant in New Haven and later became his graduate student at Harvard. When Hayes accepted a position at Minnesota, Jones, then a graduate student at Harvard, took charge under East's direction of the Connecticut corn program. He moved to New Haven early in 1915.

During his first year at New Haven Jones did little more than maintain the experiments that East and Hayes had initiated. But later, impressed by the weakness of the inbred strains and their feeble production of grain and by the vigorous production of their single crosses, he decided to try crossing two of the single crosses. Thus in 1917 he crossed the single cross of two strains of Chester's Leaming with a single cross of two strains of Burr White. Grown in 1918 this cross, which later came to be known as a "double cross," yielded more than either of its single-cross parents and considerably more than the best open-pollinated varieties.

Jones recognized that double crosses offered a means of producing hybrid seed corn at a cost within the means of progressive farmers. This fact was then quickly recognized by other corn breeders, including Henry Wallace, H. K. Hayes, and F. D. Richey. Within a few years corn-breeding programs, including the isolation of inbred strains and testing of single and double crosses, had been initiated by the U.S. Department of Agriculture and many of the state experiment stations. By 1933 hybrid corn was in commercial production on a substantial scale, and the USDA began to collect statistics on it. By 1949, 78 percent of the total U.S. corn acreage was planted in hybrid corn. By 1959, more than 95 percent was in hybrid corn, and the average yield of corn in the United States was double that of 1929.

Ironically, it turns out that Jones was not the first to make double crosses in corn. At the Heterosis Conference held in Ames, Iowa, in 1950 Shull reported that he had made a number of such crosses in 1910 and grown the hybrids in 1911. One of these crosses yielded considerably more than any of the single crosses. Shull, however, apparently saw no particular significance in the fact at that time; in 1950 he asked no credit for making double crosses before Jones and reported it only as a historical fact.

Ironically, too, once the use of double crosses established the production of hybrid corn on a highly successful scale, corn breeders found that, by developing more vigorous inbred strains than those isolated by Shull, East, and Jones, it was possible to employ single crosses instead of double crosses in the production of hybrid seed corn. Today much of the hybrid corn in the United States is represented either by single crosses or by three-way crosses, the latter being crosses of single crosses by inbred strains.

It is obvious that hybrid corn, which has revolutionized the production of corn in the United States and other parts of the world, is a method of exploiting hybrid vigor or heterosis. Thus heterosis must be considered, along with replication of the hereditary material (DNA) and photosynthesis, one of the three principal biological phenomena underlying the practice of agriculture. What, then, is the genetic basis of heterosis?

In the same year, 1917, that Jones made his first double cross, which solved the problem of hybrid seed corn production, he published a theory explaining the phenomenon of heterosis. He was at that time twenty-seven years old. Jones's theory applied the concept of chromosomal linkage of Morgan and his students to the earlier concrete explanation of hybrid vigor by Keeble and Pellew. These last two had explained the increased height of a cross of two varieties of peas over their parents in Mendelian terms. It was linkage that explained why it was not possible to combine in one race the favorable dominant factors of both parents.

Jones's theory probably gave as much stimulus to hybrid corn breeding as did his double-cross method of seed production. Hybrid corn became a practical reality when his method of seed production made it feasible and his theory of heterosis made it plausible. This combination was difficult for even the most conservative agronomists to resist. Seldom in the history of agriculture has one man made two such significant contributions, one in theory and the other in practice.

A third contribution to hybrid corn production was one in which I had the privilege of participating. It involves a method of employing cytoplasmic male sterility, of a type first described in corn by Marcus M. Rhoades, to avoid the operation of emasculation, commonly known as "detasseling," in the seed-production fields. Detasseling has been called the "peskiest and most expensive part of producing hybrid seed corn." Before cytoplasmic sterility was employed to avoid it, some one hundred and twenty-five thousand workers were engaged on the peak day of the season in removing tassels from corn plants.

By employing cytoplasmic male sterility, it was possible to eliminate as much as two thirds of the detasseling operation. To ensure fertility in the farmer's crop, sterile hybrids were mixed with fertile hybrids, involving the same inbred strains, produced in the conventional way.

Jones made still another contribution to hybrid corn production when he employed fertility-restoring genes to overcome the cytoplasmic sterility in the farmer's crop. This method employs hereditary factors in the cytoplasm to make corn sterile when sterility is a distinct asset and uses hereditary factors on the chromosomes to make it fertile when fertility is essential. A patent on the method of using genetic restorers in hybrid-seed-corn production was issued to Jones in 1956. It was the first patent on a genetic technique to be granted in the United States. The validity of the patent was challenged by the seed corn industry, but finally, after long and extensive litigation, an amicable agreement was reached: The patent's validity was generally accepted, and royalties on its use were paid.

For many years the method of employing cytoplasmic male sterility to avoid the operation of detasseling and using fertility-restoring genes to overcome this sterility in the farmer's crop was phenomenally successful. It not only drastically reduced the labor required in producing hybrid seed but also eliminated the reduction in yield of hybrid seed caused by the removal of one or more leaves in the detasseling operation. The method has probably been a factor also in making possible on an extensive scale the replacement of double crosses by higher-yielding single crosses. There is a danger—susceptibility to plant diseases—inherent in growing these genetically uniform hybrids, as Jones pointed out in an article in *American Naturalist* in 1958. But their use, combined with increased applications of fertilizer, to which the new hybrids were responsive, has undoubtedly contributed to the spectacular increase in average yields in the decade 1959–1969. This is shown in the following table, which also demonstrates the remarkable progress that has occurred between 1929 and 1969 in increasing yields of corn in the United States.

Acre Yields of Corn in the United States

Year	Percent Hybrid Corn	Bushels per Acre	Percent Increase over Previous Decade
1929	0	25.7	
1939	22.9	29.7	16
1949	78.3	37.8	27
1959	94.8	51.5	36
1969	99+	80.0	55

Eventually, however, the method became, at least for several years, the victim of its own success. In 1969 there were reports that corn hybrids carrying the Texas cytoplasmic male sterility, the type almost universally employed, were becoming susceptible to the southern corn blight fungus, *Helminthosporium maydis.* Since susceptibility to a disease determined by the cytoplasm had never previously been observed in the United States, these reports were met with skepticism on the part of some plant pathologists. In 1970, however, the blight, apparently a new mutant strain, spread over the entire eastern half of the United States. It caused a reduction in corn yields for the country as a whole of about 13 percent. Many fields in the southern states, where the infection occurred early in the season, suffered losses of 50 percent or more. Single and three-way crosses suffered greater damage from the blight than double crosses, as Jones some twenty years earlier had warned that they would when faced with a new hazard. The use of fertility-restoring genes proved not to be a factor in the susceptibility of corn hybrids to the blight. As soon as other types of cytoplasmic male sterility can be introduced into commercial hybrids, it is probable that the method will again be commonly employed.

In the meantime the blight, despite its destructive effects on the 1970 corn crop, has had one beneficial result. It has focused new attention on the importance of genetic diversity in the world's major food crops. The new dwarf varieties of wheat and rice that are revolutionizing the agriculture of underdeveloped countries have, in the case of each of these crops, dwarfing genes in common, although they are diverse in their remaining heredity. These common genetic loci may, like the universally used cytoplasmic male sterility in corn, become susceptible to new mutant pathogens with disastrous results in countries and regions already overpopulated. Recognizing this danger, the National Academy of Sciences in 1970 came forward with a proposal to study not only the problem of the corn blight, but also the genetic vulnerability of major food crops in general. The study was financed in large part by Research Corporation, to which Dr. Jones assigned his patent on the use of fertility-restoring genes, and with particular appropriateness by the Donald F. Jones Fund, which represents the corporation's share of the net proceeds from the Jones patent. The results of this study, published in 1972 in a volume entitled *Genetic Vulnerability of Major Crops,* emphasized the fact that "most major crops are impressively uniform and impressively vulnerable." Thus Donald F. Jones has left a heritage that continues to affect in tangible ways the course of applied genetics to which, while living, he made such notable contributions.

Jones's conviction that selection in self-fertilized lines is one of the most effective plant breeding methods that can be practiced in cross-pollinated plants, and his interest in exploiting heterosis was not confined to corn. During the period from 1921 to 1926, when I served as his assistant, he undertook breeding programs in numerous field and horticultural crops, including such diverse crops as alfalfa and asparagus, and strawberries and squashes. Later, when it became apparent that the use of cytoplasmic sterility in corn was becoming a resounding success, he encouraged breeders of other field crops to search for forms of cytoplasmic male sterility in the species to which they were giving attention. The success of hybrid corn also led to the exploitation of hybrid vigor in animals, especially chickens, pigs, and cattle.

Jones's research was by no means confined to practical plant breeding. His interest in theoretical genetics was as keen as his concern with crop improvement. I have mentioned his theory of heterosis. For a number of years he studied and wrote extensively on somatic segregation, especially in its relation to various kinds of atypical growths. Another subject to which he gave attention was sex differentiation in maize and other plants. In this connection he succeeded in converting maize—which is normally monoecious, having both sexes on the same plant, into a dioecious form having the two sexes on separate plants. From this he concluded that monoecism may be an intermediate step between perfect flowers and dioecism.

Donald Forsha Jones was born near Hutchinson, Kansas, on April 16, 1890. He was the second of four children of Oliver Winslow Jones and Minnie Wilcox Bush Jones. Both parents were descendants of New England families. The Winslow in Jones's father's name traces back to Kenelm Winslow, who came to Plymouth, Massachusetts, in 1629. His maternal ancestors were among the early settlers who founded Hartford, Connecticut. Jones, in one biographical sketch, has been aptly called "a Yankee from Kansas."

At the time of their marriage both parents were schoolteachers. The family subsequently moved to Mulvane, Kansas, and later to Wichita, where the father continued as a teacher and a school principal. Their home, a small farm on the outskirts of Wichita, had ample space for gardening and for a horse, a cow, a pig, and a flock of chickens. Donald and his older brother, Kenneth, later a professor at Northwestern University Medical School, had a newspaper delivery route for several years that required their getting up before daylight, hitching the horse to the buggy, and completing their deliveries in time to have breakfast at home. The family garden became Donald's special responsibility, and he tried to grow some of virtually everything. His boyhood interest in gardening was to persist throughout his life. He was an ardent and talented gardener. Even after a day's work in the experimental corn field during the summer months he was not too tired to spend the evening in his own garden. His gardening included a wide variety of vegetables, small fruits, and ornamentals, all of which responded to his gardening skill. Many of the popular articles on horticulture that he wrote were based on his own firsthand gardening experience.

After completing his secondary school education, Jones attended Kansas State Agricultural College, where he majored in horticulture. His college years apparently were neither particularly inspiring nor enjoyable, and he was not regarded as an outstanding student. However, one of the honors that he cherished most in his later years was an honorary degree, Doctor of Science, awarded to him in 1947 by his alma mater.

Graduating from college in 1911, he took a position at the Arizona Experiment Station, where one of his principal jobs was pollinating alfalfa flowers in a breeding program. He once spoke disparagingly of his role in this position as "taking the place of the bumble bee." While there he read the recently published bulletin by East and Hayes, "Heterozygosis in Evolution and Plant Breeding." Having already observed the effects of inbreeding on alfalfa, he found this publication of unusual interest, and he wrote to East inquiring about the possibility of doing graduate work at Harvard under East's direction. In the meantime, however, he took a position at Syracuse University, where he spent the year 1913–1914 teaching and working toward the master's degree. He enrolled as a graduate student at Harvard in the fall of 1914. In February 1915 he moved to New Haven to take charge under East's supervision of the plant-breeding program, which had been initiated by East in 1905 at the Connecticut station. For the next several years he divided his time between New Haven and Cambridge

Jones remained at the Connecticut Agricultural Experiment Station for the rest of his professional life, and this continuity of effort was undoubtedly one factor in his lifelong productiveness in research and publication. His technical scientific publications cover a period from 1915 to 1964 and include approximately one hundred titles. In addition he wrote many popular and semipopular articles covering a wide variety of subjects for the farm and garden press. When I joined him as a graduate assistant in 1921, he advised me also to write for these media, partly in the interest of informing the general public on new developments in agricultural science and partly as practical experience in writing, which for me it proved indeed to be.

An inveterate reader as well as a prolific writer, Jones, during the winter months, usually spent his mornings writing and reading scientific literature. His evenings at home, except during the summer when he worked in his garden until darkness, were most commonly spent in reading. Among his favorite subjects were biography and history. Even his luncheon periods were devoted partly to reading. Alternating in reading aloud to each other, he and I, in the years between 1921 and 1926, went through various works, including Darwin's *Voyage of the Beagle.*

One of the most unusual aspects of Jones's career was his close and congenial collaboration for a number of years with Edward M. East, his graduate-school mentor. The two men were quite different in temperament. Henry Wallace once described East as "sardonic, explosive, genial, intolerant, charming, stimulating." Jones was modest, soft-spoken, patient, retiring, slow to anger, tolerant, and wise. What they did have in common were keen intellects, and each admired that of the other. When Jones proposed his theory of dominant-linked factors to account for heterosis, East was so impressed that he asked his student, then still in his twenties, to join him in writing the book that he had for several years been planning on the effects of inbreeding and crossbreeding. The product of their joint efforts, *Inbreeding and Outbreeding: Their Genetic and Sociological Significance,* is one of the classics in the history of genetics. A joint paper of East and Jones, "Genetic Studies on the Protein Content of Maize," published in 1917, showed how effective selection in self-fertilized lines can be in changing the characteristics of a population. This paper was also one of the first to describe a method of breeding now known as "recurrent selection." The method has proved to be quite effective, not only in changing chemical composition but also in improving the combining ability of inbred strains. Both men were intellectually stimulating. I have always counted it rare good fortune to have had both as mentors, one in my work as a graduate assistant and the other in my graduate studies.

Like many another Yankee, Jones was almost instinctively inventive. His inventions ranged from the double cross, which made the production of hybrid seed corn practical, to innumerable small devices around his laboratory and home. One of his students once remarked that if a rootless corn plant were to turn up in his cultures, Jones would find some good use for it. This he never did, but he found an immensely practical use for cytoplasmic male sterility and for the genetic fertility-restoring factors. The latter had been in part responsible for the failure of a number of earlier corn breeders to make use of cytoplasmic sterility in avoiding detasseling.

Also from the program in applied genetics that Jones directed for some forty years came one of the important recent developments in corn improvement, the breeding of high-lysine hybrid corns. This development owes its beginning to a mutant, *opaque-2,* that affects the composition of the endosperm. Dr. Jones's associate, Dr. Ralph Singleton, had found the mutant in a New England variety of white flint corn in the early 1920s and had determined its genetic linkage relations. Jones continued to maintain a stock of *opaque-2* in hopes that this unusual characteristic would some day prove useful. His hope was realized when one of his former students, Oliver Nelson of Purdue University, with his colleague Edwin Mertz, showed that the endosperm of *opaque-2* contains about twice as much lysine and tryptophan—amino acids in which maize is notoriously deficient—as normal corn. *Opaque-2* is now the subject of numerous breeding programs in the United States and the countries of Latin America to increase the useful protein content of maize. Already, nutritional trials in Colombia have shown that advanced cases of kwashiorkor in children can be cured with a diet in which the sole source of protein is *opaque-2.* Jones was indeed a man of many dreams with a remarkable ability to make his dreams come true.

An effective worker in advancing the science of genetics, Jones served in several capacities. Before the Genetics Society of America was organized, he was secretary of the Genetics Section sponsored jointly by the Botanical Society of America and the American Society of Zoologists. Later, in 1934, he was vice president of the Genetics Society and president in 1935. He was editor of the *Proceedings of the Sixth International Congress of Genetics,* held at Ithaca, New York, in 1932. He was the second editor of *Genetics* and served from 1926–1935, longer than any other editor except George H. Shull, its founder, and during the especially exciting period of genetic research when the chromosome theory of heredity was becoming firmly established.

In Jones's later years, in addition to his duties at the Connecticut Station, he was a lecturer in genetics at Yale University and at the University of Connecticut. He was Sprague Memorial Lecturer at Michigan State College in 1935; research fellow at California Institute of Technology in 1935–1936 and again in 1946–1947; and visiting professor at the University of Washington in 1953.

Jones was the recipient of many honors. He was elected to the American Academy of Arts and Sciences in 1934, to the National Academy of Sciences in 1939, and to honorary membership in the Societa Italiana Genetica Agraria in 1955. I have already mentioned the honorary degree that he received from his alma mater in 1947. The accompanying citation reads:

"As a major contributor to the development of hybrid corn . . . he has conferred immense benefits upon a hungry world. As research scientist, teacher, and leader in scientific societies, he has inspired his colleagues and students by . . . his extraordinary achievements . . ."

The New England Council and the Governors of New England made him a charter member of the "Fellowship of Agricultural Adventurers," saying that,

"with an imagination which delved below and soared above the findings of his predecessors, he translated the learning of the laboratory into the fruitfulness of the field."

He was awarded gold medals by the Massachusetts Horticultural Society and the American Farm Bureau. In addition he was given awards by the Connecticut State Confederation of Women's Clubs, the American Seed Trade Association, the Connecticut State Grange, the New York Farmers' Club, and the Botanical Society of America.

Dr. Jones died at his home in Hamden, Connecticut, on June 19, 1963. He is survived by his wife, Eleanor March Jones, a son, Loring M. Jones, and a daughter, Mrs. Margaret Owen.

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KEY TO ABBREVIATIONS

Am. J. Bot. = American Journal of Botany
Am. Nat. = American Naturalist
Biol. Bull. = Biological Bulletin
Bot. Gaz. = Botanical Gazette
Conn. Agric. Exp. Stn. Bull. = Connecticut Agricultural Experiment Station Bulletin
Conn. Agric. Exp. Stn. Circ. = Connecticut Agricultural Experiment Station Circular
Conn. Agric. Exp. Stn. Rep. = Connecticut Agricultural Experiment Station Report
J. Am. Soc. Agron. = Journal of the American Society of Agronomy
J. Hered. = Journal of Heredity
Proc. Natl. Acad. Sci. = Proceedings of the National Academy of Sciences
Proc. ——— Int. Congr. Genet. = Proceedings of the ——— International Congress of Genetics
Sci. Mon. = Scientific Monthly
Seventh Int. Manage. Congr. = Seventh International Management Congress

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