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OLIVER EVANS NELSON JR.
1920–2001

A Biographical Memoir by

CURT HANNAH, BEN BURR, AND HUGO DOONER

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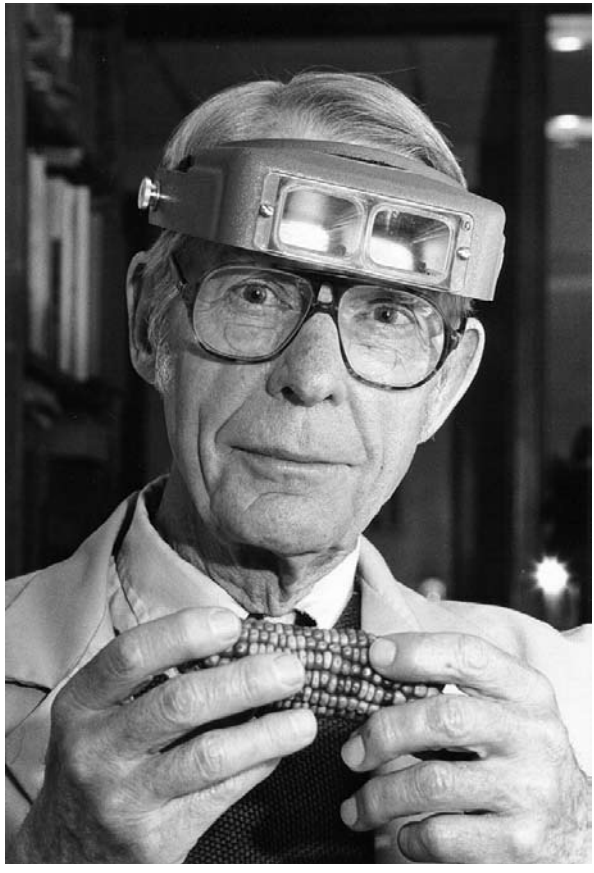
Biographical Memoir



Ronald Reagan

OLIVER EVANS NELSON JR.

August 16, 1920–November 6, 2001

BY CURT HANNAH, BEN BURR, AND HUGO DOONER

NOTED MAIZE GENETICIST Oliver Nelson of the University of Wisconsin died in a Madison hospital on November 6, 2001, after a long battle with both osteoporosis and Parkinson's disease. Having become acutely ill that afternoon, Oliver refused transport to the hospital in order to finish the communication of a paper concerning enhanced starch synthesis to the *Proceedings of the National Academy of Sciences*. He died soon after reaching the hospital. He was survived by his wife Gerda (née Hansen), whom he had married in 1963 and who supported him steadfastly during the last difficult years of his life. Gerda passed away in Madison in 2010.

Oliver Evans Nelson Jr., the first child of Oliver Evans Nelson and Mary Grant Nelson, was born in Seattle, Washington, and raised in the vicinity of New Haven, Connecticut, an area that remained dear to his heart and that he would reminisce about with great fondness. Oliver first experienced maize genetics as a summer high school assistant in the Department of Genetics at the Connecticut Agricultural Experiment Station. He graduated from Colgate University magna cum laude in botany at the age of 21 and subsequently received his M.S. and Ph.D. degrees from Yale University under the direction of the renowned plant breeder D. F. Jones.

Oliver joined the faculty at Purdue University as an assistant professor in 1947 and was promoted to professor in 1954. To the great delight of R. A. Brink and to the chagrin of his Purdue colleagues, Oliver left for the University of Wisconsin-Madison in 1969. Oliver spent the rest of his career in Madison, having "retired" to emeritus status in 1991.

Throughout his long career, Oliver pursued many aspects of maize genetics and biochemistry. Initially hired at Purdue as a popcorn breeder (at which he was quite successful—some of his better lines were used in the popcorn industry long after he ended his breeding efforts), he found that most popcorn lines carried the *Ga1-s* allele and as such were cross-incompatible with dents, carrying the *ga1* allele, when used as females (1952). This discovery led to a systematic study of the *ga1* locus. With L. R. House he showed that nonreciprocal cross-sterility was the result of poor *ga1* pollen tube growth on *Ga1-s* silks.

Oliver soon focused on the *waxy1* locus to address questions of fundamental importance to biologists of the time, as well as to test predictions about transposable elements then in vogue. Exploiting the finding of R. A. Brink and M. Demerec that the *wx1* gene functions in the male gametophyte, Oliver realized that pollen populations of sufficient size to detect rare recombination within the gene could be quickly examined. If independent mutations of the *waxy* gene occurred at different sites, he could place these relative to each other by constructing a fine structure recombination map through the occurrence of rare wild-type recombinant grains (1962,1). Looking at 50,000 pollen grains at a time, he first showed that no wild-type pollen grains could be observed in plants that had two copies of the same *waxy* allele, but that rare blue-black staining grains could be observed at frequencies 0 to 80 per 100,000 in plants heterozygous for two independent *waxy* alleles. Characteristically, he also showed for one of these

combinations that he could observe the same frequency of recombination in the seed. As he used stocks with flanking markers in this important control, this also allowed him to orient the mutations he was mapping relative to the other genes on the chromosome. Even though the frequency of recombination was not additive across the locus, he was able to construct his map using overlapping deletions. All told, the sites of 31 *waxy* mutants were mapped in this way. Among them were a number of stable transposable element-induced alleles. Oliver showed that these were distributed throughout the locus rather than being concentrated in a control region at one end of the gene (1968). The construction of the first fine structure map of a plant gene, plus that done with the *rosy* locus of *Drosophila*, provided us with the most detailed glimpse of the structure of a higher organism gene before DNA sequencing. When the *wx1* gene was cloned, Wessler and Varagona[1] remapped 13 of the mutants at the DNA level. An excellent correlation between the genetic and physical maps was observed.

Oliver considered himself a biochemical geneticist. He began his career at a time when there was great excitement to learn how genes worked and what they could tell us about biochemical pathways. Oliver saw no reason that such studies could not also be pursued in higher plants. Since starch was the major component of corn seed, it stood to reason that mutations affecting starch synthesis would have a visible mutant phenotype. He and his colleagues conducted a systematic investigation of the deficiencies of a number of kernel mutations and over the course of three decades identified the biochemical defects associated with eight starch mutants: *wx1, sh1, sh2, sh4, bt1, bt2, du1,* and *su1*. Placing these mutants in the biochemical pathways allowed us to have a better understanding of how starch synthesis occurs in the corn kernel. This accomplishment is made even more impressive

when one realizes that virtually all of this was done before recombinant DNA methodology was commonplace.

The starch work produced a number of firsts. Identification of the lesion with *wx1*, a starch-bound ADP-glucose glucosyl transferase, to our knowledge represented the first case in a higher plant in which the biochemical lesion of a gene with a visible mutant phenotype was elucidated (1962,2). At the pathway level the work with *wx1* provided the first and unexpected demonstration that amylose, the straight-chained glucose polymer is not a precursor for the branched polymer of glucose, amylopectin, a fact still not presented correctly in many plant physiology textbooks.

The elucidation of the enzyme associated with *su1*, together with subsequent cloning and characterization of the gene in the Myers-James lab at Iowa State University[2], showed that debranching of alpha 1,6 bonds in starch is essential for the synthesis of wild-type levels of starch (1984,2). This, too, was not expected, given the then current view of starch synthesis. The cloning and identification of the protein associated with *bt1* (1991), coupled with subsequent physiological/biochemical studies at Penn State University, provided the first definitive evidence that ADP-glucose, the precursor for starch, is synthesized in the cytosol (and not in the plastid) in the cereal endosperm.

As mentioned, Oliver's pursuit of *wx1* was aimed initially at understanding the nature of the relationship between the gene and its associated transposable elements. This interest persisted throughout his career at Wisconsin. This line of investigation, first involving studies of the *sh2* locus (1976) and subsequently much more detailed studies with the *bz1* gene (1977), also led to a number of first observations. These included the first reports that inserted transposable elements led to the production of a structurally altered protein. This was as expected if the elements were inserted throughout the

gene—as shown in his *wx1* recombination investigations—but was contrary to the idea originally proposed by McClintock that transposable elements act as normal regulatory elements of gene expression. Another first was the report that excision events led to a heterogeneous group of revertant alleles that displayed different protein properties, thus anticipating the alterations in coding regions created by transposon excision. These insights came before the application of recombinant DNA methodology to the study of transposable elements.

In the 1980s when the tools of molecular biology made it possible to address questions at the DNA level, Oliver's interest shifted to the transposable elements themselves. In another first that immediately became classic work, his lab in collaboration with Nina Fedoroff's isolated for the first time a plant gene by the novel procedure of transposon tagging (1984,1). The maize elements have been subsequently exported to other species and have revolutionized gene isolation procedures not only in maize but also in other plants. The second main contribution from Oliver's lab during his last decade of activity, and one that involved perhaps the largest number of students and postdocs that he had at any one time in his career, was the elucidation of many of the changes that these highly unstable elements are capable of undergoing (1988).

Perhaps the greatest acclaim given to Oliver came for work done during the period from 1962 to 1969. These studies, done primarily in collaboration with Ed Mertz of Purdue University, showed that levels of the essential amino acids, lysine, and tryptophan, could be enhanced by mutation (1964, 1965,1,2). The discovery that certain amino acids were enhanced in *opaque2* and *floury2* was of tremendous importance to maize-breeding programs; however, problems of kernel softness and yield drag precluded early use in the corn industry. Only now, through development of modified

opaque maize, or QPM, is the *o2* mutation being incorporated into corn lines of commerce.

A little-known fact about the early *opaque2* and *floury2* work exemplifies Oliver's uncanny ability to investigate biology through mutant analysis. Before the understanding of *o2* and *fl2,* biochemists at Purdue were massively screening, with little success, maize lines for amino acid content. Oliver knew that lines selected at the University of Illinois for enhanced protein content exhibited an enhanced level of zeins. Because zeins contain little to no lysine, these lines were of little value for feeding monogastric animals. These lines also exhibited a translucent phenotype. Oliver reasoned that mutants with the opposite phenotype (opaque) might have reduced zein content. If nonzein proteins increased, lysine content would increase. Accordingly, four opaque mutants were analyzed: *o1, o2, fl1,* and *fl2.* Lysine was doubled in two of the four mutants.

In addition to his many research accomplishments, Oliver was a tireless worker for the maize genetics community. When the site for the meetings of the Maize Genetics Group moved from Allerton House in central Illinois to various sites in Wisconsin and the Chicago area, Oliver generously played a major role in hosting the meetings. He chaired and wrote "A Standard For Maize Genetics Nomenclature,"[3] which remains largely unchanged today. Oliver also served as chair of the Laboratory of Genetics at UW-Madison, an associate editor for *Plant Physiology*, and devoted more than his fair share of time to grant panels in Washington.

Oliver won many prestigious awards during his career. These included election to membership the National Academy of Sciences in 1972; an honorary doctorate of agriculture from Purdue University in 1973; the Thomas Hunt Morgan Medal from the Genetics Society of America in 1997; the Stephen Hales Prize from the American Society of Plant

Physiologists in 1998; the Herbert Newby McCoy Award and the John Scott Medal in 1967; and the Holblitzele National Award in Agricultural Sciences and the Commemorative Medal of the Federal Land Bank System in 1968.

Oliver was reserved, unfailingly courteous, rigorously honest, and forthright. He was an insightful and observant scientist. His strength was the use of genetics—mutant phenotypes and segregational analysis—to answer biologically and agronomically important questions. This careful and perceptive analytical bent of his was the hallmark of his career. Oliver played an instrumental role in maize genetics, plant biology, and the maize genetics community. He taught by example. He influenced our choice of a lifelong career with the corn plant and he gave us an everlasting appreciation of the values of Mendelism and appropriate controls. Not only was he a mentor to the three of us in the early stages of our careers he also continued to provide guidance, advice, wisdom, and an unconditional friendship to us throughout the rest of his life.

NOTES

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