Stanley J. Peloquin

1921–2008

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
Philipp W. Simon

NATIONAL ACADEMY OF SCIENCES

STANLEY JOHN **PELOQUIN**

July 22, 1921–July 27, 2008

Elected to the NAS, 1984

By Philipp W. Simon

Stanley John Peloquin, the son of French-Canadian immigrants, was born in Barron, Wisconsin, on July 22, 1921. He was interested in sciences as a young man and in 1942 earned a B.S. degree in chemistry from River Falls State Teachers College (now the University of Wisconsin-River Falls). After serving in the Navy in World War II, he attended Marquette University and earned his first M.S. degree in 1948 in biology, working on invertebrate biology and doing research at Woods Hole Marine Biology Laboratory. He developed an avid interest in plant genetics under the guidance of R. A. Brink and D. C. Cooper at the University of Wisconsin-Madison, where he earned another M.S. in 1949 and went on to take a Ph.D. in 1952, concentrating on endosperm and embryo development in maize.

Stan then returned to Marquette as a biology faculty member, but after four years there decided to get back to plant genetics research. He was hired by the University of Wisconsin-Madison in the Genetics Department in 1957 for a joint USDA/ARS Geneticist/university faculty position, working with R. W. Hougas on potato germplasm and genetics. There he focused on potato haploids—cells containing a single set of chromosomes—first as an assistant professor (1957-58) and then as an associate professor (1959-61). His position was assumed fully by the university in 1962, shared jointly by the Departments of Genetics and Horticulture. He became a full professor at that time, a position he occupied until his retirement in 1994.

Professional history

Stan's scientific career can be separated into three general categories: plant genetics, potato breeding, and training of students and visiting scientists. His work had a central focus on the potato, the fourth-most important food crop in the world, where he did more than any other individual to expand the genetic and cytogenetic knowledge base and contribute to increased potato production internationally.

Stan's contributions in plant genetics began with collaborative research efforts with R. W. Hougas as co-founders of haploid potato breeding. Beginning in the 1960s, he and Hougas developed methods to isolate thousands of potato haploids. These were some of the first haploids able to be generated readily for any crop, with numbers comparable to those eventually generated for barley and maize. With the insightful method the two men devised, they used haploids to study genetic traits in potato with greater ease than had been possible in typical cultivated tetraploid potatoes. Stan's haploid method marked his first manipulation of whole chromosome sets, or ploidy. His second effort in ploidy manipulation was as founder of 2n (the basic number of chromosomes in the body cells of a species) gamete (egg or sperm cell) potato breeding. This revolutionary scientific effort, whereby he identified and characterized the basic biological mechanisms by which plants generate 2n gametes, has been the basis for our understanding of how polyploids are generated in nature. Science now recognizes 2n gametes as central to the evolution of potatoes and many, if not most, other polyploids.

One question that arises is how this process of ploidy manipulation by plants in nature is able to generate viable seeds despite large shifts in chromosome numbers via 2n gametes. Stan and fellow research geneticist R. E Hanneman, Jr., looked into the genetic bases for the production of endosperm able to sustain the development of viable seed when shifts in chromosome number result from 2n gametes. Their research led to their roles as co-founders of the endosperm balance number (EBN) concept. EBN established genetic and cytogenetic principles accounting for endosperm function in many plant species and identified the limits of, and strategies for, intercrossing potatoes from diverse ploidy levels.

Taking his cue from nature's ease in manipulating plant ploidy levels with 2n gametes by the rules of the EBN concept, Stan applied this understanding to manipulate potato ploidy levels in his breeding program. The practical application of these scientific principles include his efforts to introgress wild potato germplasm into cultivated potato by use of 2n gametes; to use potato haploids to tap useful genes from wild relatives; and to apply his knowledge of EBN to improve the agricultural performance of potatoes. Beyond his work in potatoes, his concepts and methods involving haploid breeding, 2n gametes, and EBN have been applied to several other food crops, including sweet potato, banana, and alfalfa. Furthermore, Stan took these concepts and applied them in potato to develop methods for the breeding of true-seed potato for world regions to combat post-harvest storage challenges and disease. His clonally propagated cultivars, and even more so the potato cultivars from true seed, have been revolutionary in the adaptation of potato to production of this key crop in temperate and tropical regions.

While the efforts described above were clearly led by Stan's vision, in pursuing this vision he taught numerous courses and trained many graduate students and visiting scientists. In his 37 years on the Wisconsin-Madison faculty he not only undertook a large research and potato-breeding program, but also taught Introductory Cytogenetics as sole instructor (1958-94) and was co-instructor of Chromosome Manipulations in Plants (1968-94) and the Biocore undergraduate biology courses (1968-93). His talent at conveying scientific knowledge was highlighted by his role as co-founder, with several other Wisconsin-Madison faculty, of the Plant Breeding and Genetics Program (PBGP). This highly successful program has graduated over 500 M.S. and Ph.D. students in the last 45 years. Stan was a key trainer of this faculty, where he mentored and taught 98 PBGP graduate students from 34 countries. His followers have pursued careers as prominent leaders at world food plant germplasm centers, universities, and research institutes and in the agriculture industry. His exciting research also attracted more than 20 visiting scientists from foreign countries whom he mentored with characteristic enthusiasm. These included students from leading international centers of plant germplasm enhancement. He also taught key graduate PBGP courses, instructing several thousand students in plant genetics and cytogenetics during his career. Although a busy and involved teacher and mentor, he managed to publish some 195 refereed articles and more than 250 abstracts documenting his research on plant genetics and potato breeding in national and international journals.

Advances in potato genetics

In his long and distinguished career as a genetics researcher, Stan made original, innovative, and broad contributions to the genetic improvement of the potato crop. His work had a major national and international impact on plant genetics, plant breeding, and crop production. He was broadly interested in plant reproductive biology, with a particular focus on variation in plant reproduction that alters the events of meiosis (the type of cell division involved in sexual reproduction) and, consequently, the genetic constitution of gametes and progeny. With the help of his sizable team of graduate students, Stan discovered meiotic mutants of potato, making possible a deeper understanding of genetic mechanisms underlying the origins of polyploid individuals and species in nature.

Stan and his students developed methods working with 2n gametes and haploids, and they moved genes for important horticultural traits from wild relatives of potato to cultivated potato for the betterment of agriculture. Using this knowledge and these methods, Stan developed potato germplasm with combinations of yield, adaptation, and disease-resistance traits previously unavailable. This elite plant germplasm, distributed to 85 countries by the International Potato Center (CIP) from the 1980s onward, not only increased potato yields and quality in parts of the world dependent upon this staple crop for daily sustenance but also broadened the adaptation of potato cultivation.

Because of this work, potatoes now are being grown in lowland tropical regions throughout the world where they earlier had not been able to grow, greatly expanding the food supply in those regions. For example, potato production has been expanded in Bangladesh, Brazil, Senegal, and Viet Nam using germplasm developed with Stan's potato-breeding approaches. In China, germplasm that he developed has been grown widely. In addition, he provided new high-yielding potato cultivars, adapted for both fresh-market crops and chip production grown throughout the world on vast acreages in Africa, Asia, Europe, and North and South America. The variety known as Snowden, for example, has been grown widely in the United States and has served as an important genetic source of potato processing quality by potato breeders around the world. Germplasm from his program is among the most productive throughout the world.

Breakthroughs in true potato seed

A significant applied aspect of Stan's work is his development of methods to reliably propagate potatoes from true seed rather than from tubers. True potato seed (TPS) has been suggested as an alternative to production of the crop from tubers since at least the 1940s, but the application of Stan's seminal discoveries on potato haploids and 2n gametes improved the uniformity and yield of the potato crop from TPS. This has made possible the production of a reliable and sustainable potato crop in disease-plagued regions where refrigerated tuber storage was economically impractical. Done in cooperation with CIP, this work has made the production of virus-free potatoes affordable for poor farmers in tropical countries where the production of potatoes in the past had only been possible using prohibitively expensive imported tubers.

TPS provided a means for an even broader geographic range of potato production throughout the world. As noted by Ortiz, et al., in their 2005 review of Stan's work, "the production of potatoes from true seed has increased dramatically in areas of India, Bangladesh, and China where they are grown between two crops of rice." TPS has been used in 30 countries and has accounted for tens of thousands of additional hectares of potato production with significant economic impact. For example, hybrid TPS use in Viet Nam was estimated to account for an increased household income of 1.2 percent, according to a 2001 study.

Over time, Stan's achievements were in large part realized through the collective efforts of his legions of students. His talent and sincere dedication to mentoring and training students and research scientists working with food crops throughout the world multiplied his personal impact significantly. His contagious enthusiasm and wide range of scientific knowledge and interests inspired his colleagues and peers at all levels. His superb teaching ability was recognized with teaching awards, as he instilled his passion for science in numerous graduate students who have traveled around the world to pursue careers primarily enhancing food production as researchers, teachers, and administrators. He was a prolific trainer of graduate students in the biological sciences at Wisconsin-Madison, including many now-established scientists working with food crops from around the world who came to be mentored by him and then returned to their countries to apply knowledge gained to improve vegetables, fruits, grains, and forage crop production. His scientific and applied contributions yielded significant recognition, most notably his election to the U.S. National Academy of Sciences in 1984.

Personal history

Stan was an active and outspoken supporter of the PBGP interdepartmental major from its inception in 1968 until his retirement, training most of his graduate students in that area and serving on the graduate examining committee of many more students in the program. He was much-admired and very well known as a teacher, exhibiting a contagious, exuberant enthusiasm for science and receiving several teaching awards. He leaves an indelible memory with his students, whom he considered to be his academic children, as a caring, insightful mentor, willing to discuss a wide range of topics (at length), but bringing most discussions back to his excitement with the process of scientific discovery.

Stan married Helga Sorenson, who passed away in 1972. They are survived by their three sons, Philip, John, and James, and their families. He later married Virgie Eastburn Fry, who passed away in 2012, and they are survived by her two children, David and Diane. He was a caring, supportive husband and father, a champion of his family's aspirations and hopes.

HONORS AND AWARDS

1983 Campbell-Bascom Professor of Horticulture and Genetics, University of Wisconsin-Madison

1984 Election to the U.S. National Academy of Sciences

1985 Genetics and Plant Breeding Award, National Council of Commercial Plant Breeders

1986 Honorary Life Membership, Potato Association of America

1987 College of Agricultural and Life Sciences, Excellence in Teaching Award, University of Wisconsin-Madison

1988 Outstanding Alumnus Award, University of Wisconsin-River Falls

2002 University of Naples "Federico II" Honorary Doctorate

2005 Dedication Chapter to Stanley J. Peloquin, Volume 25, *Plant Breeding Reviews*

SOURCES OF INFORMATION USED TO SUMMARIZE THE DISTINGUISHED CAREER OF STANLEY J. PELOQUIN INCLUDED:

Dedication: Stanley J. Peloquin – potato geneticist and cytogeneticist, *Plant Breeding Reviews* 25:1-20. 2005 by Rodomiro Ortiz, Luigi Frusciante, and Domenico Carputo;

Ploidy manipulation of the gametophyte, endosperm, and sporophyte in nature and for crop improvement – a tribute to Professor Stanley J. Peloquin (1921-2008), *Annals of Botany* 104: 795-807. 2009 by Rodomiro Ortiz, Philipp Simon, Shelley Jansky, and David Stelley;

Memorial Resolution of the Faculty of the University of Wisconsin-Madison on the death of Professor Stanley J. Peloquin by Philipp Simon and Shelley Jansky, December, 2008; and Stanley J. Peloquins's resume in the Department of Horticulture, University of Wisconsin–Madison.

SELECTED BIBLIOGRAPHY

1957 With R. W. Hougas. A haploid plant of the potato variety Katahdin. *Nature* 180:1209-1210.

1958 With R. W. Hougas. Fertility in two *Solanum tuberosum* haploids. *Science* 128:1340-1341.

1964 With R. W. Hougas and A. C. Gabert. The effect of the seed-parent and pollination on haploid frequency in *Solanum tuberosum*. *Crop Sci.* 4:593-595.

1968 With R. E. Hanneman. Ploidy levels of progeny from diploid-tetraploid crosses in the potato. *Amer. Potato J.* 45:255-261.

1975 With D. W. S. Mok. Three mechanisms of 2x pollen formation in diploid potatoes. *Can. J. Genet. Cytol.* 17:217-225.

With D. W. S. Mok. Breeding value of 2n pollen (diplandroids) in tetraploid x diploid crosses in potatoes. *Theor. Appl. Genet.* 46:307-314.

1976 With A. O. Mendiburu. Sexual polyploidization and depolyploidization: some terminology and definitions. *Theor. Appl. Genet.* 48:137-143.

1977 With T. P. M. den Nijs. Polyploid evolution via 2n gametes. *Amer. Potato J.* 54:377-386.

With A. O. Mendiburu. The significance of 2n gametes in potato breeding. *Theor. Appl. Genet.* 49:53-61.

1979 With M. Iwanaga. Synaptic mutant affecting only megasporogenesis in potatoes. *J. Hered.* 70:385-389.

1981 With E. L. Camadro. Cross-incompatibility between two sympatric polyploid *Solanum* species. *Theor. Appl. Genet.* 60:65-70.

1982 With M. Iwanaga. Origin and evolution of cultivated tetraploid potatoes via 2n gametes. *Theor. Appl. Genet.* 61:161-169.

1984 With H. M. Kidane-Mariam, G. C. Arndt, and A. C. Macaso-Khwaja. Comparisons between 4x x 2x hybrid and open-pollinated true potato seed families. *Potato Res.* 27:300-305.

With C. O. Okwuagwu, E. F. Leue, S. A. Hermundstad, D. M. Stelly, S. H. Schroeder, and I. E. Chujoy. Use of meiotic mutants in breeding. In P*resent and Future Strategies for Potato Breeding and Improvement: Report of the XXVI Planning Conference, December 12-14, 1983*. pp. 65-74 Lima, Peru: International Potato Center.

1985 With S. A. Hermundstad. Germplasm enhancement with potato haploids. *J. Hered.* 76:463-467.

1986 With D. M. Stelly. Formation of 2n megagametoyphytes in diploid tuber-bearing *Solanums*. *Amer. J. Bot.* 73:1351-1363.

1987 With J. E. Werner. Frequency and mechanisms of 2n egg formation in haploid *Tuberosun*-wild species F1 hybrids. *Amer. Potato J*. 64:641-654.

1988 With G. L. Yerk. 2n pollen in eleven 2x, 2EBN wild species and their haploid-wild species hybrids. *Potato Res.* 31:581-589.

1989 With L. Frusciante, A. Barone, and C. Concilio. Use of different breeding schemes and selection of parental lines for TPS production, In *Parental line breeding and selection in potato breeding*. K. M. Louwes, H. A. J. M. Toussaint, and L. W. L Dellaert , eds. pp. 178-181. Wageningen, Netherlands: Pudoc.

With G. L. Yerk, J. E. Werner, and E. Darmo. Potato breeding with haploids and 2n gametes. *Genome* 32:1000-1004.

1991 With L. Concilio. Evaluation of the 4x x 2x breeding scheme in a potato breeding program adapted to local conditions. *J. Genet. and Breed.* 45:13-18.

With R. Ortiz, R. Freyre, and M. Iwanaga. Efficiency of potato breeding using FDR 2n gametes for multi trait selection and progeny testing. *Theor. Appl. Genetics.* 82:602-608.

With K. Watanabe and M. Endo. Genetic significance of mode of polyploidization: somatic doubling or 2n gametes. *Genome* 34:28-34.

1992 With R. Ortiz. Techniques for introgressing unadapted germplasm to breeding populations, In: *Plant breeding in the 1990's.* H. T. Stalker and J. P. Murphy, eds. pp. 485-508. Oxford, UK: CABI.

1994 With R. Ortiz. Effect of sporophytic heterozygosity on the male gametophyte of the tetraploid potato (Solanum tuberosum). *Ann. Bot.* 73:61-64.

1996 With A. C. Gabert and R. Ortiz. Nature of pollinator effect in potato (*Solanum tuberosum L.*) haploid production. *Ann. Bot.* 77:539-542.

1997 With D. Carputo, A. Barune, T. Cardi, A. Sebastiano, and L. Fruisciante. Endosperm balance number manipulation for direct in vivo germplasm introgression to potato from a sexually isolated relative (*Solanum commersonii* Dun.). *Proc. Nat. Acad. Sci. U.S.A.* 94:12013-12017.

1999 With L. S. Boiteux and D. Carputo. Meiotic mutants in potato: Valuable variants. *Genetics* 153:1493-1499.

With J. A. Buso, L. S. Boiteux and G. C. C. Tai. Chromosome regions between centromeres and proximal crossovers are the physical sites of major effect loci for yield in potato: Genetic analysis employing meiotic mutants. *Proc. Nat. Acad. Sci. U.S.A.* 96:1773-1778.

2000 With J. A. Buso and L. S. Boiteux, Evaluation of 4x-2x progenies from crosses between 4x potato cultivars and 2x haploid *Tuberosum-Solanum* chacoense hybrids under long-day conditions. *Ann. Appl. Biol.* 136:35-40.

2003 With D. Carputo and L. Frusciante. The role of 2n gametes and endosperm balance number in the origin and evolution of polyploids in the tuber-bearing *Solanums*. *Genetics* 163:287-294.

2005 With H. I. Groza, B. D. Bowen, D. Kichefski, W. R. Stevenson, A. J. Bussan, and J. Jiang. Millennium Russet: A dual purpose russet potato variety. *Amer. Potato J.* 82:211-219.

2006 With D. Carputo and E. L. Camadro. Terminology for polyploids based on cytogenetic behavior: Consequences in genetics and breeding. *Plant Breed. Rev.* 26:105-124.