Dedication:
Stanley J. Peloquin
Potato Geneticist and Cytogeneticist

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Dr. Stanley J. Peloquin is known to plant breeders for his decisive contributions to genetic enhancement of potato (*Solanum tuberosum* L.) using haploids, 2*n* gametes, and wild *Solanum* species; for his pioneering work on potato cultivation through true seed; and as mentor of a new generation of plant breeders worldwide. The genetic enhancement of potato, the fourth most important food crop worldwide, benefited significantly from Peloquin's work on ploidy manipulations led by the genetic knowledge he and his co-workers, mostly former graduate students, created and systematically transformed into applied breeding methods. His scientific papers, book chapters, classes, seminars, and talks on potato as a model plant for genetic breeding and evolutionary research are a source of inspiration to all researchers in crop improvement.

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BIOGRAPHICAL SKETCH

Stan was born in Barron, Wisconsin, in 1921. He went to grade school in three small towns in Wisconsin and to a small high school at Ondossagon near Lake Superior in northern Wisconsin, where he was taught to get out of northern Wisconsin to make a living. There were 20 in his graduating class. After graduating with a degree in chemistry in 1942 from River Falls State College (now the University of Wisconsin—River Falls), he joined the U.S. Navy and served on a destroyer in the South Pacific for 3-1/2 years during the Second World War. Upon his release from the service, he enrolled at Marquette University, Milwaukee, Wisconsin, and obtained a MSc degree in biology in 1948. He then enrolled in the University of Wisconsin and studied genetics under the guidance of Dr. R. A. Brink and Dr. D. C. Cooper and was awarded a PhD degree in genetics in 1952. His thesis was entitled "Abnormal Embryo and Endosperm Development in *Zea mays* Following the Use of Pollen that has been Exposed to Mustard Gas." From 1951 to 1956, he taught biology at Marquette University. From 1957, when he joined the faculty at the University of Wisconsin, Madison, until his retirement in 1994, he taught genetics to undergraduates in the Biocore Biology Program, and two graduate level courses: cytogenetics, and, with Dr. Ted Brigham, Chromosome Manipulations in Plants. He married Helga Sorensen and reared three sons: Philip, John, and James. Some time after her passing, he married Virgie Eastburn Fry, who is the mother of two children: David and Diane. Stan and Virgie are the proud grandparents of Brandon and Brienne (from Philip), and Christopher, Julia, and Melissa (from Diane), and two great grandchildren, Gavin and David.

In 1984, Dr. Peloquin was elected to the U.S. National Academy of Sciences and was awarded a life membership by the Potato Association of America. In 1983, Dr. Peloquin was named the Campbell Bascom Professor by the University of Wisconsin and received Laurea Honoris Causa from the Università degli Studi di Napoli "Federico II" (Italy) in 2002. These recognitions he has received for his innovative research and scientific leadership are an acknowledgment of his superb skills as a potato geneticist and breeder. Peloquin always points out that potato should be seen not only as an important food (fresh or processed) but also as the raw material for the starch-processing industry, as feed because its vines can be fed to animals, and as a potential resource for medicine because of the compounds in its true seed, and as an ornamental.

RESEARCH

Peloquin's achievements are the result of fundamental, ingenious scientific insight, using potato genetics as the focal point for his research. Stan integrates his efforts with a broad range of networking activities, creating a world-famous "school" composed largely of his graduate students and research fellows. This intense collaboration has had a great impact in generating basic knowledge and for achieving practical methods for genetic enhancement.

Peloquin's early efforts were in broadening the basic knowledge about cytogenetics and genetics of potato. Stan's collaboration with Robert W. Hougas at the beginning of his career was an important first step, which led to more than 40 years of seminal potato research. Peloquin and Hougas, sometimes with early students and other collaborators, published 19 papers together that established a foundation of potato reproductive biology, genetics, and the genetics of reproductive biology that supported the broad and deep fundamental and applied developments that were to follow. Because of these early successes, Stan Peloquin set up germplasm enhancement methods relying on scaling up and scaling down chromosome sets via ploidy manipulations. Such ploidy manipulations are easily achieved in potato to transfer genes from wild *Solanum* species to the primary crop gene pool—particularly alleles for improving horticultural traits. His students in the classrooms of the University of Wisconsin still remember one of his favorite comments when teaching cytogenetics: "*The best plant with which to manipulate individual chromosome numbers is wheat. The best plant with which to manipulate sets of chromosomes is potato.*" As Stan pointed out in many of his reviews: "*The ability to obtain plants with the gamete chromosome number (haploids) and gametes with the plant chromosome number (2*n *gametes) is the basis for the ease of manipulating whole sets of chromosomes in potato.*"

Haploid and 2*n* Gamete Cytology and Cytogenetics

Scaling down the ploidy of the tetraploid potato ($2n = 4x = 48$ chromosomes) to the diploid level is achieved routinely by producing potato haploids ($2n = 2x = 24$ chromosomes). Maternal haploids can be easily obtained through parthenogenesis after interspecific hybridization of tetraploid cultivars with pollen of *S. phureja* Juz. et Buk. Haploid frequency is affected by both the maternal genotype and the pollen source, and both seed parent and pollen source influence the success of haploid production. Peloquin and co-workers indicated that the endosperm associated with a haploid embryo was always hexaploid, which clearly demonstrated the union of the two chromosome sets from *S. phureja* with the polar nuclei, and lack of fertilization of the egg. Hence, the pollen source influences haploid frequency via its effect on the endosperm. Paternal haploids are also obtained via anther culture, but maternal haploids offer more advantages for potato breeding because paternal haploid production requires gene(s) for androgenic competence, which are not always available in all tetraploid potato cultivars.

Gametes with the sporophytic chromosome number are referred to as 2*n* gametes. Some authors called them "numerically unreduced gametes," but Peloquin (and thereafter the students under his mentorship) avoided this term because normal gametes in any species have the haploid (n) number; i.e., 2*n* gametes would be 2*x* in diploids, 4*x* in tetraploids, and so on. Another reason he cautioned against the use of the term is that while chromosome number is not reduced in the formation of 2*n* gametes, the so-called "reduction division" typically does occur. The failure of students to appreciate this fact leaves them with an incomplete impression of the larger process. Premeiotic, meiotic, and postmeiotic abnormalities during gamete formation are correlated with the production of 2*n* gametes and there are at least six distinct possible modes of 2*n* gamete formation: premeiotic doubling, first division restitution (FDR), chromosome replication during meiotic interphase, second division restitution (SDR), postmeiotic doubling, and apospory. FDR and SDR mechanisms are respectively the most common modes of 2*n* pollen and 2*n* eggs formation in potato. In potato, FDR 2*n* gametes transmit on average 80% of the heterozygosity of the diploid progenitor to the tetraploid hybrid offspring. In contrast, SDR 2*n* gametes transfer on average less than 40% of the diploid heterozygosity to tetraploid hybrids.

Parallel orientation of the spindles in the second meiotic division is the most frequent mechanism of 2*n* pollen formation in most tuber-bearing *Solanum* spp. This meiotic abnormality is under the genetic control of the recessive gene *ps* (parallel spindles), which appears to be ubiquitous among *Solanum* species, but 2*n* pollen frequency could be affected by variable expressivity and incomplete penetrance. Omission of the second division after a normal first division appears to be the most common mode of SDR 2*n* egg formation in potato haploids, and haploid-species hybrids, which is controlled by a recessive meiotic mutant (*os*) in diploid potato. Genetic background and environment may affect the expressivity of this gene that also shows incomplete penetrance, and the frequency of modifier genes may enhance 2*n* egg expressivity.

Ploidy Manipulations for Genetic Enhancement

The findings of mechanisms that underlie parthenogenesis for producing maternal haploid plants and the formation of gametes with the parental chromosome number (or 2*n* gametes), established Peloquin's international prestige and credentials. Ploidy manipulations with haploids, 2*n* gametes, and wild species still remains today as one of the most impressive and exciting crop germplasm enhancement methods ensuing from cytogenetics research. In Stan's words "*the potato is unsurpassed in the facility with which sets of chromosomes can be manipulated. This allows a germplasm enhancement strategy that involves species, haploids, 2*n *gametes and endosperm balance number (EBN). The species are the source of genetic diversity, haploids provide a method for 'capturing' the diversity, and 2*n *gametes and EBN are involved in an effective and efficient method of transmitting diversity to cultivars.*" There are two main methods for ploidy manipulations in potato: unilateral sexual polyploidization (4*x*-*n* gametes × 2*x*-2*n* gametes or vice versa) and bilateral sexual polyploidization (ensuing from crosses between 2*x*-2*n* gametes producing parents). For these breeding schemes, the diploid progenitors are developed by crossing potato haploids with tuber-bearing diploid species ($2n = 2x = 24$ chromosomes). Maternal haploids, which are easily extracted through parthenogenesis from most tetraploid cultivars, are crossed with diploid species for breeding at the diploid level. The locally adapted haploid-species hybrids are selected because they possess 2*n* gametes, acceptable tuber characteristics, and sometimes additional desired attributes, e.g., disease or pest resistance. Most of the hybrids ensuing from sexual polyploidization matings in potato are tetraploids. Triploid hybrids from tetraploid-diploid or diploid-diploid crosses are very rare due to a strong triploid block in potato.

The best diploid parents for tetraploid-diploid crosses are those producing FDR 2*n* gametes because hybrid vigor associated with high yields may be maximized by multi-allelism per locus in potato. Not surprisingly, tetraploid hybrids derived from diploid progenitors producing FDR 2*n* pollen often outyield their half-sib tetraploid hybrids from intermating tetraploid progenitors. However, maximum heterozygosity does not appear to be universal and depends on the genetic background of the crossing material, because of the importance of adaptation for the optimum expression of hybrid vigor in potato.

With this knowledge, Stan and his “school”—particularly in Italy, Poland, and the Centro Internacional de la Papa (CIP, Lima, Peru)—were able to develop new potato genotypes that combine high and stable yield, plus disease or pest resistance, which also allow the widening of potato growing in areas of the world that were previously unsuitable for this crop. The potato genotypes ensuing from their work were amenable to both fresh table markets and the chipping industry. Some of these materials became parents of cultivars now grown across the world. One potato cultivar (‘Snowden’) ensuing from conventional breeding work of Peloquin and colleagues at the University of Wisconsin is a leading chipping cultivar in North America.

Endosperm Balance Number (EBN) and Hybridization Barriers

The endosperm is a distinct trait among the Angiosperms, which results from double fertilization; one male gamete unites with the egg to form the zygote and the other male gamete with the central cell to form the endosperm, thereby making this tissue necessary for normal seed development. As Peloquin pointed out many times, “One of my colleagues defines endosperm as the tissue which along with potato feeds the world.” Endosperm research by him and co-workers at the University of Wisconsin led to the Endosperm Balance Number (EBN) hypothesis to explain endosperm development in interploidy crosses, both intraspecific and interspecific. Under this theory, normal endosperm development only occurs when a balance of 2 EBN from the female parent matches with 1 EBN from the male parent in the resulting endosperm. Any deviations from this 2 maternal:1 paternal EBN ratio leads to faulty endosperm and lack of normal seed. For example, in $4x \times 2x$ crosses and $2x \times 4x$ crosses, endosperm development is regularly abnormal since the female:male ratios are 4:1 and 1:1, respectively. However, if $2n$ gametes function in the diploid, the ratio is 2:1 and endosperm development is normal. The fact that Mexican tetraploid species are easy to cross with most diploid species from South America—yielding triploid hybrids—suggested that both species sets possess 2 EBN, while they are unable to cross with Andean tetraploid species that are 4 EBN. This endosperm dosage system is typical of species possessing a “triploid block.” However, triploids from crosses between tetraploids and diploids arise occasionally from misfertilization, mitotic abnormalities in the gametophyte, and/or mitotic misdivisions in the endosperm.

The above results led to the hypothesis—tested thereafter with success by many researchers worldwide, that EBN and $2n$ gametes are more important than actual chromosome number for predicting the success of crosses and the ploidy of the resulting progeny. The EBN of a species, which initially was thought to be controlled by a few genes rather than by the whole genome, determines, therefore, the effective ploidy, and natural gene flow may occur among species with distinct chromosome numbers but the same EBN. The EBN can be assigned for most *Solanum* species on the basis of the crossing behavior of a species with a standard species of known EBN.

Further research by some of his former co-workers demonstrated that three genes control EBN in potato, and gave convincing evidence for the participation of the EBN incompatibility system and 2*n* gametes in the origin and evolution of polyploids in tuber-bearing *Solanum* species. In this regard, the EBN determined gene pools among potato and wild *Solanum* species. The primary gene pool consists of old and modern tetraploid cultivars, tetraploid Andean landraces, and tetraploid breeding populations (i.e., 4 EBN polysomic polyploid tetraploid species). Diploid cultivars or breeding populations and diploid tuber-bearing *Solanum* species (2 EBN) producing 2*n* gametes and hexaploid (4 EBN) species also belong to this primary gene pool. The secondary gene pool includes disomic tetraploid (2 EBN) and diploid (1 EBN) tuber-bearing *Solanum* species, which may cross with the crop primary gene pool after isolation barriers (mainly due to EBN) are overcome. Wild diploid non-tuber bearing *Solanum* species (1 EBN) of the series *Etuberosa* are in the tertiary potato gene pool, which could only cross with the primary crop gene pool through bridge species and embryo rescue. Other researchers expanded the EBN theory to many plant taxa, as a unifying concept to predict endosperm function in intraspecific-interploidy or interspecific crosses.

True Potato Seed (TPS)

Potato production from true (sexual) seed was not new because this propagation system was used in the Andes by the Incas. Andean farmers still grow potato from true seed for disease elimination, stock rejuvenation, and creation of new cultivars. However, another major global impact of Peloquin's research was the development of breeding methods for using true seed rather than tubers for growing potato—particularly in warm tropical environments, where potato growers are affected by the high cost of seed-tubers, and lack of clean planting materials because of high pest pressure. TPS lowers production costs, reduces the incidence of pests such as viruses that are not transmitted by true seed, and allows true seed to be the source of planting material even if parental plants are diseased. TPS technology enables low-income small landholders in the developing world to grow potato, thereby expanding the geographic range of this crop worldwide, especially in locations where transport and cold storage of seed-tubers are not feasible. 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.

Potato cultivars in modern high-input agricultural systems are homogeneous tetraploid genotypes. These cultivars, which are generally produced by cross-pollination, show a great uniformity due to vegetative propagation by tubers. In this agricultural system, tubers are harvested from a potato plant that grew from a single-sprouted tuber. Hence, TPS cultivars must combine plant characteristics for true seed production, and for tuber production from true seed propagules. Conventional potato breeding for vegetative propagation relies on selecting desired allelic combinations for further clonal multiplication, while breeding for potato production from true seed should be based on phenotypically uniform hybrid offspring with a high frequency of favorable heterogeneous allelic combinations. The genetic improvement for TPS production must, therefore, consider a breeding strategy for a sexually propagated crop that is grown for the harvest of its vegetative part, i.e., the tuber.

TPS hybrids from crosses between tetraploid parents are the most popular for potato production from true seed. Although heterogeneous gametes may result from meiosis of heterozygous progenitors, some tetraploid hybrid offspring from such crosses show very uniform plant and tuber phenotypes. Tetraploid clones are selected according to their reproductive and agronomic characteristics. Earliness, desired tuber characteristics such as color, shape, number and size, profuse flowering, fertility, and high berry and seed set are the most important attributes of the selected tetraploid parents. Specific crosses for commercial production of TPS hybrids are recommended after testing specific combining ability between locally selected parents.

Peloquin and his co-workers suggested other methods for producing tetraploid TPS hybrids through unilateral sexual or bilateral sexual polyploidization. A high frequency of $2n$ gametes will be very important for commercial TPS hybrids derived from sexual polyploidization after pollinating by hand. Furthermore, recurrent selection effectively increases $2n$ gametes frequency in diploid potatoes. Nonetheless, production costs of TPS can be lowered by eliminating pollen collection and hand pollination. Hence, since the 1980s Peloquin and his co-workers investigated new breeding systems for alternative TPS production. The cheapest material for potato production from true seed will be derived from open pollination. Open-pollinated TPS costs are significantly lower than those of TPS hybrids because the labor skills and other additional required investments are smaller for its production. However, TPS hybrids always outyield open-pollinated and selfed offspring.

The heterozygosity level in the tetraploid sporophyte affects the phenotypic expression of the diploid gametophytic generation in potato; e.g., open pollinated berry and fruit sets are correlated with pollen stainability. It appears that natural pollinators of potato such as bumblebees prefer male fertile plants, especially when pollen viability is at its highest. This finding may explain why tuber yield does not always decrease after successive open-pollinated generations derived from heterogeneous true seed offspring. A synthetic cultivar propagated by open pollination may be, therefore, achievable for potato production from TPS.

Open-pollinated offspring could result from selfing but the percentage of hybrid offspring may be increased in open-pollinated derived seedlings because of the variable rate of outcrossing in cultivated tetraploid potato. Selection of vigorous plants in artificial mixtures of hybrid and self-pollinated TPS generations proved, therefore, to be successful in the identification of hybrids in respective TPS generations. The identification of TPS hybrids may be improved by adding a marker gene in the selection scheme, e.g., interplanting a diploid first division restitution 2*n* pollen-producing male progenitor with a genetic marker (yellow tuber flesh color) among tetraploid female progenitors permitted the selection of TPS hybrids among derived open-pollinated offspring from true seed harvested from the female progenitors. Such TPS hybrids (ensuing from open pollination) had better seedling vigor, more flowers, higher pollen stainability, larger open-pollinated berry set, and greater tuber yield than their open-pollinated half-sibs. Also, the elimination of weak plants during population thinning in the TPS nursery and subsequent interplant competition in densely sown beds for production of tuberlets (the first generation tubers from seedlings) reduce dramatically the frequency of inbred genotypes.

There are some disadvantages for potato production from true seeds using transplanted seedlings, e.g., a reliable water supply is required for the successful establishment of seedling in the production field, and labor costs should be added for transplanting. Likewise, potato tuber yield from tuberlets is always higher than that recorded in TPS seedlings, but specific gravity does not change in both generations. Many small tubers are harvested from TPS seedlings, whereas few normal-size tubers are often obtained from tuber propagules. In addition, TPS seedlings require 2 to 3 extra weeks for tuber maturation as compared to tuber propagules. Hence, tuberlets rather than TPS seedlings appear to be the most promising propagules for potato production from true seed. Furthermore, tuberlets sold as "seed tubers" are suitable for developing a seed tuber system. Off-season production of tuberlets in well-controlled nursery beds will be another advantage of this seed system, because it provides propagules for the next planting season or in environments where direct sowing of TPS does not seem feasible due to short water supply, high labor cost for thinning and manual weeding, or short growing season. Lastly, selection in the seedling generation may improve the performance of tuberlets from open-pollinated and hybrid offspring. Selection for tuber color, shape, and skin in the TPS seedling nursery may lead to agronomically uniform tuberlets.

Peloquin and co-workers reported higher tuber yields in selected tetraploid hybrid offspring from bilateral sexual polyploidization than in those of commercial cultivars. However, both tetraploid and diploid hybrids ensue from diploid-diploid crosses in potato, because polyploid frequency depends on the percentage of 2*n* gametes in both parents. The formation of first division restitution 2*n* eggs through desynapsis offers an option for only tetraploid progeny ensuing from bilateral sexual polyploidization. Through their work on TPS breeding, a new method of producing inexpensive tetraploid hybrid true seed offspring through bilateral sexual polyploidization and natural insect pollination was suggested. It consists of using unrelated, locally adapted diploid haploid-species hybrids as parents—according to their combining ability, with profuse flowering, attractiveness to bumblebees (natural pollinators), and other desired attributes. The diploid male parent has high male fertility and very high frequency of (or almost only) first division restitution 2*n* pollen, and a heterozygous monogenic dominant marker tightly linked to the centromere. The female parent combines male and female fertility, self-incompatibility, very high frequency (or almost only) 2*n* egg production, and lacks a dominant marker (recessive genotype). Both diploid haploid-species parents are grown following an interplanting field design to allow natural pollination and gene flow between them. TPS are harvested only from female parents and are grown in a nursery to eliminate those showing poor vigor and lacking dominant phenotype of the male progenitor. Hence, the tuberlet harvest will include mostly (if not only) tetraploid hybrids for potato production in the field. With this TPS scheme, emasculation, pollen collection, and hand pollination are eliminated, thereby reducing by 50% the costs of producing hybrid tetraploid seed. It would be desirable to select diploid parents that are able to set 10,000 hybrid seeds per plant with this method for producing TPS.

THE MENTOR

Stan Peloquin was among the most prolific trainers of graduate students in the history of the University of Wisconsin—Madison. A total of 93 graduate students (51 PhD, 42 MSc) and 27 visiting scientists from 34 countries were guided by Stan. Many of them returned to their country of origin or pursued a professional career in international agriculture. Through their work, they help to enhance food production in the developing world. Many of his students are now heads of advanced research organizations or lead international agricultural research institutes.

Stan has the ability to infuse a "love" for research in science to young professionals. He is fiercely loyal and devoted to the students' best interest. His enthusiasm and broad interest stimulate not only his students but also colleagues and peers. His former students and visiting research fellows know Stan as someone who enjoys the company of others, has strong education principles, and has a great desire to convey his knowledge. He derives intense satisfaction from the success of each and every student or visiting scientist who comes to his laboratory at the University of Wisconsin.

His students and visiting fellows can never forget that their professional education and careers were developed, molded, and launched under his strong and vibrant personality. Many feel that much of their success was related not only to what they learned from him about science but also about life. We all learned one principle: "*hard work always pays off.*"

Professor Stanley J. Peloquin has devoted a lifetime to merging basic cytogenetic and genetic research to achieve direct applicability in crop improvement. His plant breeding philosophy of "*putting genes into a usable form*" is a prime example of farsightedness in science. His efforts are an inspiration to us all and we proudly dedicate this volume of *Plant Breeding Reviews* to him and his achievements.

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