

# Perspectives

## Anecdotal, Historical and Critical Commentaries on Genetics

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### Meiotic Mutants in Potato: Valuable Variants

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**P**HENOTYPIC variations in the meiotic process, under control of typical Mendelian inheritance, have been found in many plant and animal species (Kaul and Murthy 1985; Hawley 1993; Dawe 1998; Lindsey 1999). A number of comprehensive reviews surveying research activities with these natural and induced mutants in plants emphasize their value in cytological, developmental, biochemical, and molecular investigations of the meiotic process *per se* (Golubovskaya and Mashenkov 1985; Dawe 1998). Strikingly, no reference was made to the use of meiotic mutants in genetics, germplasm transfer, breeding, and evolution. The meiotic variants found in potato (*Solanum tuberosum* L.) and its more than 150 tuber-bearing relatives are unique tools for investigating crucial problems in both basic and applied research in this crop species (Peloquin 1983). This *Perspectives* considers the application of these inherited variations affecting microsporogenesis and megasporogenesis in potato and their utility in genetics, cytology, germplasm transfer, breeding, and evolution of the fourth most important food crop in the world.

**Potato biology:** The cultivated potato is a tetraploid ( $2n = 4x = 48$ ) with four sets of similar chromosomes (where  $n$  is the gametic chromosome number and  $x$  is the basic number). The main cultivated germplasm for long-day conditions is derived from *S. tuberosum* Group Tuberosum, whereas *S. tuberosum* Group Andigena is adapted for short-day environments. The wild tuber-bearing relatives form a polyploid series with species having 24, 36, 48, 60, and 72 chromosomes—more than 70% of them are diploids ( $2n = 2x = 24$ ).

The tetrasomic inheritance of the cultivated potato is infinitely more complicated than that of  $2x$  relatives. Fortunately, haploid plants ( $2n = 2x = 24$ ) of tetraploids ( $2n = 4x = 48$ ) can be obtained with ease from the

cultivated tetraploids, and these haploids can be crossed to most of the diploid ( $2n = 2x = 24$ ) species to capture their genetic diversity. In addition to simple disomic inheritance, the employment of haploids has the great advantage for improvement of  $2x$  hybrid populations. These  $2x$  hybrids obtained by this approach can be crossed to the  $4x$  potato via functioning of  $2n$  gametes (gametes with the sporophytic chromosome number) to obtain  $4x$  progeny (Peloquin *et al.* 1989b).

The occurrence of postzygotic barriers may sometimes prevent interspecific and/or interploidy crosses, causing abortion of hybrid endosperm. This results in sexual isolation of a number of  $2x$  and  $4x$  species. The endosperm balance number (EBN) hypothesis, formulated by Johnston *et al.* (1980), explains why some closely related species fail to produce hybrid offspring. It states that each *Solanum* species has an effective ploidy, the EBN, and after interspecific crosses normal endosperm development occurs only when there is a 2:1 maternal to paternal EBN ratio in the hybrid endosperm. Thus, successful crosses will occur only when the parents have identical EBN. Diploid species with EBN = 1, and  $4x$  species with EBN = 2, are, respectively, sexually isolated from Tuberosum haploids (EBN = 2) and cultivated potato (EBN = 4).

**Description and genetic characteristics of meiotic mutants in potatoes:** The mutants identified in potato affect major aspects of nuclear and cytoplasmic events during micro- and megasporogenesis. Some key characteristics of meiotic mutants should be noted: (1) Almost all of these mutant phenotypes are controlled by a single locus (2) the mutations are invariably recessive; (3) sometimes the character associated with a certain genotype fails to manifest—*i.e.*, penetrance is not always 100%; (4) the number of meiocytes that express the parental genotype can vary from 1 to 100%—*i.e.*, variable expressivity is the rule, not the exception, with meiotic mutants; and (5) phenotypic expression is significantly modified by genetic, environmental, and developmental factors.

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**Mutants affecting microsporogenesis:** In the normal sequence of events in microsporogenesis in *Solanum* species, the first meiotic division is not followed by cytokinesis, two spindles in the second division are oriented so that their poles define a tetrahedron, and cytokinesis results in a tetrad of four  $n$  microspores (Figure 1). After meiosis, the microspores separate, and each forms a male  $n$  gametophyte. In plants homozygous for the meiotic mutation *parallel spindles* (*ps/ps*), some sporocytes have parallel spindles in the second division, and after cytokinesis two  $2n$  microspores are formed, which give rise to  $2n$  gametophytes. A modification of this occurs when second-division spindles are tripolar, and one  $2n$  and two  $n$  microspores are formed. Another recessive mutation, named *premature cytokinesis* (*pc*), also affects microsporogenesis. The first division in many sporocytes is followed by cytokinesis, the second division does not occur, except that chromatids fall apart, and a dyad of two  $2n$  microspores is formed.

The significance of the *ps* and *pc* mutations resides in their genetic consequences. The *ps* allele controls a process that is essentially a first-division restitution (FDR) mechanism. All loci from the centromere to the first crossover that are heterozygous in the parent remain heterozygous in the gametes. One-half of the heterozygous parental loci beyond the first crossover will be heterozygous in the gametes (in  $2x$  *Solanum* species there is normally only one crossover per chromosome arm). In contrast, the mutation *pc* is genetically equivalent to a second-division restitution (SDR) mechanism. All the loci from the centromere to the first crossover will be homozygous in the gametes, and all loci past the first crossover that are heterozygous in the parent will remain heterozygous in the gametes. From cytological observations (*e.g.*, chromosome structure and frequency and location of chiasmata on chromosome arms), it has been estimated that the percentage heterozygosity transmitted by the gametes is roughly 80% with FDR, in contrast to less than 40% with SDR. FDR gametes are expected to resemble each other and the parental clone from which they came. In contrast, SDR is expected to produce a heterogeneous population of highly homozygous gametes.

Another meiotic mutation, named *synaptic-3* (*sy-3*), was found in the progeny from crosses between two diploid *ps/ps* clones. It is characterized by almost complete lack of chiasmata (with probably no crossing over). In some *sy-3* clones, only univalents are present at metaphase I, and they are distributed randomly into telophase I nuclei. This phenomenon would ordinarily lead to almost complete male sterility. However, when the *sy-3* mutation is combined with the *ps* mutation (*i.e.*, double homozygous genotype *sy-3/sy-3, ps/ps*), a high frequency of functional  $2n$ -pollen grains is formed. No matter how unequal the distribution of univalent chromosomes is in the first division, the *parallel spindles* mechanism in the second division ensures a symmetric incor-

poration of two sets of 12 chromosomes in each pair of  $2n$  microspores (Figure 1). The genetic significance of this combination of meiotic mutations resides in the opportunity they provide for incorporating the almost intact genotype of the  $2x$  parent into all the  $2n$  gametes.

**Mutations affecting megasporogenesis:** During normal megasporogenesis in *Solanum* species, the first and second meiotic divisions are each followed by cytokinesis. As a result, four  $n$  megaspores are formed (Figure 1). Three of these megaspores degenerate and one becomes the functional megaspore and, after three mitotic divisions, forms the female gametophyte. Two meiotic mutants, resulting in the formation of  $2n$  eggs, have been identified in potato. One, named *omission of the second meiotic division* (*os*), is the predominant mechanism of  $2n$ -egg formation in *Solanum* species. A second mutation was described as *failure of cytokinesis* (*fc*), which takes place after the second meiotic division and is followed by nuclear fusion. Both of these variants are genetically equivalent to SDR mechanisms. Synaptic variants such as *sy-3* are also expressed in megasporogenesis, but restitution rarely results in a functional  $2n$  megaspore. For a review of synaptic mutants in potato, see Jongedijk and Ramanna (1988).

**Use of meiotic mutants in potato breeding:** The most significant contribution of meiotic mutants is their role as essential elements for the development of new breeding methods. The overall breeding strategy with meiotic mutants involves three main components: the wild and  $2x$  cultivated species are the "source" of genetic diversity; haploids of *Tuberosum* and *Andigena* provide a method for "capturing" the genetic diversity; and  $2n$  gametes are an effective and efficient way to "transmit" genetic diversity to cultivated forms. Genetic diversity includes both valuable qualitative and quantitative traits, as well as the allelic variation necessary to broaden the genetic base of the cultivated potato. The most successful new breeding scheme involves obtaining  $4x$  progeny from  $4x-2x$  crosses, where the  $2x$  parent forms  $2n$  pollen via the meiotic mutant *ps*. The essential ingredients of the breeding scheme, designated unilateral sexual polyploidization (USP), are illustrated in Figure 2. It is important to point out that normally, after USP,  $3x$  plants are not recovered because the  $5x$  endosperm associated with the  $3x$  embryo degenerate owing to EBN unbalance. The potentially wide application of the USP scheme and the often high levels of heterosis for tuber yield are strong indicators of its effectiveness. The yield of the USP-derived progenies regularly exceeds those of their respective  $4x$  parents (Tai 1994). Furthermore, individual clones selected from the  $4x-2x$  families have yields significantly higher than those of the respective  $4x$  parental cultivars (Buso *et al.* 1999c). The most successful use of USP has been by the largest potato-breeding program in the world at Rozalin, Poland. They used  $2x$  clones, involving several species that possessed multiple disease resistance genes and desirable tuber quality.

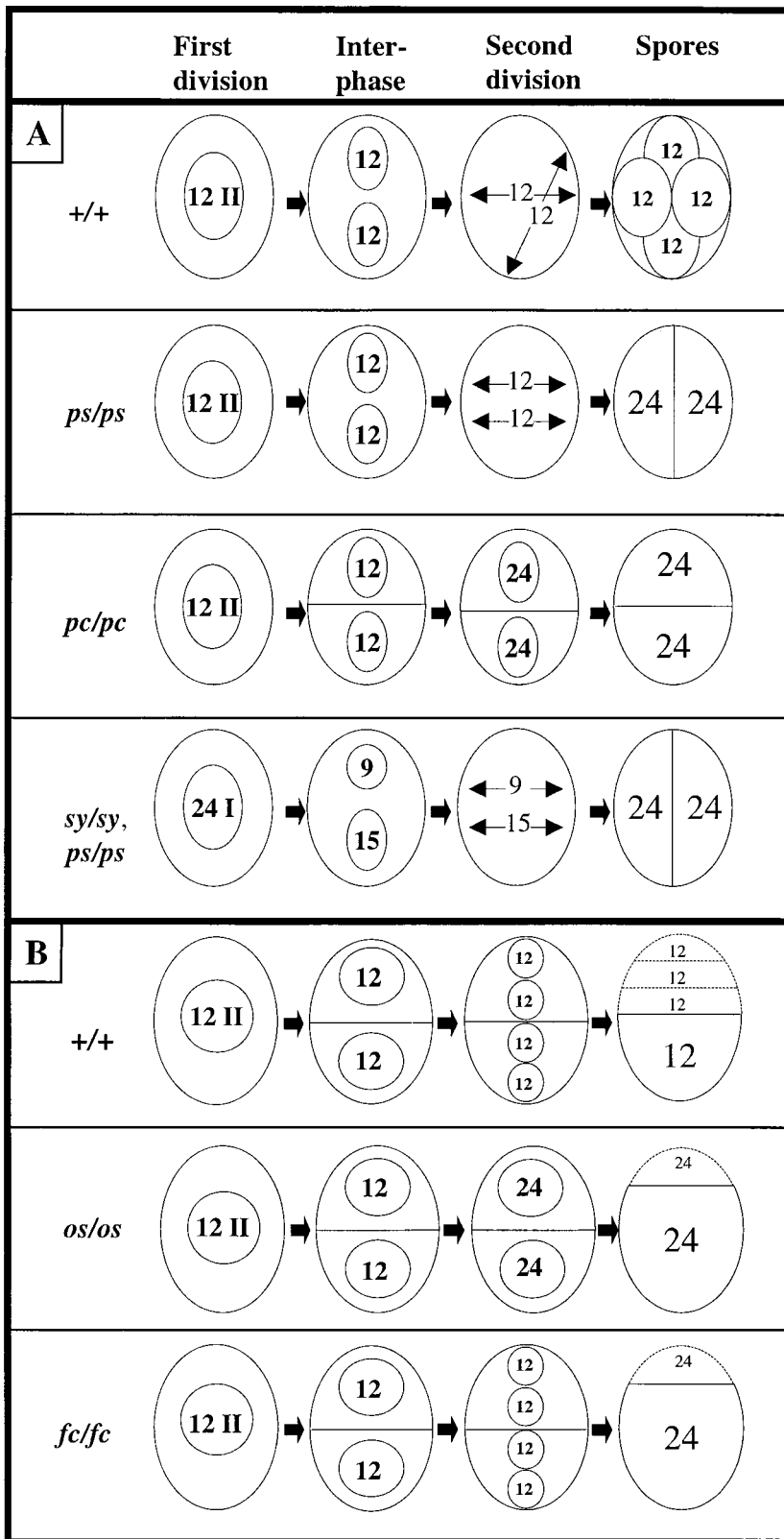


Figure 1.—Cytological consequences of meiotic mutants. (A) Microsporogenesis: ( $+/+$ ) wild type; ( $ps/ps$ ) parallel spindles; ( $pc/pc$ ) premature cytokinesis; ( $sy/sy; ps/ps$ ) synaptic-3 and parallel spindles in the same genotype. (B) Megasporesogenesis: ( $+/+$ ) wild type; ( $os/os$ ) omission of the second meiotic division; ( $fc/fc$ ) failure of cytokinesis.

USP was five times more effective than the conventional  $4x-4x$  (intra-Tuberosum) crosses in developing parental lines and cultivars (Zimnoch-Guzowska *et al.* 1999).

An alternative breeding scheme with meiotic mutants,

called bilateral sexual polyploidization (BSP), involves obtaining  $4x$  progeny from  $2x-2x$  crosses, where one  $2x$  parent forms  $2n$  eggs and the other  $2n$  pollen. The BSP strategy has great potential, providing the opportunity

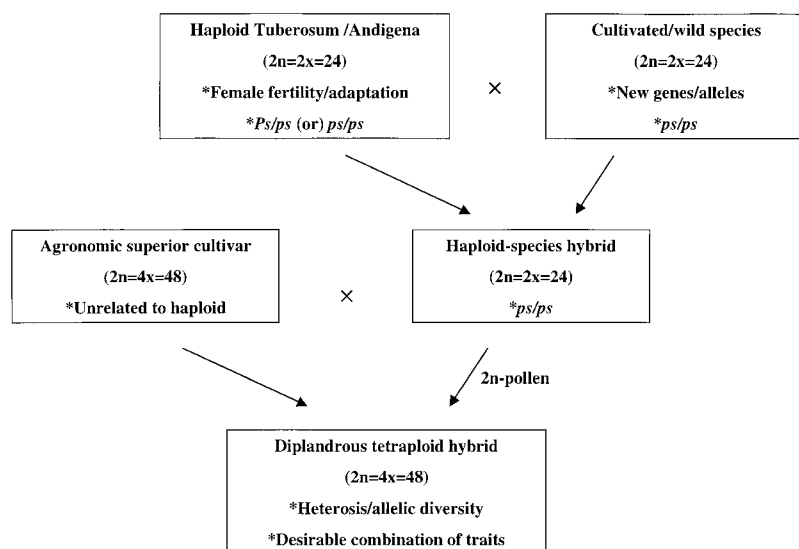


Figure 2.—Breeding strategy to obtain 4x hybrids from 4x–2x crosses.

to incorporate (via conventional or transgenic approaches) different desirable traits in the two 2x parents and then to combine them in the 4x progeny. In addition, tuber yields of 4x progenies derived from the BSP scheme also exceed those of standard 4x cultivars (Werner and Peloquin 1991).

**Germplasm transfer with meiotic mutants:** Among economic plants, the potato is unexcelled in the abundance of related germplasm resources. Several points need particular emphasis:

1. Any desirable trait for plant breeding appears to be available in related species. This includes resistance/tolerance to major biotic and abiotic stresses, important tuber quality characteristics, and all the allelic diversity needed to broaden the genetic base of the cultivated forms (Hanneman 1989).
2. Potato is also the easiest organism in which to incorporate the related germplasm into cultivated forms. Cytological investigations indicated very little differentiation between the chromosomes of the cultivated potato and those of most wild relatives. For example, when haploids of the cultivated potato are crossed with 24-chromosome wild species, the F<sub>1</sub> hybrids are vigorous and, most importantly, chromosome pairing and crossing over are essentially normal (Peloquin *et al.* 1989a).
3. The 4x–2x breeding scheme is an effective and efficient method of germplasm transfer from the cultivated and wild 2x species to 4x cultivars. The availability of so many traits in the wild germplasm, the widespread occurrence of the *ps* allele, the ease with which diploid 2n-gamete-producer species hybridize with 4x potato, and the ease of scaling-up interploid crosses strongly favor the 4x–2x approach as a valuable scheme for germplasm transfer. In fact, many investigators have used the USP strategy to transfer monogenic and polygenic traits from the wild germ-

plasm to the Tuberosum gene pool (for review see Ortiz 1998).

The formation of 2n gametes also provides a useful tool for transferring genes of interest from species that have developed reproductive isolating mechanisms. Several 2x species with EBN = 1 cannot be crossed with *S. tuberosum* haploids or other 24-chromosome species with EBN = 2. Similarly, some 4x species with EBN = 2 (which behave as diploids) cannot be crossed with *S. tuberosum* (EBN = 4). Crossing schemes based upon 2n gametes, ploidy manipulations, and ploidy bridges can be successfully employed for germplasm transfer among these incongruent species. For example, transferring of genes from the frost-tolerant species *S. commersonii* (2n = 2x = 24, 1EBN) was performed crossing a 4x(2EBN) clone of *S. commersonii* with 2x(2EBN) genotypes (Carputo *et al.* 1997). Triploid hybrids were generated and, through the function of 2n gametes, they were successfully crossed to the cultivated potato. The resulting 5x progeny could be easily crossed with *S. tuberosum* to continue the backcross program. It is important to point out that, in this example, 2n gametes represent balanced functional gametes of an odd-ploidy parent and also a tool for allowing the establishment of a compatible maternal to paternal EBN ratio after 3x(2EBN)–4x(4EBN) crosses.

**Use of meiotic mutants in genetics:** Meiotic mutants have been used to elucidate several areas of genetic research. The first involves gene-centromere mapping by half-tetrad analysis with 4x–2x crosses, where the 2x parent forms 2n pollen by either FDR (*ps/ps*) or SDR (*pc/pc*) (Mendiburu and Peloquin 1979). Since two of four strands of a bivalent are recovered together in 4x progeny from crossing a 4x nulliplex (*aaaa*) with a 2x heterozygous (*Aa*), the frequency of 4x nulliplex progeny provides an estimate of gene-centromere map distance. Through half-tetrad analysis, a number of phe-



notypic and isozyme loci have been mapped (Ortiz 1998).

The second application involves pyramiding of distinct meiotic mutations in the same genetic background. For example, clones with the doubly homozygous genotype *ps/ps*, *sy-3/sy-3* are able to produce  $2n$  gametes by a mechanism equivalent to FDR without crossover (FDR-NCO). These gametes transmit the parental genotype virtually intact to their progenies. The FDR-NCO  $2x$  clones provide a homogeneous sample of heterozygous gametes for testing the parental value of  $4x$  clones (Pelouquin 1983). Factorial  $4x-2x$  crosses using  $2x$  (FDR-NCO) male parents allow the unique opportunity to estimate the relative contribution of the random meiotic products (from the  $4x$  parents) and the “somatic” (non-recombinogenic) male genome to the phenotypic expression of quantitative traits.

Another application of meiotic mutants has been to permit genetic inference about the chromosomal (physical) location of quantitative trait loci (QTL) controlling important traits in potato. A large range of  $4x$  cultivars was crossed with a collection of full-sib  $2x$  clones able to transmit different fractions of their heterozygosity via  $2n$  gametes. Tuber yield of the progenies was then determined at different environments in three continents. One group of progenies was derived from FDR with crossing-over (FDR-CO) clones, where the  $2x$  parent transmits about 80% of the heterozygosity to the  $4x$  progeny. The other group was derived from FDR-NCO clones in which the  $2x$  parent transmits almost 100% of its heterozygosity and epistasis to  $4x$  progeny. Therefore, we would expect higher yields with 100% transmission of heterozygosity *vs.* 80% heterozygosity. However, no significant difference in total tuber yield between the two groups has been found in any of the experiments (Buso *et al.* 1999a,b). These results are interpreted to signify that loci with a major effect on yield are located between centromeres and proximal crossovers, since these regions are in common between the two groups of  $2x$  clones. This proximal hypothesis was first formulated by Tai and De Jong (1997) after comparing progenies derived from  $2x$  (FDR-CO) clones *vs.* progenies from their vegetatively (colchicine) doubled counterpart parents. Previous experiments with FDR-CO *vs.* SDR-derived families can now be reinterpreted as additional evidence for the proximal physical location of QTL affecting yield. In this latter case, the expected genetic superiority of the FDR-CO gametes was confirmed (Mok and Pelouquin 1975), which parallels their ability to transmit higher levels of heterozygosity at proximal regions. All the genetic analyses using meiotic mutants thus far are converging to one interesting notion: QTL with a major effect on yield are predominantly located in genomic regions with reduced levels of recombination (Buso *et al.* 1999a). In this context, breeding programs should develop strategies to maximize the transfer of heterozygosity to proximal loci, since

theoretical models also indicated that deleterious mutations would preferentially accumulate in these regions of the  $4x$  potato chromosomes.

Another genetic application of the meiotic mutants of the potato takes advantage of the simpler structure of  $2n$  gametes produced by  $2x$  genotypes, which makes quantitative genetic analyses much easier compared with the tetrasomic inheritance of the  $4x$  potato. For example, several  $4x-2x$  mating designs involving FDR and SDR  $2n$  gametes have been proposed by Tai (1994) for biometric studies and for placement of QTL in linkage maps.

**Application of meiotic mutants in cytology:** The nature of cytokinesis after the second meiotic division in microsporogenesis in dicots has been discussed for many years. The two competing hypotheses have been cell-plate formation *vs.* cleavage furrow formation. The meiotic mutant *ps* provided for an easier cytological examination of this problem compared with the normal complex tetrahedral arrangement. It was found that cytokinesis differed from both cell-plate formation and cleavage furrow (Stelly 1983). The *ps* mutant also has provided excellent material for an analysis of the role of  $\alpha$ -tubulin and F-actin in cytokinesis during microsporogenesis (Genuardo *et al.* 1998). The results suggested the key role for nonspindle cytoskeleton array occurring during telophase II to ensure  $2n$ -pollen formation. The meiotic mutant *pc* and the various synaptic mutants should provide valuable material for further research in this area.

**Meiotic mutants and evolution of *Solanum* species:** Polyploidy is a very important evolutionary mechanism in the Angiosperms. Likewise, polyploidization has been of considerable importance in the speciation process in potato. The ploidy level in the genus *Solanum* extends from  $2x$  to  $6x$ . Two mechanisms for the origin of polyploids have been proposed: (1) asexual by somatic doubling and (2) sexual through the functioning of  $2n$  gametes. The genetic evidence strongly favors sexual polyploidization in *Solanum* species (Den Nijs and Pelouquin 1977). We feel strongly that the high frequency of meiotic mutations that result in the formation of  $2n$  gametes provides the basis for the origin and evolution of the cultivated  $4x$  potato and for polyploids among the wild *Solanum* species.

We hypothesized that if *parallel spindles* were involved in the origin of the  $4x$  cultivated potato, then the frequency of *ps* allele should be higher in the  $4x$  than in the  $2x$  progenitors (Iwanaga and Pelouquin 1982). We examined a large number of plant introductions and thousands of plants of possible  $2x$  progenitors of  $4x$  Tuberosum and  $4x$  Andigena. The gene frequency for *ps* in the  $2x$  was 0.39 for *S. sparsipilum*, 0.34 for Group Stenotomum, and 0.28 for Group Phureja. In contrast, the gene frequency in  $4x$  Tuberosum was 0.69 and in  $4x$  Andigena was 0.82. The results convincingly support the hypothesis. Similar results were obtained with wild

species. The gene frequency in  $4x$  *S. gourlayi* was 0.80, 0.46 in  $2x$  *S. gourlayi*, and 0.37 in *S. infundibuliforme*, which are the two possible parents of  $4x$  *S. gourlayi* (Camadro and Peloquin 1980).

The high gene frequencies for meiotic mutants giving rise to  $2n$  pollen and  $2n$  eggs provide the opportunity for two important evolutionary events: (1) since these are inherited variations, we can have multiple origins of polyploidy and (2) they allow for continuous introgression of  $2x$  genes into  $4x$  and  $6x$  gene pools. An interesting feature of the *ps* plants is the simultaneous production of functional  $n$  and  $2n$  pollen. They thus have the best of all possible worlds in that  $n$  pollen allows them to hybridize with  $2x$  and via  $2n$  pollen with  $4x$  and  $6x$  plants.

The evolutionary advantage of sexual polyploidization over asexual polyploidization includes heterosis for plant vigor and yield, genetic variability, minimal inbreeding, change to establish new inter- and intralocus interactions, and high fertility. Of course, to obtain  $4x$  offspring from a cross between two  $2x$  individuals, both  $2n$  pollen and  $2n$  eggs are needed. We screened plants of  $2x$  wild species and haploids of  $4x$  *Tuberosum* for the frequency of plants producing  $2n$  eggs by the meiotic mutant *as* (Werner and Peloquin 1991). One-half of the haploids produced  $2n$  eggs and only about 24% of the wild  $2x$  species plants. Again, this supports the hypothesis that  $2n$  eggs were involved in the origin of cultivated  $4x$  potatoes.

During a cytogenetic investigation of intra- and inter-specific  $F_2$  hybrids, abnormal meiotic behavior was found in both types of hybrids (Wang and Peloquin 1999). This included poor pairing at pachytene, high frequency of univalents at metaphase I not related to poor pairing at pachytene, and increased chiasma frequency (5–10 ring bivalents per meiocyte *vs.* the normal with 1–2 ring bivalents per meiocyte). Further research established that all three variations were meiotic mutants controlled by recessive alleles. Thus, these meiotic variants are under strict genetic control. Therefore, caution must be taken in interpreting meiotic variations in interspecific hybrids as evidence of extensive genome differentiation between *Solanum* species, because they may, in fact, be the result of genetic lesions in one or a few genes.

**Future directions:** This *Perspectives* documents the value of meiotic mutants in potato research—particularly in the areas of new breeding methods, germplasm transfer from wild species to cultivated forms, and evolution of polyploid *Solanum* species. More important, at a recent international potato meeting held in Italy, with 570 delegates from 44 countries, it was clear that use of meiotic mutants to solve potato research problems would significantly accelerate in the future. We also believe that this broad exploitation of meiotic mutants is possible in other polysomic polyploid species such

as alfalfa, clover, cassava, sweet potatoes, bananas, and sugar cane.

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## LITERATURE CITED

- Buso, J. A., L. S. Boiteux, G. C. C. Tai and S. J. Peloquin, 1999a Chromosome regions between centromeres and proximal cross-overs are the physical sites of major effect loci for yield in potato: genetic analysis employing meiotic mutants. *Proc. Natl. Acad. Sci. USA* **96**: 1773–1778.
- Buso, J. A., F. J. B. Reifschneider, L. S. Boiteux and S. J. Peloquin, 1999b Effects of  $2n$ -pollen formation by first meiotic division restitution with and without crossover on eight quantitative traits in  $4x$ - $2x$  potato progenies. *Theor. Appl. Genet.* **98**: 1311–1319.
- Buso, J. A., L. S. Boiteux and S. J. Peloquin, 1999c Multitrait selection system using populations with a small number of inter-ploid ( $4x$ - $2x$ ) hybrid seedlings in potato: degree of high-parent heterosis for yield and frequency of clones combining quantitative agronomic traits. *Theor. Appl. Genet.* **99**: 81–91.
- Camadro, E. L., and S. J. Peloquin, 1980 The occurrence and frequency of  $2n$  pollen in three diploid *Solanums* from northwest Argentina. *Theor. Appl. Genet.* **56**: 11–17.
- Carputo, D., A. Barone, T. Cardi, A. Sebastiano, L. Frusciante *et al.*, 1997 Endosperm balance number manipulation for direct germplasm introgression to potato from a sexually isolated relative (*Solanum commersonii* Dun.). *Proc. Natl. Acad. Sci. USA* **94**: 12013–12017.
- Dawe, R. K., 1998 Meiotic chromosome organization and segregation in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **49**: 371–395.
- Den Nijs, T. P. M., and S. J. Peloquin, 1977  $2n$  gametes in potato species and their function in sexual polyploidization. *Euphytica* **26**: 585–600.
- Genuardo, G., A. Errico, A. Tiezzi and C. Conicella, 1998  $\alpha$ -Tubulin and F-actin distribution during microsporogenesis in a  $2n$  pollen producer of *Solanum*. *Genome* **41**: 636–641.
- Golubovskaya, I. N., and A. S. Mashnenkov, 1985 The cytogenetic evidence of the gene control of meiosis, pp. 723–738 in *Pollen: Biology and Implications for Plant Breeding*, edited by D. L. Mulcahy and E. Ottaviano. Elsevier, New York.
- Hanneman, Jr., R. E., 1989 Potato germplasm resources. *Am. Potato J.* **66**: 655–668.
- Hawley, R. S., 1993 Meiosis is an “M” thing: twenty years of meiotic mutants in *Drosophila*. *Genetics* **135**: 613–618.
- Iwanaga, M., and S. J. Peloquin, 1982 Origin and evolution of cultivated tetraploid potatoes via  $2n$  gametes. *Theor. Appl. Genet.* **61**: 161–169.
- Johnston, S. A., T. M. Den Nijs, S. J. Peloquin and R. E. Hanneman, Jr., 1980 The significance of genic balance to endosperm development in interspecific crosses. *Theor. Appl. Genet.* **57**: 5–9.
- Jongedijk, E., and M. S. Ramanna, 1988 Synaptic mutants in potato, *Solanum tuberosum* L. I. Expression and identity of genes for desynapsis. *Genome* **30**: 664–670.
- Kaul, M. L. K., and T. G. K. Murthy, 1985 Meiotic mutants in higher plants. *Theor. Appl. Genet.* **70**: 449–466.
- Lindsey, D., 1999 Larry Sandler: personal recollections. *Genetics* **151**: 1233–1237.
- Mendiburu, A. O., and S. J. Peloquin, 1979 Gene-centromere mapping by  $4x$ - $2x$  matings in potato. *Theor. Appl. Genet.* **54**: 177–180.
- Mok, D. W. S., and S. J. Peloquin, 1975 Breeding value of  $2n$  pollen (diplandroids) in tetraploid  $\times$  diploid crosses in potatoes. *Theor. Appl. Genet.* **46**: 307–314.
- Ortiz, R., 1998 Potato breeding via ploidy manipulation. *Plant Breed. Rev.* **16**: 15–86.
- Peloquin, S. J., 1983 Genetic engineering with meiotic mutants, pp. 311–316 in *Pollen: Biology and Implications for Plant Breeding*, edited by D. L. Mulcahy and E. Ottaviano. Elsevier Science, Amsterdam.
- Peloquin, S. J., S. H. Jansky and G. L. Yerk, 1989a Potato cytogenetics and germplasm utilization. *Am. Potato J.* **66**: 629–638.

- Peloquin, S. J., G. L. Yerk, J. E. Werner and E. Darmono, 1989b Potato breeding with haploids and  $2n$  gametes. *Genome* **31**: 1000–1004.
- Stelly, D. M., 1983 (I)  $2n$  female gametophytes in potato; and (II) Microsporocyte cytokinesis in potato. Ph.D. Thesis, University of Wisconsin-Madison.
- Tai, G. C. C., 1994 Use of  $2n$  gametes, pp. 109–132, in *Potato Genetics*, edited by J. E. Bradshaw and G. R. Mackay. CAB International, Wallingford, UK.
- Tai, G. C. C., and H. De Jong, 1997 A comparison of performance of tetraploid progenies produced by diploid and their vegetatively doubled (tetraploid) counterpart parents. *Theor. Appl. Genet.* **94**: 303–308.
- Wang, H., and S. J. Peloquin, 1999 Phenotypic and cytogenetic analyses of  $F_2$  progenies among four Argentine  $2x$  species. Proceedings of the 14th Trien. Conf. Euro. Assoc. for Potato Res., Sorrento, Italy, May 2–7, 1999, pp. 572–573.
- Werner, J. E., and S. J. Peloquin, 1991 Occurrence and mechanisms of  $2n$  egg formation in  $2x$  potato. *Genome* **34**: 975–982.
- Zimnoch-Guzowska, E., M. Sieczka, H. Jakuczun and L. Domansky, 1999 Diploid and tetraploid parental line breeding focused on resistance to pathogens and quality traits. Proceedings of the 14th Trien. Conf. Euro. Assoc. for Potato Res., Sorrento, Italy, May 2–7, 1999, pp. 329–330.