Annals of Botany **104**: 795–807, 2009
doi:10.1093/aob/mcp207, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY Founded 1887

INVITED REVIEW

Ploidy manipulation of the gametophyte, endosperm and sporophyte in nature and for crop improvement: a tribute to Professor Stanley J. Peloquin (1921–2008)

Rodomiro Ortiz[1,*], Philipp Simon[2], Shelley Jansky[2] and David Stelly[3]

[1]*International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico,* [2]*United States Department of Agriculture/Agricultural Research Service (USDA/ARS), Department of Horticulture, University of Wisconsin-Madison, 1575 Linden Drive, Madison, WI 53706, USA and* [3]*Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843, USA*

Received: 11 May 2009 Returned for revision: 13 July 2009 Accepted: 21 July 2009 Published electronically: 17 August 2009

• *Background* Emeritus Campbell-Bascom Professor Stanley J. Peloquin was an internationally renowned plant geneticist and breeder who made exceptional contributions to the quantity, quality and sustainable supply of food for the world from his innovative and extensive scientific contributions. For five decades, Dr Peloquin merged basic research in plant reproduction, cytology, cytogenetics, genetics, potato (*Solanum tuberosum*) improvement and education at the University of Wisconsin-Madison. Successive advances across these five decades redefined scientific comprehension of reproductive variation, its genetic control, genetic effects, evolutionary impact and utility for breeding. In concert with the International Potato Center (CIP), he and others translated the advances into application, resulting in large benefits on food production worldwide, exemplifying the importance of integrated innovative university research and graduate education to meet domestic and international needs.

• *Scope* Dr Peloquin is known to plant breeders, geneticists, international agricultural economists and potato researchers for his enthusiastic and incisive contributions to genetic enhancement of potato 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 expanded germplasm utilization and advanced reproductive genetic knowledge, which he and co-workers, including many former students, systematically transformed into applied breeding methods. His research on plant sexual reproduction included subjects such as haploidization and polyploidization, self- and cross-incompatibility, cytoplasmic male sterility and restorer genes, gametophytic/sporophytic heterozygosity and male fertility, as well as endosperm dosages and seed development. By defining methods of half-tetrad analysis and new cytological techniques, he elucidated modes, mechanisms and genetic controls and effects of 2*n* gametes in *Solanum*. Ramifications extend to many other crops and plants, in both basic and applied sciences.

• *Achievements* Based upon a foundation of genetics, cytogenetics and plant reproductive biology, Dr Peloquin and co-workers developed methods to use 2*n* gametes and haploids for breeding, and used them to move genes for important horticultural traits from wild tuber-bearing *Solanum* species to cultivated potato for the betterment of agriculture. The resulting potato germplasm included combinations of yield, adaptation, quality and disease resistance traits that were previously unavailable. This elite plant germplasm was utilized and distributed to 85 countries by the CIP, because it not only increased potato yields and quality, it also broadened the adaptation of potato to lowland tropical regions, where humanity has benefited from this addition to their food supply.

Key words: 2*n* gametes, endosperm balance number, haploid, *Solanum*, true potato seed.

INTRODUCTION

Writing about Emeritus Campbell-Bascom Professor Stanley J. Peloquin (Fig. 1) presents a significant challenge as his innovative science, mentoring role and impact on people spans generations and reaches across the world. Dr Peloquin was born in Barron, Wisconsin (USA), on 22 July, 1921 and died on 27 July, 2008 in Madison, Wisconsin. After World War II, he enrolled at Marquette University, Milwaukee, Wisconsin, and obtained an MSc degree in biology in 1948. He then enrolled at the University of Wisconsin, Madison, and studied genetics under the guidance of Professor R. A. Brink and 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, and in 1957 joined the faculty at the University of Wisconsin, Madison, until his retirement in 1994. Dr Peloquin was a faculty member in the Laboratory of Genetics, but his majority appointment was in the Department of Horticulture – a field that he helped to advance although he had no formal training in the subject.

In 1984, Dr Peloquin was elected to the US National Academy of Sciences and was awarded an honorary life membership by the Potato Association of America. In 1983, he was named the Campbell-Bascom Professor by the University of Wisconsin and he received *Laurea Honoris Causa* from the

* For correspondence. E-mail r.ortiz@cgiar.org

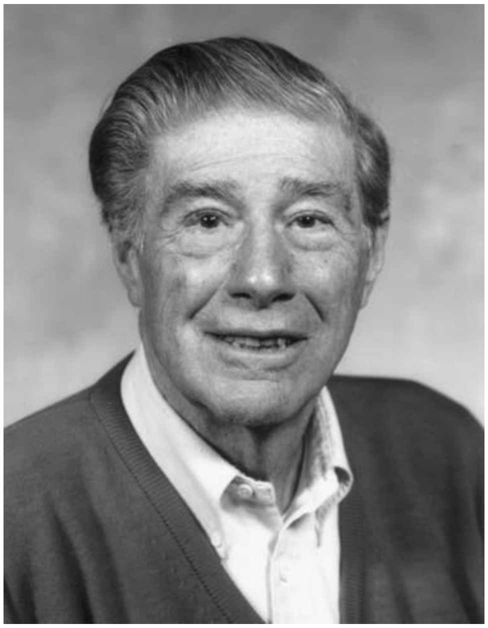

FIG. 1. Emeritus Campbell-Bascom Professor Stanley J. Peloquin (1921–2008).

Università degli Studi di Napoli 'Federico II' (Italy) in 2002. He was recognized for his innovative research and scientific leadership and they serve as an acknowledgment of his superb skills as a plant geneticist and potato breeder. This article reviews his achievements in science, education, potato improvement and production.

HAPLOIDS

Haploids are individuals having the same number of chromosome sets as a gamete, or half as many as a somatic cell. The scientific contributions of Dr Peloquin in plant genetics began with his research efforts, along with Professor R. W. Hougas, into potato breeding using haploids (Hougas *et al.*, 1958; Peloquin and Hougas, 1958). They initially found a plant with a somatic chromosome number of 24 among progeny of a cross between the tetraploid ($2n = 4x = 48$) potato cultivar 'Katahdin' and the cultivated South American diploid ($2n = 2x = 24$) species *Solanum phureja* Juz. & Bukasov (Hougas and Peloquin, 1957). This plant resembled the female parent 'Katahdin' and lacked any of the distinctive characters of the *S. phureja* male parent. They concluded that this 24-chromosome plant was a haploid of 'Katahdin', and it arose through parthenogenesis. Following this finding, they developed methods to isolate thousands of potato haploids from diverse tetraploid genotypes (Hougas *et al.*, 1964). These were among the first readily generated haploids in any crop, with numbers comparable with those generated for barley and maize (Kotch and Peloquin, 1987). With the method devised by Peloquin and Hougas, haploids were used to study genetic traits in potato with better resolution than is possible in typical cultivated $4x$ potato (Peloquin and Hougas, 1960). Haploid production was the first type of ploidy manipulation carried out by Dr Peloquin and co-workers and the first of his many discoveries resulting from research involving interspecific hybridization.

Decapitation of the pistillate parent was found to increase haploid frequency (Peloquin and Hougas, 1959). However, the 'pollinator' effect (Peloquin *et al.*, 1996) is the main factor affecting the frequency of potato maternal haploids. Maternal haploids from $4x$–$2x$ crosses were associated with hexaploid ($6x$) endosperm; $2n$ pollen was not a requisite (Peloquin *et al.*, 1996). This association of decreased embryo ploidy level with increased endosperm ploidy level suggested a common basis, specifically that the absence of egg cell fertilization was coincident with fertilization of the central cell ($4x$) by both monoploid ($1x$) sperm cells or, if pollen tube mitosis failed, by a single combined equivalent ($2x$). Subsequent development of a functional $6x$ primary endosperm would allow for parthenogenetic development of the associated virgin egg cell, if not induce it. This 'pollinator' effect is heritable (Ortiz *et al.*, 1992*b*). Genetic markers such as pigmentation on seeds allow early identification and elimination of hybrids. Consequently, potential haploids among the progeny of cultivar × pollinator crosses are readily detected. 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 available in all tetraploid potato cultivars (Ortiz, 1998).

Potato haploids provide promising material for genetic studies (Werner and Peloquin, 1991*a*; Kotch *et al.*, 1992; Ortiz *et al.*, 1993*a*), cytogenetic analyses (Peloquin *et al.*, 1989*a*) and germplasm enhancement of this important tuber crop (Hermundstad and Peloquin, 1985*a*). The crossability of haploids appears to be similar to that of the cultivated diploid species, and most haploid–diploid species hybrids are vigorous plants. Many of these hybrids produce large attractive tubers (Hermundstad and Peloquin, 1986) and are male-fertile (Hermundstad and Peloquin, 1985*b*). An effective method of incorporating germplasm of wild $2x$ *Solanum* species into the cultivated potato is through hybridization with haploids of $4x$ *Solanum tuberosum*. This procedure provides for the introduction of desirable traits and genetic diversity from wild species into potato (Jansky *et al.*, 1990). Haploid and wild species genotypes can be evaluated for parental value based on the presence of good tuberization, desirable traits, fertility and $2n$ gametes in their hybrid progeny. Haploid–wild species hybrids may be intercrossed and evaluated at the $2x$ level to take advantage of diploid genetic ratios. Selected $2x$ genotypes may then be brought to the $4x$ level through sexual polyploidization using $2n$ gametes.

2*n* GAMETES

Professor Peloquin's second major contribution to ploidy manipulation was as the founder of potato breeding using $2n$ gametes (Peloquin *et al.*, 1989*b*). In the 1950s, large-scale testing of various parents for interploid $4x$–$2x$ cross fertility revealed that certain parents consistently departed from the expected failure. Although few or no triploid progeny resulted, many tetraploid progeny were obtained from specific parental combinations, and the numbers were heavily dependent on the $2x$ genotype (Hanneman and Peloquin, 1967). This discovery led to diverse lines of innovative basic and applied research, including reproductive biology, cytology, cytogenetics, inheritance, quantitative genetics, population genetics, evolution, experimental breeding, applied breeding and agricultural production. They provided new insights into the basic biological mechanisms by which plants generate 2*n* gametes (Peloquin *et al.*, 1999) and generate polyploids in nature. Science now recognizes 2*n* gametes as central to the evolution of potatoes and most other polyploidy crop species (Harlan and de Wet, 1975; den Nijs and Peloquin, 1977; Veilleux, 1985; McCoy and Echt, 1992; Ortiz *et al.*, 1992*b*; Bretagnolle and Thompson, 1995; Katsiotis and Forsberg, 1995; Ortiz, 1997; Ramsey and Schemske, 1998; Hancock, 2005; Heslop-Harrison and Schwarzacher, 2007).

Differences among diploid parents for the ability to produce 4*x* progeny from 4*x*–2*x* crosses was shown to be heritable and resulted from their production of various percentages of diploid pollen, as opposed to haploid (monoploid) pollen. To distinguish categorically the diploid pollen from haploid pollen, the former were dubbed 2*n* pollen. The definition recognized that the ploidy levels of 2*n* gametophytes would depend on parental ploidy levels, as do the ploidy levels of haploids. Thus, given a diploid parental plant, haploid pollen would be monoploid and 2*n* pollen would be diploid; given a tetraploid parent, haploids would be diploid, and 2*n* pollen would be tetraploid.

Early research on the inheritance of 4*x*–2*x* crossability led to the definition of three single-gene mutants, and to the development of an important conceptual distinction between mechanisms and modes of 2*n* gamete formation. The most important of these, the *parallel spindles* (*ps*) mutant, affects relative orientations of meiosis-II spindles in the coenocytic microsporocytes, generates meiotic products genetically equivalent to first division restitution (FDR) gametes, and is under control of the Mendelian recessive *ps* (Mok and Peloquin, 1975*a*). The high *ps* frequency in 4*x* potato cultivars supports the hypothesis that 2*n* pollen was involved in the origin of the cultivated 4*x* gene pool, as a higher *ps* frequency in modern tetraploid cultivars (0·6–0·82) than in the ancestral 2*x* population (0·3–0·47) can be expected if they arose from sexual polyploidization but not if they were produced by somatic doubling (Iwanaga and Peloquin, 1982). Mok and Peloquin (1975*b*) also described two less frequent mechanisms, premature cytokinesis-1 and -2, which are under the genetic control of recessive non-allelic *pc-1* and *pc-2* mutants and lead to second division restitution (SDR) 2*n* pollen. Parallel spindles at anaphase II is the most frequent mechanism for producing 2*n* pollen in potato and in other tuber-bearing *Solanum* species (Watanabe and Peloquin, 1989, 1992).

The findings of Mok and Peloquin (1975*a*, *b*) underscored the fact that 2*n* gamete populations are defined not only by their parental genes but also by the mechanisms by which they form. Moreover, those mechanisms can be grouped according to the genetic expectations, e.g. FDR versus SDR mechanisms. These differences in genetic ramifications underlined the need for being specific when describing 2*n* gametes. Professor Peloquin recognized that the term 'unreduced' has two connotations, one numerical and one genetic, and so he avoided the term to describe any type of 2*n* pollen or gamete. Unfortunately, not all researchers realized this fact and its significance, and thus applied it too liberally. Likewise, many scientists, including geneticists, fail to recognize that genetic reduction normally occurs in both the 'reductional' and the 'equational' divisions of meiosis. Fortunately, these terms have become nearly obsolete.

For 4*x*–2*x* crosses, surveys of numerous wild and artificial diploid genotypes for 2*x*–4*x* cross fertility revealed variability among diploids for 4*x* progeny production (Hanneman and Peloquin, 1968). The differences were largely attributable to differing frequencies of functional 2*n* megagametophytes, and intercrosses initially hinted at simple inheritance, but also to a multiplicity of underlying mechanisms and genes. The biological and genetic dissection of 2*x*–4*x* crossability was much slower than that of 4*x*–2*x* crossability, due to the much greater difficulty of detailed cytological characterization, which for megagametogenesis conventionally relied on microtome sections. However, Iwanaga and Peloquin (1979) established FDR 2*n* megagametophyte production by a sex-specific synaptic mutant. Progress quickened following a robust stain-clearing method was developed to facilitate and expedite cytological analysis of megagametogenesis (Stelly *et al.*, 1984). This enabled direct cytological screening of mature megagametophyte populations to determine 2*n* megaspore frequencies, and cytological analysis of megasporocyte and megagametophyte development to delineate multiple mechanisms of formation (Stelly and Peloquin, 1985, 1986*b*). Whereas 2*n* pollen arises predominantly by way of parallel spindles (FDR), 2*n* megagametophytes seem to arise most commonly by omission of the second division (SDR) (Stelly and Peloquin, 1986*a*). It is controlled by the recessive meiotic mutant (*os*) in diploid potato (Werner and Peloquin, 1990). The *os* gene frequency was found to vary from 0·28 to 0·76 among 2*x* wild *Solanum* species (Ortiz and Peloquin, 1991*a*). Other mechanisms of 2*n* megagametophyte formation in potato are failure of cytokinesis at telophase II followed by nuclear restitution, and synaptic abnormalities followed by nuclear restitution and a normal second division, which are genetically equivalent to SDR and FDR, respectively (Werner and Peloquin 1987, 1991*b*).

DIPLOID TUBER-BEARING *SOLANUM* SPECIES AND POTATO GENETIC ENHANCEMENT

Professor Peloquin viewed the utilization of germplasm resources in breeding programmes as one of the greatest opportunities in modern agriculture, and one of its greatest challenges. Diploid wild species and cultivars of *Solanum* constitute a vast genetic reservoir of genetic diversity in potato breeding (Jansky and Peloquin, 2006). However, ploidy and other naturally occurring barriers markedly hinder gene transfer from the diploids into agriculturally suitable types. Dr Peloquin was a leading force in circumventing these barriers. A key strategy was systematically to screen parts of the exotic 2*x* potato gene pool for 4*x*–2*x* or 2*x*–4*x* crossability and 2*n* gametes (2*n* pollen). The facile generation of tetraploid progeny provided quick avenues for hybridization and introgression, but many of the immediate F_1 hybrids were outstandingly impressive in production capacity, but ill-suited in terms of maturity, tuber type and certain other traits related to domesticated production. Back-crossing of certain hybrids to cultivars was shown to mitigate significantly the agricultural shortcomings of original 4*x*–2*x* hybrids. The resulting hybrid populations were of such vigour and disease resistance that they served as an important impetus for development of 'true-potato seed' (TPS) in tropical areas. Moreover, transmission of most potato viruses is rare via true botanical seed, but common through tubers, so the novel genotypes were also relatively free of pathogenic viruses. These remarkable benefits contributed significantly to the revolutionary practice of producing potatoes from TPS, especially in tropical climates.

Efforts to use diploids in the synthesis of F_1 hybrids suitable for traditional clonal production led to the discovery that agriculturally more suitable types were derived more expeditiously by crossing the exotic $2x$ plants to haploids of potato cultivars. The haploids tuberize under field conditions in temperate regions, facilitating both evaluation and maintenance. These attributes greatly complemented shortcomings of the diploid species. Most cultivar haploids were found to be pollen-sterile, relegating them to use as female parents, and the exotic materials as pollen parents to produce 'haploid-species hybrids'. Many of these haploid-species hybrids were discovered to produce $2n$ gametes, which greatly facilitated subsequent transfer of the diploid germplasm into $4x$ cultigens. Collectively, these advances established that diploid species germplasm could be used to create female-fertile $2n$ gamete-producing haploid-species hybrids with acceptable tuber characteristics and other desired attributes, such as host plant resistance to pathogens or pests; these haploid-species hybrids provided a conduit to synthesis of $4x$ offspring valuable as clones and parents. In short, these efforts establish new breeding schemes based on sexual polyploidization.

PLOIDY MANIPULATIONS: TERMINOLOGY AND THEORY

As a perceptive educator and scientist, Dr Peloquin was astutely aware of the inadequacies of a number of terms widely used to describe meiosis, polyploid formation, constitution, breeding and genetics. The desired accuracy could be achieved only if the terminology were linked to cytogenetic behaviour, and such accuracy was essential to discussions of genetics and the breeding of polyploid crops (Carputo *et al.*, 2006). Cognizant that scientific vocabulary, once established, exhibits considerable inertia, he understood that adoption by the broader scientific community of more accurate and specialized terms would occur only with increased comprehension and common usage. He endeavoured to provide both, and vociferously encouraged others to do likewise. He regularly used enhanced terminology in daily communications with students, research assistants and peers, as well as in the laboratory's presentations and publications. Moreover, he was quick to challenge inappropriate usage of the older terms.

Perhaps his most challenging terminology endeavour was to improve usage of the deeply entrenched terms 'allopolyploidy' and 'autopolyploidy', and in many cases replace them with terms 'disomic' and 'polysomic' polyploidy. The underlying aim was to establish terminology that emphasized meiotic behaviour and genetic consequences, rather than ancestral origins and cytogenetic composition. Allopolyploidy and autopolyploidy allude to cytogenetic constitution and ancestry, but there is no measure by which to distinguish between them. If their definitions are based on interspecific versus intraspecific ancestry, then they are subject to the basis upon which taxonomists choose to define separate species. Moreover, genomic constitution does not determine behaviour. For example, the pattern of inheritance followed by a newly formed interspecific polyploid hybrid, even if an allopolyploid, might be disomic, polysomic, intermediate or highly distorted. This lack of a consistent relationship between constitution and genetic behaviour was underlined by the discovery in wheat and then other species that single chromosomes and single genes could shift the meiotic pairing and inheritance from disomic to polysomic in at least some 'allopolyploids' (Dvorak *et al.*, 2006). The terms disomic and polysomic polyploidy relate directly to patterns of meiotic chromosome pairing and subsequent genetic ratios, which are readily quantified and highly pertinent to genetic manipulation. Their accountability, relevance to functional ramifications, and instructive focus on disomic versus polysomic patterns of meiotic pairing and inheritance made them preferable for teaching and scientific presentations concerned with cytogenetics, genetics and breeding.

Mendiburu and Peloquin (1976) defined sexual polyploidization and depolyploidization (haploidization) as the processes through which euploid zygotes are formed and whose chromosome numbers are respectively increased above or decreased below the ploidy level that would be expected if each parent contributed a gamete carrying half the parental pre-meiotic (somatic) chromosome number. These definitions helped to communicate the existence of plant reproductive variations and their significance as evolutionary and *in vivo* breeding mechanisms. Sexual polyploidization leads to massive genetic innovation, which should be regarded as its most significant difference from somatic doubling.

Dr Peloquin and co-workers devised genetic enhancement methods that take advantage of ploidy manipulations, i.e. scaling up and scaling down chromosome sets. Ploidy manipulations with *S. tuberosum* haploids, $2n$ gametes and wild species remain as one of the most impressive and exciting crop germplasm enhancement methods ensuing from cytogenetics research (Ortiz *et al.*, 2005). Such ploidy manipulations are easily achieved in potato, where they enable the transfer of genes from wild *Solanum* species to the primary crop gene pool, particularly alleles for improving horticultural traits. In the breeding scheme, hybridization between cultivar haploids and wild species captures the genetic diversity from $2x$ species. Many of the $2x$ progeny tuberize and are thus easily screened and maintained as clones. Their $2n$ gametes transmit much or all of the diversity to $4x$ progeny through unilateral or bilateral sexual polyploidization. Unilateral events involve either $2n$ pollen ($4x \times 2x$ crosses), or $2n$ megagametopytes ($2x \times 4x$ crosses), whereas bilateral events involve both ($2x \times 2x$ crosses). Most progeny from unilateral sexual polyploidization matings in potato are tetraploids, whereas those from bilateral sexual polyploidization usually include diploids and tetraploids, the frequencies being dependent on the relative frequencies of $2n$ gametophytes. In potato (and many other species) $3x$ hybrids from $4x \times 2x$, $2x \times 4x$, or $2x \times 2x$ crosses are very rare (Hanneman and Peloquin, 1968), which makes this method of gene transfer both highly effective and quite efficient. Moreover, tetraploid progeny can be visually selected by their larger size and increased vigour relative to diploid sibs.

Relative levels of performance among some tetraploids from sexual polyploidization were stunningly superior to cultivars, while those of others were not. These differences were related to their origin, and particularly to the underlying mode of $2n$ gamete formation behind sexual polyploidization. The observations corresponded to the principle that a high level of heterozygosity is directly related to heterosis for crop yield in polysomic polyploids. The breeding of polyploid cultivars for polygenic traits where non-additive effects are important should generally aim at maximizing heterozygosity due to allelic diversity. In potato, FDR $2n$ gametes transmit on average 80 % of the heterozygosity of the $2x$ parent to the $4x$ hybrid offspring whereas SDR $2n$ gametes transfer on average less than 40 % of the $2x$ heterozygosity to $4x$ hybrids. In this regard, the better diploid parents for $4x \times 2x$ crosses would be those producing FDR $2n$ gametes, because hybrid vigour associated with high yields may be maximized by multiple alleles per locus in potato. In his last journal article, Dr Peloquin estimated that FDR gametes were more than twice as effective as SDR gametes in transmission of heterozygosity after estimating the transmission of heterozygosity on an individual chromosome basis through pachytene analysis (Peloquin *et al.*, 2008). Their cytological models rely on relative chromosome length, euchromatin and heterochromatin content, centromere location, and observations of usually one chiasma per bivalent from early research in his laboratory (Yeh *et al.*, 1965).

SELF-INCOMPATIBILITY AND CROSS-INCOMPATIBILITY

Gametophytic self-incompatibility controlled by multi-allelic *S* genes may hamper inbreeding (either through selfing or sib-mating) in $2x$ potato species (Cipar *et al.*, 1964*a*). There may be some self-compatible $2x$ variants (Cipar *et al.*, 1964*b*), but they can seldom be selfed over more than a few generations (i.e. beyond S_5) due to inbreeding depression. However, one of Dr Peloquin's former students, Dr Robert E Hanneman Jr, identified and characterized a dominant self-compatibility locus in a $2x$ wild potato species (Hosaka and Hanneman, 1998*a*, *b*). This valuable genetic resource can be useful for the development of inbred lines for breeding and genetics research.

Dr Peloquin undertook further self-incompatibility research with his graduate students in other plant species such as *Lilium longiflorum* (Thumb.) or Easter lily (Ascher and Peloquin, 1968). They chose this species because it possesses several advantages for investigating the nature of self-incompatibility; for example, the large hollow styles permit analyses of proteins and enzymes from pollen tubes removed from the styles after selfing or crossing along with their corresponding styles, as well as from pollen grains and from styles of non-pollinated flowers (Desborough and Peloquin, 1968*a*). Research by Dr Peloquin's students included the influence of age and temperature on incompatible and compatible pollen tube growth in Easter lily (Ascher and Peloquin, 1966*a*, *b*, 1970). They found inactivation of self-incompatibility following temperature pretreatments of styles (Hopper *et al.*, 1967; Hopper and Peloquin, 1976), and X-ray inactivation of the stylar component of the self-incompatibility reaction (Hopper and Peloquin, 1968).

Tuber-bearing *Solanum* species are separated by geographical and ecological barriers throughout the American continent. Nonetheless, there are some sympatric species that share the same niches but do not readily cross. For example, $4x$ *S. gourlayi* Hawkes and $6x$ *S. oplocense* Hawkes from Argentina are difficult to hybridize due to pollen–pistil incompatibility on the stigma, in the first third of the style and in the first two-thirds of the style (Camadro and Peloquin, 1991). Cross-incompatibility genes in pistils and dominant specific complementary genes in pollen grains appear to control such interactions. Likewise, Camadro *et al.* (2004) indicated that other major forces strengthening external hybridization barriers are nuclear-cytoplasmic male sterility, and the endosperm.

MALE FERTILITY, CYTOPLASMIC MALE STERILITY AND RESTORER GENES

Low male fertility and seed set is common in cultivar haploids and in offspring from inter-haploid matings (Ross *et al.*, 1964). Likewise, male sterility may occur in hybrids from crosses between *S. tuberosum* haploids and either $2x$ cultivated relatives or some wild *Solanum* species (Hanneman and Peloquin, 1981; Hermundstad and Peloquin, 1985*b*). Often, male sterility in interspecific hybrids results from the interaction of sensitive *S. tuberosum* cytoplasm with the nuclear dominant gene *Ms* from some $2x$ species.

Variation in male fertility among $4x$–$2x$ families resided in the $4x$ cultivar female parents, because the FDR $2n$ pollen-producing male parents had the same genotype (*Ms*/*ms*) for the *Ms* locus (Iwanaga *et al.*, 1991). The *Ms* gene was deduced to be located far from the centromere. A male fertility restorer (*Rt*) gene also occurs among cultivars and its frequency was estimated to be 0·20 in Tuberosum Group clones. Ortiz *et al.* (1993*b*) found that tetrad sterility associated with lack of microspore release from sporads could result also from interactions between *S. stoloniferum* Schltdl. & Bouché cytoplasm and male sterility genes. In contrast, Andigena Group and *S. demissum* Lindley cytoplasm did not interact with the *Ms* gene to produce male sterility in potato.

This knowledge about male sterility and restorer of fertility loci provides an opportunity to circumvent genetic–cytoplasmic male sterility by conventional methods. For example, haploids from $4x$ Tuberosum Group cultivars carrying both *Rt* and *ps* alleles could be crossed with $2x$ cultivars or wild species producing FDR $2n$ pollen and carrying the *Ms* gene. Some of their derived haploid-species hybrids will be male-fertile and FDR $2n$ pollen producers and can be used for the incorporation of $2x$ germplasm with desirable attributes to the $4x$ level by unilateral sexual polyploidization via $4x \times 2x$ crosses.

Dr Peloquin expanded his interest in cytoplasm–nuclear interactions to maize (*Zea mays* L.) through the research of one of his students. Ellsworth and Peloquin investigated the influence of the cytoplasm on ear number expression on the main stalk in the progeny of five maize inbred lines (Ellsworth and Peloquin, 1972). Their research indicates that maize breeders interested in increasing ear number per plant could improve success rates by screening for beneficial cytoplasmic–genotypic interactions.

GAMETOPHYTIC/SPOROPHYTIC HETEROZYGOSITY AND MALE FERTILITY

Tetrasomic plant species such as $4x$ potato routinely produce gametophytes that have two copies of each gene and are thus heterozygous or homozygous for every locus. As a result, gametophytic heterosis may occur. Levels of heterozygosity in the tetrasomic $4x$ sporophyte as well as the proportions of heterozygosity that are transmitted may have an effect of pollen vigour and viability. In addition, solanaceous self-incompatibility systems are rendered ineffective by heterozygosity of the *SI* locus.

Simon and Peloquin (1976) found that FDR $2n$ pollen was more vigorous than SDR $2n$ pollen and haploid (n) pollen, both before and after storage. They demonstrated that $2n$ gametes per se were not necessarily advantageous, as no superiority for vigour was found in SDR $2n$ pollen compared with n pollen. Further research by Ortiz and Peloquin (1994), using $4x$ hybrid offspring from $4x \times 2x$ and $4x \times 4x$ crosses free of cytoplasmic–genetic male sterility showed FDR $2n$ pollen-producing $2x$ parents produced hybrid offspring with significantly higher pollen stainability than those derived from $4x \times 4x$ crosses. The superiority of such pollen populations seems probably to be due to a higher level of heterozygosity in the sporophyte, a proportion of which would be transmitted to haploid pollen, or to vigour of the parent and sporophytic effects on pollen. As argued by Stephenson *et al.* (2001), pollen depends upon the sporophyte for the resources necessary to develop, germinate and initiate tube growth, so the level of heterozygosity in the pollen-producing parent could affect pollen performance by affecting the ability of the sporophyte to provision its pollen. As already mentioned, with FDR $2n$ pollen, 80 % of the heterozygosity and a large fraction of epistasis of the $2x$ parent can be transmitted to its $4x$ hybrid offspring in potato. Such findings are important for the production of open-pollinated (OP) TPS because pollen stainability is significantly correlated with fruit set in potato.

ENDOSPERM BALANCE NUMBER

The endosperm is a unique feature of angiosperms and clearly reflects a reproductive strategy with immense evolutionary ramifications. Endosperm arises after double fertilization, where one of the two male gametes delivered by a pollen tube unites with the egg to form the zygote, and the other unites with the central cell to form the endosperm. Normal seed development *in vivo* is contingent on endosperm. Clearly, this specialized tissue has played a significant role in the evolution of angiosperms because of its physiological and genetic relationships to the embryo and overall seed development. One manifestation of this close developmental relationship is its abnormal development, and consequent seed inviability, that normally follows interploidy crosses. In many angiosperm taxa, interploid $4x \times 2x$ and $2x \times 4x$ crosses fail to produce viable triploid progeny, i.e. a ‘triploid block’ (Marks, 1966).

In contrast to other researchers at the University of Wisconsin-Madison who had attempted to define factors governing angiosperm reproductive controls in relationship to ploidy, Dr Peloquin and his former student Dr Robert E. Hanneman Jr used potato and its relatives to develop a distinctly different approach. They and their students delved into the factors governing viable endosperm and seed production as related to ploidy level when shifts in chromosome number result from $2n$ gametes or sporophyte ploidy level. These studies led to their co-founding of the endosperm balance number (EBN) concept (Johnston *et al.*, 1980). Conceptually, this EBN hypothesis placed control over endosperm function in many plant species at a level beyond ploidy level per se, and beyond that of maternal versus paternal genome dosage. These principles led to significant practical benefits, by enabling relatively reliable predictions on the limits of and strategies for intercrossing potatoes from diverse ploidy levels (Ehlenfeldt and Ortiz, 1995).

According to the EBN concept, sustained endosperm development occurs only when two EBN factors from the female parent unite with one EBN factor from the male parent. Any deviations from the 2 : 1 ratio of maternal–paternal EBN factors lead to faulty endosperm and inviable seed. For example, in $4x \times 2x$ crosses and $2x \times 4x$ crosses, endosperm development is regularly abnormal as the female–male ratios are 4 : 1 and 1 : 1, respectively. However, if $2n$ gametes function in the $2x$ parent of $4x \times 2x$ or $2x \times 4x$ crosses, then the ratio is 2 : 1 and endosperm development is normal.

The genetic basis of EBN has yet to be elucidated. However, it appears that EBN is controlled by a few genes rather than the whole genome (Ehlenfeldt and Hanneman, 1988; Camadro and Masuelli, 1995). Crossing behaviour in *Solanum* species further suggests that the system is multi-genic and regulates both interspecific and intraspecific crosses. Endosperm dosage systems therefore explain many aspects of species evolution, but the system appears to have originated as an ancient means of promoting the fidelity of ploidy levels for each species, or at least the avoidance of sexual sterility associated with triploidy. Interestingly, $2x$ *Solanum* species with one EBN that do not form $2n$ gametes are sexually isolated from $2x$ two-EBN species. EBN-based isolation may be artificially overcome for breeding purposes by scaling the ploidy levels up or down or using $2n$ gametophytes (Carputo *et al.*, 1997). For example, $3x$ F_1 hybrids [derived from an *in vitro* doubled clone of a $2x$ one-EBN ($2n = 3x$, two-EBN) and $2x$ two-EBN clones] can be successfully used in crosses to tetraploid cultivated potato, resulting in $5x$ or near $5x$ BC_1 progenies. Selected $5x$ BC_1 clones may be further back-crossed both as male and as female parents with $4x$ potato cultivars.

ISOZYMES, HALF-TETRAD ANALYSIS AND CYTO-TECHNIQUES

Acid gel electrophoresis of tuber proteins and esterase isozymes from *Solanum* tubers were used for potato cultivar identification and genetic research (Desborough and Peloquin, 1966, 1967, 1968*b*, 1969*a*, *b*). Further research by Simon and Peloquin (1980) elucidated the inheritance of electrophoretic variants of tuber proteins in *S. tuberosum* haploids. Desborough and Peloquin (1968*a*) electrophoretically characterized proteins and enzymes of styles, pollen and pollen tubes of self-incompatible cultivars of Easter lily, but did not associate any proteins with self-incompatibility.

The centromere plays a very important role in delivering the chromosome complement to the daughter cells at cell division. Although it is highly desirable to map the positions of centromeres relative to genes by linkage analysis, there are very few methods to do so. Half-tetrad analysis of $4x \times 2x$ offspring can be used for gene–centromere mapping of loci that are heterozygous in the $2x$ parent (Mendiburu and Peloquin, 1979). Two of the four product strands from each meiotic bivalent in the $2x$ parent are transmitted via the $2n$ gamete to the $4x$ progeny, thus providing a convenient sample of half of the meiotic 'tetrad' for genotyping. The nulliplex (*aaaa*) $4x$ individuals that result from a cross between a nulliplex $4x$ parent and a heterozygous (*Aa*) FDR $2n$ gamete-producing $2x$ parent allows one to estimate the gene–centromere map distance. Following this method, Mok *et al.* (1976) were able to map the self-incompatibility locus (*S*) very close to the centromere. Additional research using half-tetrad analysis led to gene–centromere mapping of isozyme loci (Douches and Quiros, 1987), and host plant resistance genes to cyst nematode (H_1) Potato Virus X (*Rx*) and Potato Virus Y (*Ry*) (Wagenvoort and Zimnoch-Guzowska, 1992). Ortiz and Peloquin (1993) added non-nulliplex $4x$ parents for gene–centromore mapping of the flower pigmentation locus in potato. Comparative gene–centromere mapping enabled an estimate of meiotic recombination in normal synaptic and desynaptic $2x$ potatoes producing $2n$ pollen, and revealed desynapsis could reduce crossing-over by 73 % (Bastiaanssen *et al.*, 1996). They suggested that half-tetrad analysis may be a promising additional approach because accurate centromere positions in relation to other loci were not available in the saturated genetic maps of potato. Further research by Park *et al.* (2007) showed that in potato only one crossover occurred per chromosome arm, and proved that strong recombination interference occurs between the centromere and the telomere. Conversely, Stelly and Peloquin (1986*a*), Werner *et al.* (1992) and Bastiaanssen *et al.* (1998) used half-tetrad analysis with previously mapped loci relative to their centromeres to determine the modes of $2n$ megagametophyte formation in potato. These analyses exemplify the tripartite relationship among genotype, mode of $2n$ gamete formation and gene–centromere distance.

Dr Peloquin and co-workers also developed several techniques for cytological and cytogenetic research that are also useful for classroom teaching. Among these are methods for germinating potato pollen on artificial media (Mortenson *et al.*, 1964), a modified Giesma staining technique for identifying somatic chromosomes of $2x$ potatoes (Mok *et al.*, 1974), and a stain-clearing technique for observation within whole ovules of potato and thus populations of megasporocytes and megagametophytes (Stelly and Peloquin, 1985; Stelly *et al.*, 1986*b*).

THE POTATO: HIS MODEL CROP FOR CHROMOSOME MANIPULATIONS AND GENETIC ENHANCEMENT

Dr Peloquin orchestrated numerous demonstrations that $2n$ gametes and EBN have contributed intrinsically to the origins and extreme genetic diversity in *Solanum* at multiple ploidy levels. Their implicit evolutionary roles in nature underlined their potential utility in genetic improvement of potato. Dr Peloquin thus developed an experimental breeding programme that he ran in parallel with a more-or-less conventional one. In the experimental programme, Dr Peloquin, co-workers and students hoped to incorporate wild potato germplasm into agriculturally elite types of potato, using $2n$ gametes, haploids and EBN to improve the agricultural performance of potatoes. The conventional programme was successful in its own right, and provided a 'measuring stick' for the experimental programme. The two breeding programmes were superb teaching tools through which students gained indelible experience.

Dr Peloquin and his students elucidated the mechanisms of ploidy manipulations and developed new breeding methods based on such knowledge. They stated that sexual polyploidization results in greater genetic variability, fitness and heterozygosity than does somatic doubling and that the EBN system acts as a screen for either *n* or $2n$ gametes, depending on the EBN of parental clones (Carputo *et al.*, 2003). Indeed, in nature, EBN in combination with $2n$ gametes ensures ploidy integrity of $2x$ ancestral species while providing the flexibility for either unilateral or bilateral sexual polyploidization.

The superiority of progeny arising from sexual polyploidization involving FDR $2n$ gametes was revealed by Kidane-Mariam and Peloquin (1974) and, in particular, Mok and Peloquin (1975*c*). Relative to SDR $2n$ gametes from diploids and haploid (*n*) gametes from tetraploids, FDR $2n$ gametes from diploids were superior in breeding value and were more homogeneous; SDR $2n$ gametes could be superior to *n* gametes of $4x$ parents, but were as heterogeneous. Replicated yield trials that were used to contrast clonal families created with vs. without the involvement of $2n$ gametes clearly established the significance of FDR $2n$ pollen in applied potato breeding and that non-additive gene action contributes significantly to tuber yield (Mendiburu and Peloquin, 1977*a*). Further research showed that heterozygosity, epistasis and genetic diversity, if present in the parental $2x$ genotype, are largely maintained in $2n$ gametes formed by FDR, which accounts for the extremely heterotic responses that can occur upon sexual polyploidization (Mendiburu and Peloquin, 1977*b*).

The discovery of high general combining ability in $4x \times 2x$ crosses for $2x$ clones that produce FDR $2n$ pollen contrasted sharply with the breeding behaviour in conventional $4x \times 4x$ crosses, where epistasis and specific combining ability are predominant. This raised the question of whether general combining ability could be selected among elite $4x$ clones, and perhaps even improved by breeding. Although such improvements would potentially enhance breeding of conventional potato cultivars, it was clear that they would be especially valuable in the synthesis of parents for high-performing F_1 seed as TPS cultivars, for which FDR $2n$ pollen producers had demonstrable promise. Dr Peloquin and co-workers devised an innovative approach that minimized genetic variation among $2n$ pollen grains, such that the performance of the progeny means and dispersion from $4x \times 2x$ crosses reflected the gametic input from the respective $4x$ parent, only.

To create uniform populations of $2n$ pollen, the Peloquin laboratory identified diploid clones that combined a mechanism for FDR $2n$ pollen formation, conferred by the *ps* mutation, with absence or reduction of recombination, conferred by a mutant affecting homologous chromosome synapsis and recombination (Okwuagwu and Peloquin, 1981). Nearly all stainable pollen from the double mutants is FDR-NCO 2*n* pollen, i.e. FDR 2*n* pollen with no crossing-over (FDR-NCO), or at least reduced crossing over. These diploid clones provided ideal testers to assess the breeding value of elite 4*x* cultivars, and to estimate the relative contributions of random meiotic products from 4*x* parents to quantitative traits (Buso *et al.*, 1999*a*, 2000).

In most instances, FDR-NCO 2*n* gametes are expected to be genetically superior to conventional FDR 2*n* gametes, i.e. with crossing over (FDR-CO), because they transmit to the progeny, without disruption by recombination, almost 100 % of the parental heterozygosity. FDR-CO gametes transfer approx. 80 % of the parental heterozygosity and a large fraction of the epistatic interactions.

FDR gametes from a given parent are expectedly equivalent for genes residing between centromeres and proximal crossover sites (Buso *et al.*, 1999*c*). Research on 4*x* × 2*x* progeny from FDR 2*n* pollen showed that most loci controlling yielding ability must be between their respective centromeres and proximal chiasmata. Quantitative trait loci (QTL) in these low-recombination chromosome regions may be relatively intractable to conventional 4*x* × 4*x* crosses, which may account for the slow progress in increasing total tuber yield. Conversely, high heterosis for yield has been observed after incorporating genetic diversity through 4*x* × 2*x* crosses, and shown to be transmissible via FDR 2*n* gametes.

Peloquin *et al.* (2009) coined the term ‘horizontal linkage’ to describe the intact transmission of blocks of all genes between the centromere and the first crossover to offspring via FDR 2*n* gametes. His research provided support for the concept that horizontal linkage provides a powerful mechanism to exploit non-additive genetic variation, especially for potato yield. Because FDR 2*n* gametes effectively transmit dominant and epistatic interactions to offspring, producing uniform, high-yielding offspring, they are especially valuable to potato breeders. In addition, horizontal linkage is likely to play an important role in the evolution of polyploid species.

In potato, progeny testing is an imperative step for the selection of parental clones at any ploidy level because the parent–offspring correlation is low for tuber yield and other important traits, i.e. parents per se cannot provide a reliable prediction about the performance of their hybrid offspring (Buso *et al.*, 2003). Both Ortiz *et al.* (1991*b*) and Buso *et al.* (1999*b*) showed the advantages of unilateral sexual polyploidization for multi-trait selection and progeny testing in potato breeding, e.g. fewer replications and locations are required to evaluate tuber yield in 4*x* × 2*x* than in 4*x* × 4*x* hybrid offspring. Likewise, research by Darmo and Peloquin (1991) and Buso *et al.* (2002) demonstrated the feasibility of the 4*x* × 2*x* breeding approach for producing outstanding hybrid offspring and to select promising individuals therein, highlighting this method for the genetic enhancement of the potato as a viable alternative to the conventional 4*x* × 4*x* crosses in both tropical and temperate areas of the world. However, as pointed out by Ortiz *et al.* (1991*a*) selection of parents must be done in each location in which the final product, either a family or a clone, will be used for further breeding or by farmers, respectively.

The concepts and methods developed by Dr Peloquin involving haploid breeding, 2*n* gametes and EBN have been extended to cassava, sweet potato, banana, alfalfa, other forages, berry fruits and other plants of economic importance (Ortiz, 2003). In potato, Dr Peloquin used them to breed not only clonal potato cultivars, but also true-seed potato cultivars suited to world regions with pests and pathogens that otherwise preclude production. His clonally propagated 4*x* 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.

POTATO GENETICS AND CONVENTIONAL BREEDING FOCUSING ON END-USERS

Dr Peloquin and his students often focused on end-user traits as the topic for their potato genetic research. They elucidated the inheritance of potato crisp colour – an important trait in determining the quality and acceptability of cultivars for processing (Thill and Peloquin, 1994), tuberization under long day-lengths (Jansky *et al.*, 2004) or tuber greening – a problem in retail markets (Parfitt and Peloquin, 1981). Epistasis appears to account for most of the genetic variation of the above tuber traits. His breeding research with his students included new potato uses, e.g. vines for silage (Parfitt *et al.*, 1982), or traits for human nutrition, e.g. ascorbic acid (Davies *et al.*, 2002), which could improve tuber resistance to oxidative damage during chilling or cold storage.

Dr Peloquin together with his colleague Don Kichefski of the University of Wisconsin potato research farm at Rhinelander provided new high-yield 4*x* potato cultivars propagated by tuber division and adapted for fresh market and chipping, which have been grown on many hectares in North America. ‘Snowden’, for example, has been grown on 100 000 ha and has served as an important source of potato processing quality by potato breeders around the world. Potato-bred germplasm by Dr Peloquin’s programme is among the most productive throughout the world, as shown by releases in the tropics of the high-yielding 4*x* × 2*x* derived DTO-2, DTO-28 and DTO-33 by Centro Internacional de la Papa (CIP, Lima, Peru) in the 1980s, and of the conventionally bred 4*x* cultivars ‘Wischip’ (1973), ‘Rhinered’ (1976), ‘Oneida’ (1977), ‘Langlade’ (1984), ‘Snowden’ (1990), ‘Niska’ (1991), ‘AC Glacier Chip’ (2001), ‘Red Companion’ (2002), ‘Red Pearl’ (2004), ‘Millennium Russet’ (2005), ‘White Pearl’ (2006) and Megachip (2007) in North America.

TRUE POTATO SEED

A significant applied aspect of Dr Peloquin’s achievements in potato improvement is his development of methods to propagate potatoes reliably from true seed (TPS) rather than tubers. TPS has been suggested as an alternative to the production of the crop from tubers since at least the 1940s but Dr Peloquin’s perceptive and very valuable application of his seminal discoveries on potato haploids and 2*n* gametes improved the uniformity and yield of the potato crop from TPS, resulting in a reliable and sustainable potato crop developing regions of the world that are plagued by pests and lack refrigerated tuber storage facilities. In cooperation with the International Potato Center (CIP), this research made the production of virus-free potatoes possible at an affordable cost for poor farmers in the tropical developing world where the production of potatoes in the past had only been possible with prohibitively expensive imported tubers.

TPS has provided a means for extending the geographical range of potato production throughout the world. 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 accounts for in excess of an estimated 10 000 ha in India and 15 000 ha in China, for example. An economic analysis by CIP of hybrid TPS use in Viet Nam indicated that about 10 % of the total potato production area (grown by small-scale farmers) utilized TPS and this increased their average yield by 75 %, compared with traditional clonal potato production; it benefited 100 000 rural households; and this single technology accounted for an increased household income of 1·2 %. Similar economic benefits were estimated from the utilization of TPS in India and Indonesia.

TPS research in the Peloquin laboratory ranged from genetic to horticultural in nature. Open-pollinations (OPs) were explored as a means to reduce seed production costs, while trying to retain uniformity and mean performance (Kidane-Mariam *et al.*, 1985). Selfing rates were examined to select an appropriate TPS breeding method (Camadro and Peloquin,1982). Distinct crossing schemes were assessed for their ability to produce uniform TPS offspring (Macaso-Khwaja and Peloquin, 1983). The effects of inbreeding on TPS, OP pollen fertility and tuber yield were examined by Arndt *et al.* (1990) and Shonnard and Peloquin (1991*a*). Genetic markers were used to select hybrid TPS seedlings (Arndt and Peloquin, 1990), whereas the effects of seedling selection and planting methods on TPS performance were studied by Shonnard and Peloquin (1991*b*). Their research led to TPS cultivar options such as OP from $4x$ potato cultivars and FDR-derived $4x$, or TPS hybrids resulting from $4x \times 2x$ crosses, among others.

Based on this accumulated knowledge, Ortiz and Peloquin (1991*b*) proposed an inexpensive, $4x$ hybrid TPS production strategy from $2x \times 2x$ crosses: one haploid-species hybrid (female parent) would be selected for male fertility, self-incompatibility, a high frequency of $2n$ megagametophytes and no $2n$ pollen, and an unrelated haploid species for male fertility and high $2n$ pollen production. In addition, the two parents would be selected for profuse flowering, attractiveness to bumble-bees and other desirable characteristics. The male and female parents would be planted on adjacent hills with bumble-bees as pollinators. The elimination of emasculation, pollen collection and hand pollination could reduce $4x$ hybrid TPS costs by more than 50 %.

CULTIVATING A NEW GENERATION OF SCIENTISTS

The efforts described above reflect visionary insight and leadership of the late Emeritus Campbell-Bascom Professor Stanley J. Peloquin. During these pursuits, he trained large numbers of students and visiting scientists while pursuing these achievements (Fig. 2). Many of the international students and scientists were supported via sustained research interactions with the CIP. The underlying research collaboration model with the CIP combined the international network and mission of the CIP with the cross-section of elite scientific training at a top-tier university and was immensely successful in terms of impacting research, education and real-world needs.

A huge part of Dr Peloquin's impact was his classroom teaching and mentoring of undergraduate and graduate students (Fig. 2). Dr Peloquin was closely involved in establishing the BioCore undergraduate course sequence, and a co-founder of the Plant Breeding and Genetics Program at the University of Wisconsin-Madison. The latter program has been highly successful, with 500+ MSc and PhD degrees awarded over the past 40 years. Dr Peloquin also taught key graduate student courses in the Plant Breeding and Plant Genetics Program, where he enthusiastically instructed several thousand students in plant genetics and cytogenetics (Table 1). Dr Peloquin was among the first group of faculty who began teaching the Biology Core Curriculum (Biocore) at the University of Wisconsin-Madison in the 1960s.

FIG. 2. Left: Dr Peloquin and one of his former graduate students at potato harvest time in Rhinelander, northern Wisconsin, during the autumn season in the early 1990s. Right: Professor Peloquin teaching about potato science to his students at the University of Wisconsin-Madison in the early 1990s (photographs courtesy of Wolfgang Hoffmann).

TABLE 1. *Teaching by Professor Stanley J. Peloquin at the University of Wisconsin-Madison*

Course	Level	Period	Average class size
Introductory Cytogenetics	Advanced undergraduate/ graduate course with lecture and hands-on laboratory	1958–1994	30 students per year
Chromosome Manipulations in Plants	Advanced graduate-level course with lecture	1968–1994	18 students
Plant Genetics	Advanced graduate level-course with lecture	1978–1994	18 students
Cellular Biology	Advanced undergraduate/ graduate-level course with lecture	1980–1985	160 students
Organismal Biology	Advanced undergraduate/ graduate-level course with lecture	1968–1975	160 students
Ecology, Genetics and Evolution	Advanced undergraduate course with lecture and hands-on laboratory	1988–1993	160 students

He taught his first course (Biocore 204 – Organismal Biology) in BioCore in 1967 together with Professors Stanley Beck (Department of Entomology), Oliver Smithies (Laboratory of Genetics) and John Heslop-Harrison (Department of Botany). Dr Peloquin taught almost continuously in the programme until 1993, and following his retirement, he helped recruit one of his former students (Phil Simon), who has continued Dr Peloquin's legacy teaching in this programme.

As Dr Peloquin would attest, the programme's impact was largely due to the collective efforts and innovations of his students and visiting scientists. Dr Peloquin mentored and trained 90+ Plant Breeding and Plant Genetics graduate students from 34 countries, who pursued careers as prominent leaders and educators at world food plant germplasm centres, universities, research institutes and companies (see full list in Supplementary Information to this article, available online). Additionally, Dr Peloquin trained more than 20 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 the production of vegetables, fruits, grains and forage crops. He trained more potato researchers than anyone else in the world, and he was among the most prolific trainers of graduate students in the biological sciences at the University of Wisconsin-Madison.

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 undergraduate workers, graduate students, colleagues and peers at all levels. His superb teaching ability was recognized with teaching awards as he instilled the thrill of science into numerous undergraduate and graduate students who subsequently travelled around the world to pursue careers as researchers, teachers and administrators. Dr Peloquin's scientific and applied contributions yielded 195 referred papers (list available in the dedication to volume 25 of *Plant Breeding Reviews*; Ortiz *et al.*, 2005), in excess of 250 abstracts, and numerous honours, most notably his election in 1984 to the United States National Academy of Sciences.

SUPPLEMENTARY DATA

A list of graduate students trained by Professor Stanley J. Peloquin and a list of his visiting scientists are available online at www.aob.oxfordjournals.org.

LITERATURE CITED

Arndt GC, Peloquin SJ. 1990. The identification and evaluation of hybrid plants among open pollinated true seed families. *American Potato Journal* **67**: 293–304.

Arndt GC, Rueda JL, Kidane-Mariam HM, Peloquin SJ. 1990. Pollen fertility in relation to open pollinated true seed production in potatoes. *American Potato Journal* **67**: 499–505.

Ascher PD, Peloquin SJ. 1966*a*. Effect of floral aging on the growth of compatible and incompatible pollen tubes in *Lilium longiflorum* (Thumb.). *American Journal of Botany* **53**: 99–102.

Ascher PD, Peloquin SJ. 1966*b*. Influence of temperature on incompatible and compatible pollen tube growth in *Lilium longiflorum*. *Canadian Journal of Genetics and Cytology* **8**: 661–664.

Ascher PD, Peloquin SJ. 1968. Pollen tube growth and incompatibility following intra- and inter-specific pollinations in *Lilium longiflorum*. *American Journal of Botany* **55**: 1230–1234.

Ascher PD, Peloquin SJ. 1970. Temperature and the self-incompatibility reaction in *Lilium longiflorum* Thumb. *Journal of the American Society of Horticultural Science* **95**: 586–588.

Bastiaanssen HJM, Ramanna MS, Sawor Z, Mincione A, Steen A, Jacobsen E. 1996. Pollen markers for gene-centromere mapping in diploid potato. *Theoretical and Applied Genetics* **93**: 1040–1047.

Bastiaanssen HJM, van der Berg L., Ramanna MS. 1998. Postmeiotic restitution in 2*n*-egg formation of diploid potato. *Heredity* **81**: 20–27.

Bretagnolle F, Thompson JD. 1995. Tansley Review No. 78. Gametes with the somatic chromosome number: mechanisms of their formation and their role in the evolution of autopolyploid plants. *New Phytologist* **129**: 1–22.

Buso JA, Reifschneider FJB, Boiteux LS, Peloquin SJ. 1999*a*. Effects of 2*n* pollen formation by first-meiotic division restitution with and without crossover on eight quantitative traits in 4*x*–2*x* potato progenies. *Theoretical and Applied Genetics* **98**: 1311–1319.

Buso JA, Boiteux LS, Peloquin SJ. 1999*b*. Multitrait selection system using populations with a small number of interploid (4*x*–2*x*) hybrid seedlings in potato: Degree of high-parent heterosis for yield and frequency of clones combining quantitative agronomic traits. *Theoretical and Applied Genetics* **99**: 81–91.

Buso JA, Boiteux LS, Tai GCC, Peloquin SJ. 1999*c*. Chromosome regions between centromere and proximal crossovers are the physical sites of major effect loci for yield in potato: genetic analysis employing meiotic mutants. *Proceedings of the National Academy of Sciences of the USA* **96**: 1773–1778.

Buso JA, Boiteux LS, Tai GCC, Peloquin SJ. 2000. Direct estimation of the effects of meiotic recombination on potato traits via analysis of 4*x*–2*x* progenies from synaptic mutants with 2*n*-pollen formation by FDR without crossing over. *Theoretical and Applied Genetics* **101**: 139–145.

Buso JA, Aragão FAS, Reifschneider FJB, Boiteux LS, Peloquin SJ. 2002. Assessment under short-day conditions of genetic materials derived from three potato breeding strategies: 4*x*-4*x* (intra-Tuberosum), 4*x*-2*x* (FDR 2n-pollen), and 4*x*-4*x* (diplandrous tetraploid). *Euphytica* **126**: 437–446.

Buso JA, Boiteux LS, Peloquin SJ. 2003. Tuber yield and quality of 4*x*-2*x* (FDR) potato progenies derived from the wild diploid species *Solanum berthaultii* and *Solanum tarijense*. *Plant Breeding* **122**: 229–232.

Camadro EL, Masuelli RW. 1995. A genetic model for the endosperm balance number (EBN) in the wild potato *Solanum acaule* Bitt. and two related diploid species. *Sexual Plant Reproduction* **8**: 282–288.

Camadro EL, Peloquin SJ. 1981. Cross-incompatibility between two sympatric polyploid *Solanum* species. *Theoretical and Applied Genetics* **60**: 65–70.

Camadro EL, Peloquin SJ. 1982. Selfing rates in two wild polyploid *Solanums*. *American Potato Journal* **59**: 197–203.

Camadro EL, Carputo D, Peloquin SJ. 2004. Substitutes for genome differentiation in tuber-bearing *Solanum*: interspecific pollen-pistil incompatibility, nuclear-cytoplasmic male sterility, and endosperm. *Theoretical and Applied Genetics* **109**: 1369–1376.

Carputo D, Barone A, Cardi T, Sebastiano A, Frusciante L, Peloquin SJ. 1997. Endosperm balance number manipulation for direct *in vivo* germplasm introgression to potato from a sexually isolated relative (*Solanum commersonii* Dun.). *Proceedings of the National Academy of Sciences of the USA* **94**: 12013–12017.

Carputo C, Camadro EL, Peloquin SJ. 2003. The role of 2*n* gametes and endosperm balance number in the origin and evolution of polyploids in the tuber-bearing *Solanum*s. *Genetics* **163**: 287–294.

Carputo C, Camadro EL, Peloquin SJ. 2006. Terminology for polyploids based on cytogenetic behavior: consequences in genetics and breeding. *Plant Breeding Review* **26**: 105–124.

Cipar MS, Peloquin SJ, Hougas RW. 1964*a*. Inheritance of incompatibility in hybrids between *Solanum tuberosum* haploids and diploid species. *Euphytica* **13**: 163–172.

Cipar MS, Peloquin SJ, Hougas RW. 1964*b*. Variability in the expression of self-incompatibility in tuber-bearing diploid *Solanum* species. *American Potato Journal* **41**: 155–162.

Darmo E, Peloquin SJ. 1991. Use of 2*x Tuberosum* haploid-wild species hybrids to improve yield and quality in 4*x* cultivated potatoes. *Euphytica* **53**: 1–9.

Davies CS, Ottman MJ, Peloquin SJ. 2002. Can germplasm resources be used to increase the ascorbic acid of stored potatoes? *American Journal of Potato Research* **79**: 295–299.

Desborough S, Peloquin SJ. 1966. Disc electrophoresis of tuber proteins from *Solanum* species and interspecific hybrids. *Phytochemistry* **5**: 727–733.

Desborough S, Peloquin SJ. 1967. Esterase isozymes from *Solanum* tubers. *Phytochemistry* **6**: 989–994.

Desborough S, Peloquin SJ. 1968*a*. Disc-electrophoresis of proteins and enzymes from styles, pollen and pollen tubes of self-incompatible cultivars of *Lilium longiflorum*. *Theoretical and Applied Genetics* **38**: 327–331.

Desborough S, Peloquin SJ. 1968*b*. Potato variety identification by use of electrophotetic patterns of tuber proteins and enzymes. *American Potato Journal* **45**: 220–229.

Desborough S, Peloquin SJ. 1969*a*. Acid gel electrophoresis of tuber proteins from *Solanum* species. *Phytochemistry* **8**: 425–429.

Desborough S, Peloquin SJ. 1969*b*. Tuber proteins from haploids, selfs and cultivars of Group *Tuberosum* separated by acid gel electrophoresis. *Theoretical and Applied Genetics* **39**: 43–47.

Douches DS, Quiros CF. 1987. Use of 4*x*-2*x* crosses to determine gene-centromere map distances of isozyme loci in *Solanum* species. *Genome* **29**: 519–527.

Dvorak J, Deal KR, Luo M-C. 2006. Discovery and mapping of wheat *Ph1* suppressors. *Genetics* **174**: 17–27.

Ehlenfeldt MK, Hanneman RE Jr. 1988.. Genetic control of endosperm balance number (EBN):Three additive loci in a threshold-like system. *Theoretical and Applied Genetics* **75**: 825–832.

Ehlenfeldt MK, Ortiz R. 1995. On the origins of endosperm dosage requirements in *Solanum* and other angiosperma genera. *Sexual Plant Reproduction* **8**: 189–196.

Ellsworth RL, Peloquin SJ. 1972. The influence of the cytoplasm on ear number expression in corn. *Crop Science* **12**: 388–389.

Hancock JF 2005. Contributions of domesticated plant studies to our understanding of plant evolution. *Annals of Botany* **96**: 953–963.

Hanneman RE, Peloquin SJ. 1967. Crossability of 24-chromosome potato hybrids with 48-chromosome cultivars. *European Potato Journal* **10**: 62–73.

Hanneman RE, Peloquin SJ. 1968. Ploidy levels of progeny from diploid-tetraploid crosses in the potato. *American Potato Journal* **45**: 255–261.

Hanneman RE, Peloquin SJ. 1981. Genetic-cytoplasmic male sterility in progeny of 4*x*–2*x* crosses in cultivated potatoes. *Theoretical and Applied Genetics* **59**: 53–56.

Harlan JR, de Wet JMJ. 1975. On Ö. Winge and a prayer. The origins of polyploidy. *Botanical Review* **41**: 361–390.

Heslop-Harrison JS, Schwarzacher T. 2007. Domestication, genomics and the future for banana. *Annals of Botany* **100**: 1073–1084.

Hermundstad SA, Peloquin SJ. 1985*a*. Germplasm enhancement with potato haploids. *Journal of Heredity* **76**: 463–467.

Hermundstad SA, Peloquin SJ. 1985*b*. Male fertility and 2n pollen production in haploid-wild species hybrids. *American Potato Journal* **62**: 479–487.

Hermundstad SA, Peloquin SJ. 1986. Tuber yield and tuber traits of haploid-wild species F_1 hybrids. *Potato Research* **29**: 289–297.

Hosaka K, Hanneman RE Jr. 1998*a*. Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 1. Detection of an *S* locus inhibitor (*Sli*) gene. *Euphytica* **99**: 191–197.

Hosaka K, Hanneman RE Jr. 1998*b*. Genetics of self compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 2. Localization of an *S* locus inhibitor (*Sli*) gene on the potato genome using DNA markers. *Euphytica* **103**: 265–271.

Hopper JE, Peloquin SJ. 1968. X-ray inactivation of the stylar component of the self-incompatibility reaction in *Lilium longiflorum*. *Canadian Journal of Genetics and Cytology* **10**: 941–944.

Hopper JE, Peloquin SJ. 1976. Analysis of stylar self-incompatibility competence by use of heat induced inactivation. *Theoretical and Applied Genetics* **47**: 291–297.

Hopper JE, Ascher PD, Peloquin SJ. 1967. Inactivation of self-incompatibility following temperature pretreatments of styles in *Lilium longiflorum*. *Euphytica* **16**: 215–220.

Hougas RW, Peloquin SJ. 1957. A haploid plant of the potato variety Katahdin. *Nature* **180**: 1209–1210.

Hougas RW, Peloquin SJ. 1958. The potential of potato haploids in breeding and genetic research. *American Potato Journal* **35**: 701–707.

Hougas RW, Peloquin SJ, Ross RW. 1958. Haploids of the common potato. *Journal of Heredity* **49**: 103–106.

Hougas RW, Peloquin SJ, Gabert AC. 1964. The effect of the seed-parents and pollinator on haploid frequency in *Solanum tuberosum*. *Crop Science* **4**: 593–595.

Iwanaga M, Peloquin SJ. 1979. Synaptic mutant affecting only megasporogenesis in potatoes. *Journal of Heredity* **70**: 385–389.

Iwanaga M, Peloquin SJ. 1982. Origin and evolution of cultivated tetraploid potatoes via 2*n* gametes. *Theoretical and Applied Genetics* **61**: 161–169.

Iwanaga M, Ortiz R, Cipar MS, Peloquin SJ. 1991. A restorer gene for genetic cytoplasmic male sterility in cultivated potatoes. *American Potato Journal* **68**: 19–28.

Jansky SH, Peloquin SJ. 2006. Advantages of wild diploid *Solanum* species over cultivated diploid relatives in potato breeding programs. *Genetic Resources and Crop Evolution* **51**: 1–6.

Jansky SH, Yerk GL, Peloquin SJ. 1990. The use of potato haploids to put 2*x* wild species germplasm in a usable form. *Plant Breeding* **104**: 290–294.

Jansky SH, Davis GL, Peloquin SJ. 2004. A genetic model for tuberization in potato haploid-wild species hybrids grown under long day conditions. *American Journal of Potato Research* **81**: 335–339.

Johnston SA, den Nijs TPN, Peloquin SJ, Hanneman RE Jr. 1980. The significance of genetic balance to endosperm development in interspecific crosses. *Theoretical and Applied Genetics* **57**: 5–9.

Katsiotis A, Forsberg RA. 1995. Discovery of 2n gametes in tetraploid oat *Avena vaviloviana*. *Euphytica* **81**: 1–6.

Kidane-Mariam HM, Peloquin SJ. 1974. The effect of direction of hybridization (4*x* X 2*x* vs. 2*x* X 4*x*) on yield on cultivated potatoes. *American Potato Journal* **51**: 330–336.

Kidane-Mariam HM, Arndt GC, Macaso-Khwaja AC, Peloquin SJ. 1985. Comparisons between $4x \times 2x$ hybrid and open-pollinated true potato seed families. *Potato Research* **28**: 35–42.

Kotch GP, Peloquin SJ. 1987. A new source of haploid germplasm for genetic breeding research. *American Potato Journal* **64**: 137–141.

Kotch GP, Ortiz R, Peloquin SJ. 1992. Genetic analysis by use of potato haploid populations. *Genome* **35**: 103–108.

Macaso-Khwaja AC, Peloquin SJ. 1983. Tuber yield of families from open-pollinated and hybrids true potato seed. *American Potato Journal* **60**: 645–651.

Marks GE. 1966. The enigma of triploid potatoes. *Euphytica* **15**: 285–290.

McCoy T, Echt C. 1992. Chromosome manipulations and genetic analysis in *Medicago*. *Plant Breeding Review* **10**: 169–197.

Mendiburu AO, Peloquin SJ. 1976. Sexual polyploidization and depolyploidization: some terminology and definitions. *Theoretical and Applied Genetics* **48**: 137–143.

Mendiburu AO, Peloquin SJ. 1977*a*. The significance of 2*n* gametes in potato breeding. *Theoretical and Applied Genetics* **49**: 53–61.

Mendiburu AO, Peloquin SJ. 1977*b*. Bilateral sexual polyploidization in potatoes. *Euphytica* **26**: 573–583.

Mendiburu AO, Peloquin SJ. 1979. Gene centromere mapping by 4*x*–2*x* matings in potato. *Theoretical and Applied Genetics* **54**: 177–180.

Mok DWS, Peloquin SJ. 1975*a*. The inheritance of three mechanisms of diplandroid (2*n* pollen) formation in diploid potatoes. *Heredity* **35**: 295–302.

Mok DWS, Peloquin SJ. 1975*b*. Three mechanisms of 2*n* pollen formation in diploid potatoes. *Canadian Journal of Genetics and Cytology* **17**: 217–225.

Mok DWS, Peloquin SJ. 1975*c*. Breeding value of 2*n* pollen (diplandroid) in tetraploid x diploid crosses in potato. *Theoretical and Applied Genetics* **46**: 307–314.

Mok DWS, Lee HK, Peloquin SJ. 1974. Identification of potato chromosomes with giemsa. *American Potato Journal* **51**: 337–341.

Mok DWS, Peloquin SJ, Mendiburu AO. 1976. Genetic evidence for mode of 2*n* pollen formation and S-locus mapping in potatoes. *Potato Research* **19**: 157–164.

Mortenson LR, Peloquin SJ, Hougas RW. 1964. Germination of *Solanum tuberosum* pollen on artificial media. *American Potato Journal* **41**: 322–328.

den Nijs TPM, Peloquin SJ. 1977. Polyploid evolution via 2*n* gametes. *American Potato Journal* **54**: 377–386.

Okwuagwu CO, Peloquin SJ. 1981. A method of transferring the intact parental genotype to the offspring via meiotic mutants. *American Potato Journal* **58**: 512.

Ortiz R. 1997. Occurrence and inheritance of 2n pollen in *Musa*. *Annals of Botany* **79**: 449–453.

Ortiz R. 1998. Potato breeding via ploidy manipulations. *Plant Breeding Review* **16**: 15–86.

Ortiz R. 2003. Analytical breeding. *Acta Horticulturæ* **622**: 235–247.

Ortiz R, Peloquin SJ. 1991*a*. Breeding for 2*n* egg production in haploid x species 2*x* potato hybrids. *American Potato Journal* **68**: 691–703.

Ortiz R, Peloquin SJ. 1991*b*. A new method of producing 4*x* hybrid true potato seed. *Euphytica* **57**: 103–107.

Ortiz R, Peloquin SJ. 1993. Mapping the flower pigmentation locus in potato. *Journal of Genetic Breeding* **47**: 171–173.

Ortiz R, Peloquin SJ. 1994. Effect of sporophytic heterozygosity on the male gametophyte of the tetraploid potato (*Solanum tuberosum*). *Annals of Botany* **73**: 61–64.

Ortiz R, Freyre R, Peloquin SJ, Iwanaga M. 1991*a*. Adaptation to day length and yield stability of families from 4*x* × 2*x* crosses in potato. *Euphytica* **56**: 187–198.

Ortiz R, Peloquin SJ, Freyre R, Iwanaga M. 1991*b*. Efficiency of potato breeding using FDR 2*n* gametes for multi trait selection and progeny testing. *Theoretical and Applied Genetics* **82**: 602–608.

Ortiz R, Bruederle LP, Vorsa N, Laverty T. 1992*a*. The origin of polysomic polyploids via 2n pollen in *Vaccinium* section *Cyanococcus*. *Euphytica* **61**: 241–246.

Ortiz R, Iwanaga M, Camadro EL. 1992*b*. Utilización potencial de progenie autofecundada de IvP-35 como inductor de haploides en papa por cruzamientos 4*x*-2*x*. *Revista Latinoamericana de Papa* **5/6**: 46–53.

Ortiz R, Douches DS, Kotch GP, Peloquin SJ. 1993*a*. Use of haploids and isozyme markers for genetic analysis in the polysomic polyploid potato. *Journal of Genetic Breeding* **47**: 283–288.

Ortiz R, Iwanaga M, Peloquin SJ. 1993*b*. Male sterility and 2*n* pollen in 4*x* progenies derived from 4*x* x 2*x* and 4*x* x 4*x* crosses in potato. *Potato Research* **36**: 227–236.

Ortiz R, Frusciante L, Carputo D. 2005. Dedication: Stanley J. Peloquin potato geneticist and cytogeneticist. *Plant Breeding Review* **25**: 1–20.

Parfitt DE, Peloquin SJ. 1981. The genetic basis for tuber greening in 24-chromosome potatoes. *American Potato Journal* **58**: 299–304.

Parfitt DE, Peloquin SJ, Jorgensen NA. 1982. The nutritional value of pressed potato vine silage. *American Potato Journal* **59**: 415–423.

Park T-H, Kim J-B, Hutten RCB, van Eck HJ, Jacobsen E, Visser RGF. 2007. Genetic positioning of centromeres using half-tetrad analysis in a 4*x*–2*x* cross population of potato. *Genetics* **176**: 85–94.

Peloquin SJ, Hougas RW. 1958. Fertility in two *Solanum tuberosum* haploids. *Science* **128**: 1340–1341.

Peloquin SJ, Hougas RW. 1959. Decapitation and genetic markers as related to haploidy in *Solanum tuberosum*. *European Potato Journal* **2**: 176–183.

Peloquin SJ, Hougas RW. 1960. Genetic variation among haploids of the common potato. *American Potato Journal* **37**: 89–297.

Peloquin SJ, Jansky SH, Yerk GL. 1989*a*. Potato cytogenetics and germplasm utilization. *American Potato Journal* **66**: 629–638.

Peloquin SJ, Yerk GL, Werner JE, Darmo E. 1989*b*. Potato breeding with haploids and 2*n* gametes. *Genome* **32**: 1000–1004.

Peloquin SJ, Gabert AC, Ortiz R. 1996. Nature of pollinator effect in potato (*Solanum tuberosum* L.) haploid production. *Annals of Botany* **77**: 539–542.

Peloquin SJ, Boiteux LS, Carputo D. 1999. Meiotic mutants in potato: valuable variants. *Genetics* **153**: 1493–1499.

Peloquin SJ, Boiteux LS, Simon PW, Jansky SH. 2008. A chromosome-specific estimate of transmission of heterozygosity by 2*n* gametes in potato. *Journal of Heredity* **99**: 177–181.

Peloquin SJ, Simon PW, Jansky SH. 2009. The concept of horizontal linkage and its application to genetics and breeding. In: Mohan RH. ed. *Recent advances in heredity*. Kerala: Global Research Network, in press.

Ramsey J, Schemske DWS. 1998. Pathways, mechanisms and rates of polyploidy formation in flowering plants. *Annual Review of Ecology and Systematics* **29**: 467–501.

Ross RW, Peloquin SJ, Hougas RW. 1964. Fertility of hybrids from *Solanum phureja* and haploid *S. tuberosum* matings. *European Potato Journal* **7**: 81–89.

Shonnard G, Peloquin SJ. 1991*a*. Performance of true potato seed families. I. Effect of level of inbreeding. *Potato Research* **34**: 397–407.

Shonnard G, Peloquin SJ. 1991*b*. Performance of true potato seed families. II. Comparison of transplants versus seedlings. *Potato Research* **34**: 409–418.

Simon PW, Peloquin SJ. 1976. Pollen vigor as a function of mode of 2*n* gamete formation in potatoes. *Journal of Heredity* **67**: 204–208.

Simon PW, Peloquin SJ. 1977. The incidence of paternal species on the origin of callus in anther culture of *Solanum* hybrids. *Theoretical and Applied Genetics* **50**: 53–56

Simon PW, Peloquin SJ. 1980. Inheritance of electrophoretic variants of tuber proteins in *Solanum tuberosum* haploids. *Biochem. Genet.* **18**: 1055–1061.

Simon PW, Peloquin SJ. 1977. The incidence of paternal species on the origin of callus in anther culture of *Solanum* hybrids. *Theoretical and Applied Genetics* **50**: 53–56.

Stelly DM, Peloquin SJ. 1985. Screening for 2n female gametophytes, female fertility and 2*x* x 4*x* crossability in potatoes (*Solanum* spp.). *American Potato Journal* **62**: 519–529.

Stelly DM, Peloquin SJ. 1986*a*. Diploid female gametophytes formation in 24- chromosome potatoes. Genetic evidence for the prevalence of second meiotic division restitution mode. *Canadian Journal of Genetics and Cytology* **28**: 101–108.

Stelly DM, Peloquin SJ. 1986*b*. Formation of 2n megagametophytes in diploid tuber-bearing Solanums. *American Journal of Botany* **73**: 1351–1363.

Stelly DM, Peloquin SJ, Palmer RG, Crane CF. 1984. Mayer's hemalum-methyl salicytate: a stain-clearing technique for observation within whole ovules. *Stain Technology* **59**: 155–161.

Stephenson AG, Hayes CN, Jannsson MH, Winsor JA. 2001. The performance of microgametophytes is affected by inbreeding depression and hybrid vigor in the sporophytic generation. *Sexual Plant Reproduction* **14**: 77–83.

Thill CA, Peloquin SJ. 1994. Inheritance of potato chip color at the 24 chromosome level. *American Potato Journal* **71**: 629–646.

Veilleux RE. 1985. Diploid and polyploid gametes in crop plants: mechanisms of formation and utilization in plant breeding. *Plant Breeding Review* **3**: 253–288.

Wagenvoort M, Zimnoch-Guzowska E. 1992. Gene-centromere mapping in potato by half-tetrad analysis: map distances of H_1, *Rx*, and *Ry* and their possible use for ascertaining the mode of 2n-pollen formation. *Genome* **35**: 1–7.

Watanabe K, Peloquin SJ. 1989. Occurrence of 2*n* pollen and *ps* gene frequencies in cultivated groups and their related wild species in tuber-bearing *Solanums*. *Theoretical and Applied Genetics* **78**: 329–336.

Watanabe K, Peloquin SJ. 1992. Cytological basis of 2*n* pollen formation in a wide range of 2*x*, 4*x*, and 6*x* taxa from tuber-bearing *Solanum* species. *Genome* **36**: 8–13.

Werner JE, Peloquin SJ. 1987. Frequency and mechanisms of 2*n* egg formation in haploid *Tuberosum*-wild species F1 hybrids. *American Potato Journal* **64**: 641–654.

Werner JE, Peloquin SJ. 1990. Inheritance of two mechanisms of 2*n* egg formation in 2*x* potatoes. *Journal of Heredity* **81**: 371–374.

Werner JE, Peloquin SJ. 1991*a*. Significance of allelic diversity and 2*n* gametes for approaching maximum heterozygosity in 4*x* potatoes. *Euphytica* **58**: 21–29.

Werner JE, Peloquin SJ. 1991*b*. Occurrence and mechanisms of 2*n* egg formation in 2*x* potato. *Genome* **34**: 862–870.

Werner JE, Douches DS, Freyre R. 1992. Use of half-tetrad analysis to discriminate between two types of *2n* egg formation in a potato haploid. *Genome* **35**:741–745.

Yeh BP, Peloquin SJ, Hougas RW. 1965. Pachytene chromosomes of the potato (*Solanum tuberosum* Group Andigena). *American Journal of Botany* **52**: 1014–1020.