Potato has a variety of reproductive uniquenesses besides its clonal propagation by tubers. These traits are controlled by a different kind of genetic control. The reproductive information has been applied to enable interspecific hybridization to enhance valuable traits, such as disease and pest resistances, from the tuber-bearing Solanum gene pool. While progress has been made in potato breeding, many resources have been invested due to the requirements of large populations and long time frame. This is not only due to the general pitfalls in plant breeding, but also due to the complexity of polyploid genetics. Tetraploid genetics is the most prominent aspect associated with potato breeding. Genetic maps and markers have contributed to potato breeding, and genome information further elucidates questions in potato evolution and supports comprehensive potato breeding. Challenges yet remain on recognizing intellectual property rights to breeding and germplasm, and also on regulatory aspects to incorporate modern biotechnology for increasing genetic variation in potato breeding.

**Key Words:** polyploidy, tetrasomic inheritance, reproductive biology, potato genome.
different species, such as *Brassica* (Nishiyama and Inomata 1966, Nishiyama *et al.* 1991), *Impatiens* (Arisumi 1982), and *Trifolium* (Hussain and Williams 2008), and the concept can be applied to many different taxa in relation to interspecific hybridization.

**2n gametes:** The common occurrence of 2n gametes is a unique feature of tuber-bearing *Solanum* (Iwanaga and Peloquin 1982, Watanabe and Peloquin 1989, 1991, Watanabe *et al.* 1991). The 2n gametes are gametes with a somatic chromosome number, often mixed with unreduced gametes. Unreduced gametes are gametes without genetic recombination during the process of gamete formation, which implies no genetic reduction and no reduction of chromosome number. The 2n gametes contribute to polyploidization and enable introgression from diploid to polyploidy taxa (Carputo *et al.* 2003, den Nijs and Peloquin 1977). Ploidy manipulation can be systematically performed with knowledge of the EBN and use of 2n gametes to utilize the wild species gene pool in cultivated potato breeding (Hanneman 1994, Johnston and Hanneman 1982). The 2n gametes occur widely in angiosperm and they are likely a common mechanism of polyploidization (Harlan and De Wet 1975). Furthermore, 2n gametes have been used for ploidy manipulation in breeding in many taxa of higher plants (Dewitte *et al.* 2012).

The 2n gamete formation is genetically controlled by simple genetic mechanisms, such as parallel spindles (ps) and premature cytokinesis (pc) in microsporogenesis, which are recessive. The ps gene results in meiotic variation at the second metaphase with parallel orientation of spindle fibers of two chromosome division plates; consequently, the two microspores end up with an unreduced number of chromosomes after cytokinesis instead of a four microspore formation, which is genetically equivalent to first division restitution (FDR) in meiosis (Mok and Peloquin 1975a, 1975b). The pc gene induces premature cytokinesis right after the first division, which is genetically equivalent to second division restitution (SDR). The frequency of 2n pollen varies in different environments, but selection of diploid breeding lines with stable 2n pollen production is feasible (Watanabe *et al.* 1994, 1995b, 1996a, 1996b). Female 2n gametes have been reported and they exhibit simple inheritance (Iwanaga 1984, Werner and Peloquin 1991).

The genetic significance of 2n gametes is that they are crucial for potato germplasm enhancement. Heterozygosity and allelic interactions are important for many traits, so it is essential to support conservation transmission of parental heterozygosity to the progeny (Carputo *et al.* 2003). FDR 2n gametes transmit 100% of parental heterozygosity between a centromere and first crossing-over and 50% from the crossing-over to the distal end of a chromosome (**Fig. 1**). Likewise, SDR 2n gametes transmit 0% of parental heterozygosity between a centromere and first crossing-over and 100% from the crossing-over to the distal end of a chromosome. Overall, FDR 2n gametes, a result of the ps gene, average 80% of the parental heterozygosity, and the SDR gametes, a result of the pc gene, average 40% of the parental

---

**Table 1.** Reproductive features associated with potato breeding using tuber-bearing *Solanum* spp.

| Feature                        | Association with breeding                                      | Key references                                                                 |
|-------------------------------|----------------------------------------------------------------|--------------------------------------------------------------------------------|
| Tetraploid                     | Complex and large segregating population                      | Allard (1960), Bradshaw (1994)                                                 |
| Odd ploidyies (3x, 5x)         | Ending up with further sexual hybridization                   | Marks (1966)                                                                   |
| 2n gametes                    | Facilitating use of diploid gene pool in tetraploids by interploidy crosses | den Nijs and Peloquin (1977)                                                   |
| Dihaploid                     | Assisting capturing diversity and selection at diploid level   | Hermansen and Verdenius (1973), Ortiz and Peloquin (1994)                      |
| Endosperm Balance Number (EBN) | Providing prediction of hybridization success                 | Johnston *et al.* (1980), Johnston and Hanneman (1982)                         |
| Poor flowering in common cultivars | No cross hybridization                               | Ross (1986)                                                                    |
| Male sterility in common cultivars | Unilateral hybridization                                | Iwanaga *et al.* (1991a), Salaman (1910)                                       |
| Self-incompatibility at diploids | Limitation of crossing counterparts with the same incompatibility allele | Kaufmann *et al.* (1991), Pal and Nath (1942)                                  |

---

**Fig. 1.** Percentage of genetic constituents which can be transmitted by alternative genetic modes of 2n gametes. FDR and SDR indicate first division restitution and second division restitution, respectively. Based on one cross-over occurrence at a chromosome arm on potato, FDR 2n gametes can transmit an average of 80% and SDR results in an average 40% of parental genetic constituent.
hybridity (Mok and Peloquin 1975c).

**Haploids:** Dihaploids from tetraploids, which are diploid, occur naturally (Hougas and Peloquin 1958) and also can be introduced by pseudogametic parthenogenesis using special pollinators (Hermsen and Verdenieu 1973). Haploid production efficiency varies by pollinator (Peloquin et al. 1996). Haploids from tetraploids often do not flower and are also male-sterile due to inbreeding during the processes of haploidization. Haploidization can also be induced by another culture, but often the derived haploids do not have vigor compared with the ones by pseudogametic parthenogenesis (Ortiz and Peloquin 1994). However, those tissue culture-based haploids facilitated genetics study at the diploid level (Veilleux 1999) and germplasm enhancement for disease and pest resistances (Wenzel and Uhrig 1981).

Selection of haploids can lead to diploid breeding lines to obtain wild diploid genetic variation (Carputo et al. 2003, Hougas and Peloquin 1958) and F1 hybrids between the haploids, and wild species can be used as bridging genotypes to transfer useful traits from diploids to the tetraploid cultivated gene pool (Watanabe et al. 1995b). In addition, this type of haploid has been used to study the segregation of traits at the tetraploid level if many haploids are produced from one tetraploid genotype.

**Self-incompatibility:** Self-incompatibility occurs commonly in tuber-bearing Solanum species, especially at the diploid level. Self-incompatibility of diploid wild species results in genetic variation within a taxon, and allows outcrossing sexual reproduction with heterozygosity and vegetative propagation (tubers) under variable climatic conditions (Cipar et al. 1964). The locus S with multiple alleles controls gametophytic self-incompatibility (reviewed by Xu et al. 1990). The genetic structure of the S gene is rather simple: the S1 allele consists of two exons and one intron of 117bps with a total size of 786 bps (Kauffman et al. 1991). The S locus was identified on chromosome I (Gebhardt et al. 1991). A rare self-incompatibility-inducing mutant gene, Sli, has also been identified, and this unique mutant gene can enable pure genetic lines to be established to study the segregation of heterozygosity in potatoes (Hosaka and Hanneman 1998). The Sli gene was mapped at the distal end of chromosome XII; thus, the Sli gene is independent of the S locus.

**Male sterility:** Male sterility occurs often in tetraploid cultivars and related taxa (Grun et al. 1962). It is the consequence of nuclear-cytoplasm interactions; the dominant Ms gene interacts with the cytoplasm of S. tuberosum Group Tuberosum cultivars to cause male sterility and the dominant Rt gene restores fertility (Iwanaga et al. 1991a). For example, the diploid hybrids between S. tuberosum Group Tuberosum haploids × Group Phureja yield all or almost all male sterile progeny with the dominant Ms from Group Tuberosum influencing Tuberosum cytoplasm but the reciprocal cross results in fertile filial lines. The occurrence of male sterility often results in difficulties for potato breeders, as the choice of parental lines can restrict the introgression of traits. However, once information on the genotypes associated with male-sterility is organized, prediction can be made easily to choose parental lines for germplasm enhancement.

2. **Tetraploid genetics**

While progress has been made in potato breeding, many resources have to be invested due to the requirements of large populations and long time frame. This is not only due to the general pitfalls in plant breeding, but also due to the complexity of polyploid genetics. Tetraploid genetics is the most prominent aspect associated with potato breeding (Ortiz and Watanabe 2004, Table 2). Often, a trait controlled by a single gene can be quantitatively scored by phenotype due to its specificity in segregation (Fig. 2). Here, the term “polysomic polyploidy” from Mackey (1970) is used instead of the word “autopolyploid” used by Grant (1971), Stebbins (1950), and other botanists. Tetrasomic behavior of chromosomes and corresponding genetic segregation have been reported (Matsubayashi 1991, Swaminathan and Magoon 1961). However, variation was observed in frequency of quadrivalent formation in tetraploid cultivars.

Inter-locus interaction (epistasis) and heterozygosity are important factors in potato breeding, while additive components also contribute to quantitative traits. Identification of individual chromosomes is very difficult by conventional cytogenetic methods, while monitoring recombination and introgression is also difficult by phenotypic evaluation at the tetraploid level. Theoretical prediction of segregation has been supported by cytogenetic and genetic research, and these findings were tested and applied in potato breeding (Ross 1986).

There are four unique aspects of polyploids: 1) genotypic variation at a locus, 2) possibility of multiple alleles in a locus of the same genotype, 3) possibility of the occurrence of

| Feature          | Species example          | Segregation          | Multivalent in meiosis | Chromatid segregation | Fertility          | Key references                                      |
|------------------|--------------------------|----------------------|------------------------|------------------------|-------------------|----------------------------------------------------|
| Tetrasomic cultivars | tetraploid S. tuberosum | Tetrasomic and variable | Yes                     | Possible               | Low to medium | Allard (1960) Bradshaw (1994) Ortiz and Watanabe (2004) |
| Disomic species (4x, 6x) | polyploid 4x: S. acaule, S. stoloniferum, 6x: S. demissum | Disomic               | No                      | No                     | Very high       | Watanabe and Orrillo (1994)                         |

Table 2. Comparison of inheritance in tetraploid potatoes and polyploidy wild Solanum species
allelic interactions with multiple alleles, and 4) occurrence of chromatid segregation as well as chromosome segregation (Allard 1960, Bradshaw 1994).

1) Due to tetrasomic conditions, one locus accommodates four alleles, and with a diallelic locus, \( A \) and \( a \), five classes of genotype are possible: \( AAAA \), \( AAAa \), \( AAaa \), \( Aaaa \), and \( aaaa \). If an additive effect of an allele occurs, then one locus can result in considerable quantitative segregation (Fig. 2).

2) A diversity of multiple alleles is possible: each allele can have a different function, such as \( a_1 \), \( a_2 \), \( a_3 \), and \( a_4 \).

3) These different alleles can interact, resulting in various allelic interactions: diallelic, \( a_1a_2 \), \( a_1a_3 \), \( a_1a_4 \), \( a_2a_3 \), \( a_2a_4 \), \( a_3a_4 \); triallelic, \( a_1a_2a_3 \), \( a_1a_2a_4 \), \( a_1a_3a_4 \), \( a_2a_3a_4 \); or tetralelic \( a_1a_2a_3a_4 \). Thus, heterosis is not the only result of interaction between two alleles, but there a wide range of possibilities.

4) A locus distal to the centromere with a chance of crossing-over can be involved in chromatid segregation. For example, a locus with a diallelic condition and genotype \( Aaaa \) produces gametic output at a 1 : 1 ratio to \( Aa \) : \( aa \) by chromosome segregation and 15 : 12 : 11 by chromatid segregation, assuming random assortment of the homologous chromosomes and chromatids. Thus, a rare gametic genotype and zygotic progeny phenotype are possible. Another example is \( AAaa \) genotype which produces \( AA : aa = 1 : 1 \) with chromosome segregation and \( AA : Aa : aa = 3 : 8 : 3 \) ratio with chromatid segregation and larger phenotypic ratio could be expected as 208 : 1 if \( AAaa \) genotypes are inter-mated.

Even with chromosome segregation, tetrasomic tetraploid genetics is far more complicated than the diploid situation; moreover, the outcrossing nature and high heterozygosity of tetraploid potato cultivars cause more complications in segregation. Potato breeding objectives often involve quantitative traits which are highly influenced by the environment. Considering a wide range of phenotype variation with tetrasomic inheritance and environmental effects, a large true seed population is needed in crosses and subsequent phenotypic selection for successful potato breeding.

### 3. Interspecific hybridization

The genetic base of the potato cultivars is narrow, and could be very susceptible to new strains of pests and diseases, such as potato late blight, which resulted in the Great Irish Famine. While there are many wild relatives of potato, due to the variety of reproductive mechanisms resulting in genetic isolation from cultivated potato, germplasm enhancement has been developed with a variety of methods using the knowledge of reproductive biology and genetics (Jansky 2000). Further challenges in potato breeding are associated with the use of wild relatives with different reproductive and genetic characteristics (Table 1). Differences in ploidy can be overcome with the selection and use of \( 2n \) gametes, alleviating the elements listed in Table 1. However, technical trials are needed for successful interspecific sexual hybridization among distantly related genera. Past efforts are discussed below on the attempts to generate hybrids between non-tuber-bearing and tuber-bearing genera.

---

**Fig. 2.** One variation and complexity of zygotic outputs in polysomic polyploids. Assuming a diallelic model with complete dominant \( A \) and recessive \( a \) at a locus, genotypic and phenotypic segregation are displayed in the crosses from heterozygous parental genotypes. Ovals indicate genotypic segregation and squares show phenotypic segregation. Increase of ploidy requires far larger progeny population size for specific phenotypic selection.
Accumulated knowledge of reproductive biology and genetics of *Solanum* species, including some non-tuber-bearing species, has made it possible to use disomic tetraploid species (2EBN) (Iwanaga et al. 1991b, Watanabe et al. 1992, 1995c) and distantly related diploid wild species (1EBN), which often furnish high levels of important resistance. These species cannot be crossed directly with cultivated potato lines, as hybrids result in odd ploidy which do not allow for further introgression.

Embryo rescue combined with rescue pollination (second compatible pollination) can break down major cross incompatibility barriers in many wild *Solanum* species that contain resistance (*R*) genes of potential value, which cultivated potatoes do not have (Iwanaga et al. 1991b, Watanabe et al. 1992, 1994, 1995c). Yield performance also can be high due to introduction of unique alleles from a wild gene pool (Fig. 2). The sexual filial progeny have a use in interspecific hybridization. Previous approaches, including somatic hybrids, required complicated ploidy manipulation and/or bridging to introgress the valuable genes from these species, while the current new strategy uses simpler method(s). Developments in enhancement methods indicate the feasibility of introgression of tetraploid wild species, such as *S. acaule* and *S. stoloniferum* (Watanabe et al. 1992), and diploid non-tuber-bearing wild species, such as *S. brevidens* (Watanabe et al. 1995c), while generalization of these methods can be exploited to achieve genotype-independent success. Alleviating the problems in obtaining successful filial generations using different wild species also provides an opportunity for comparison of genetic efficiency with somatic fusion-derived hybrids using such species as *S. brevidens*, which furnishes many relevant resistances for potato breeding, such as resistance to potato leaf roll virus, tuber soft rot, and early blight.

This approach has been used by the potato breeding community for germplasm enhancement with wild species, as can be found easily in various papers. Protoplast fusion is another approach for using distantly related taxa. However, there has not been significant cultivar developed via this approach (Millam et al. 1995).

4. *Germplasm enhancement at the diploid level using haploids and 2n gametes and high heritability of traits from 2x to 4x*

Potato genetic improvement has been achieved by establishing systematic germplasm enhancement methods and breeding approaches. The International Potato Center (CIP) has contributed to international collaboration by establishing research networks with broad participation (Watanabe et al. 1995a). Germplasm enhancement with diploid tuber-bearing *Solanum* species, including some diploid cultivated taxa, has been performed in many potato breeding programs (Watanabe et al. 1995b, 1996a, 1996b, 1999a, 1999b, 1999c). The methods alleviate some of the bottlenecks that occur in conventional breeding at the tetraploid level. These involve two major biological tools: 1) haploids from 4x cultivars and 2) 2n gametes. Haploids from tetraploids can be obtained easily by pseudogametic parthenogenesis using a haploid inducing pollinator (Hermansen and Verdenius 1973, Hougas and Peloquin 1958), and are used to capture useful genes from wild or exotic germplasm. Breeding at the diploid level with disomic inheritance facilitates simultaneous selection for target resistance traits as well as some agronomic characteristics (Ortiz and Peloquin 1994). Transmission of useful traits from diploid breeding lines has been successfully achieved by the use of 2n gametes, especially using FDR 2n pollen, which occurs widely and frequently in the diploid tuber-bearing *Solanum* species. Furthermore, the concept of an EBN greatly assisted prediction of success in interspecific and/or interploidy crosses (Carputo et al. 2003, Hanneman 1994).

Using the above strategy, many potato cultivars have been established with successful quantitative disease and insect pest resistances (Watanabe et al. 1999a, 1999b, 2005). These resistance sources from wild species were transmitted to tetraploid breeding lines in a few years via germplasm enhancement methods (Watanabe and Watanabe 2000). Bacterial wilt, early blight, potato tuber moth, and root-knot nematode have been successfully introgressed into potato breeding lines. Consequently, multiple resistant diploid clones have been generated and used for tetraploid potato breeding.

Prediction of heterozygosity transmission by 2n gametes, which is associated with effective transmission of quantitative traits, is shown in Table 3. The estimation of transmission rate of quantitative traits from diploids to tetraploids via different genetic modes of 2n gametes is given in Table 3. A simple genetic model is presented as percentage of 2n gametes with desirable allelic combination for QTLs, assuming complete dominance at each locus and dominant alleles are responsible for the trait, an additive effect over loci and P value, and probability of crossing-over between a locus of interest and the centromere. The expected outcome was the percentage of progenies with high frequencies of alleles/loci responsible for a quantitative trait.

| # loci | FDR p = 0 | FDR p = 0.5 | FDR p = 1.0 | SDR p = 0 | SDR p = 0.5 | SDR p = 1.0 |
|-------|-----------|-------------|-------------|-----------|-------------|-------------|
| 1     | 100       | 87.5        | 75.0        | 50        | 75.0        | 100         |
| 2     | 100       | 76.6        | 56.3        | 50        | 56.3        | 100         |
| 3     | 100       | 67.0        | 42.2        | 50        | 42.2        | 100         |
| 4     | 100       | 58.6        | 31.6        | 50        | 31.6        | 100         |
| 5     | 100       | 51.3        | 23.7        | 50        | 23.7        | 100         |
| 6     | 100       | 44.9        | 17.8        | 50        | 17.8        | 100         |
| 7     | 100       | 39.3        | 13.3        | 50        | 13.3        | 100         |
| 8     | 100       | 34.4        | 10.0        | 50        | 10.0        | 100         |
| 9     | 100       | 30.1        | 7.5         | 50        | 7.5         | 100         |
| 10    | 100       | 26.3        | 5.6         | 50        | 5.6         | 100         |

Table 3. Transmission estimation of multiple loci with heterozygosity by 2n gametes. FDR is first division restitution and SDR is second division restitution. The p indicates the frequency of a crossing-over between the centromere and a locus.
By comparison with 4x × 4x mating, 4x × 2x crosses are favored when high allelic frequency for the resistance do not exist in the tetraploids. On the other hand, when a high allelic frequency occurs in the tetraploids, 4x × 4x is favored over 4x × 2x. The overall outcome from the simulation showed that 4x × 2x with FDR was generally more desirable. The results can be used in conjunction with the existing genetic map information to determine an optimum population size in 4x × 2x progenies (Watanabe et al. 1999a, 1999b, Watanabe and Watanabe 2000).

II. Molecular markers and Genome research

1. Genome research

The potato genetic and genome research communities established research resource databases together with other plant science groups. The SOL Genomics Network (SGN) (http://solgenomics.net/, Mueller et al. 2005) was derived from the Tomato Genetics Cooperative (TGC) but now supports all Solanaceae species. The SGN provides information on maps & markers, genes, genomes & sequences, breeding tools, pathways, and phenotypes all in one site.

Potato genome research has been effectively supported by tomato genome information due to the high synteny between their genomes and their close molecular evolutionary relationship (Bonierbale et al. 1988). Tomato genome information has been employed for marker exploitation for potatoes, such as COS (Conserved Ortholog Set) (http://solgenomics.net/markers/cos_markers.pl) (Fulton et al. 2002) and COSII (http://solgenomics.net/markers/cosii_markers.pl) (Wu et al. 2006). The COS was developed originally by screening an extensive tomato expression sequence tag (EST) database against the Arabidopsis genomic sequence. The first COS contained 1,025 genes that are single or low copy in both genomes. The COSII was the result of extensive expansion of comparative assessment of the genome database. Lindqvist-Kreuze et al. (2013) applied the COS to 300 genes using eight accessions of tuber-bearing Solanum species. These gene sequences were mapped with a BLASTN algorithm. They found that the majority of the genes are single copy and corresponded well with the tomato genome, but some showed repetitiveness with unexpected location in the potato genome. The effectiveness of COS markers has been proven by different taxa beyond Solanum, such as Lycium (Levin et al. 2009), Manihot esculentum (Castelblanco and Fregene 2006), Rosaceae (Cabrera et al. 2009), and Theobroma cacao (Khun et al. 2012).

The Potato Genome Sequence Consortium (PGSC) was established (http://www.potatogenome.net/index.php/Main_Page) and all of the genome information has been released (PGSC 2011). The PoMaMo database (Meyer et al. 2005) once supported genome research, but now it is integrated into the potato genome under the PGSC. The database is available at http://solanaceae.plantbiology.msu.edu/pgsc_download.shtml (Sharma et al. 2013).

Diploid potato has an estimated genome size of 844 Mb (Bennett et al. 1997, PGSC 2011). The PGSC has sequenced two diploid potato genotypes: the heterozygous diploid S. tuberosum Group Tuberosum genetics line RH89-039-16 (RH) and the doubled monoploid S. tuberosum Group Phureja clone DM1-3 (DM). The major achievements are as follows:

1) Sequence information was assembled with 86% of the whole genome of the doubled-monoploid potato clone, and 39,031 protein-coding genes were predicted.
2) A palaeopolyploid origin was also proposed with two major gene duplication events.
3) Presence of potato-specific genes was indicated for 2,642 genes.
4) Sequence of the heterozygous diploid clone indicated that gene presence/absence variants and other potentially deleterious mutations occur frequently and are a likely cause of inbreeding depression.
5) Tuber development evolved from gene family expansion, tissue-specific expression, and recruitment of genes to new metabolic pathways.

Potato research has benefitted from overall advances in the plant sciences and biotechnology. Here are some examples: carbohydrate metabolism, plant hormone interaction with tuberization, tissue culture for germplasm conservation and clean seed tuber production, pathogen detection methods, and transgenic approaches (Watanabe et al. 1997). Tuberization is controlled by day length (Rodríguez-Falcón et al. 2006, Seabrook et al. 1991) and plant hormones, such as gibberellin and jasmonic acid (Amador et al. 2001, Pruski et al. 2001). Each potato genotype tuberizes under only the given day-length requirement with specific physiological conditions. While simplified in vitro studies have been conducted, so far no elucidation of the genetic system of tuberization has been reported and it is considered a complicated genetic system (Brown 2007, Struik et al. 1999).

A novel finding in the plant science community has opened a new arena for studying tuberization. The mobile FLOWERING LOCUS T (FT) protein is a main component of long-range ‘florigen’, or flowering hormone, which was originally identified in Arabidopsis thaliana (Kobayashi et al. 1999). Trangenic short-day tuberizing potato genotypes with FT induce tuberization under long-day conditions (Navarro et al. 2011). Using the genome sequence (PGSC 2011) and information on FT, Kloosterman et al. (2013) identified the potato genomic element StSP6A, which induces mobile tuberization signal. The StSP6A signal resulted in the induction of tuber development at the stolon termini. They have postulated that diverse allelic variation of the gene is closely associated with the domestication of potatoes to diverse latitudes with corresponding different day lengths.
2. Potato genetic map

The first potato genetic map was reported in 1988 using tomato RFLP (restriction fragment length polymorphism) markers (Bonierbale et al. 1988). Since potatoes are highly heterozygous, F1 mapping can be conducted using two heterozygous genotypes. Two linkage maps were obtained from a cross between a diploid clone of S. tuberosum Group Phureja and a diploid hybrid line from S. tuberosum Group Tuberosum × (S. tuberosum Group Phureja × S. chacoense). The alignment of the RFLP loci shows a high level of similarity to that of the tomato map and the major differences were paracentric inversions on three chromosomes.

Generation and uses of molecular markers in potato genome studies are listed in Table 4. With advances in molecular marker knowledge in general, the potato genetics community also has applied different markers. Many maps have been constructed and used for identifying specific loci, and markers have been used in breeding for specific traits.

AFLP (amplified fragment length polymorphism) markers are highly transferable between potato populations.

| Marker type | Number of loci or markers | cM | References | Comments |
|-------------|---------------------------|----|------------|----------|
| RFLP (restriction fragment length polymorphism) | 135 | 1189 | Bonierbale et al. (1988) | First potato map |
| RFLP | 141 | 690 | Gebhardt et al. (1989) | High heterozygosity observed in diploid genetics lines |
| RFLP | 304 | 1034 | Gebhardt et al. (1991) | Increase of mapped loci |
| RFLP | 1030 (average 1.2 cM interval) | 1276 | Tanksley et al. (1992) | Highly saturated map for comparison with tomato |
| RFLP, transposons, isozymes | 175 | 1120 | Jacobs et al. (1995) | Integration of known loci and new markers |
| AFLP (amplified fragment length polymorphism) | 770 | – | Vos et al. (1995) | AFLP used on potatoes and high resolution is possible |
| RGL (resistance gene-like fragment) | Concept generation for landmark | – | Leister et al. (1996) | Applicability for disease and pest resistances |
| SSR | 89 | – | Milbourne et al. (1998) | Fingerprinting |
| ISSR (inter simple sequence repeat) | 4 | – | Prevost and Wilkinson (1996) | Validation for fingerprinting |
| RAPD (random amplified polymorphism), RFLP | 100 | 606 | Hosaka and Hanneman (1998) | An example of target-trait-specific rapid generation of mapping |
| COS (Conserved Ortholog Set) | 1025 | – | Fulton et al. (2002) | Further validation of tomato-potato orthology |
| SSR | 156 | – | Ghislain et al. (2004) | 15 SSR marker sets selected as highly informative |
| SSR (simple sequence repeat, microsatellite) | 61 | – | Feingold et al. (2005) | EST-based SSR |
| Multiple gene family homologues (P450) | 15 primer pairs produced 27 loci | – | Yamanaka et al. (2003, 2005) | Simple approach to make a marker and map |
| AFLP | 10,305 (10,365 with markers such on CAPS, SCAR) | 751 maternal/773 paternal | Van Os et al. (2006) | Small number of progeny individuals with 130 and 381 AFLP primer combinations made over 10,000 markers |
| NB-LRR disease resistance gene homologues | 738 RGLs | 47 R genes physically mapped | Bakker et al. (2011) | BAC-based physical map of R genes |
| NB-LRR R genes | 438 | 370 R genes physically mapped | Jupé et al. (2012) |
| BAC physical map | 2800 contigs | 1.64 times the coverage of the genome | de Boer et al. (2011) | Foundation for genome sequencing |
| SNP (single nucleotide polymorphism), SSR, AFLP, DArT (diversity array technology) | 2469 | 936 | Sharma et al. (2013) | Integration of genetic and physical maps |
Microsatellite markers (also known as simple sequence repeats—SSRs) have assisted progress in mapping the potato genome (Provan et al. 1996), and are valuable for fingerprinting closely related genotypes (Milbourne et al. 1998). AFLP showed greater merit than multilocus SSRs for fingerprinting in a comparative study of RAPD (random amplified polymorphic DNA), ISSR (inter simple sequence repeat), AFLP, and SSR (McGregor et al. 2000) These can be made from the EST database (Feingold et al. 2005) and made more systematically by potato genome information (PGSC 2011).

With further advancement of genome research in plants, many relevant technologies can be applied to potato. DAfT (diversity array technology) (Wenzl et al. 2004) benefits potato genetics. Finally, new sets of markers have been applied with advances in genome sequencing (PGSC 2011). Single nucleotide polymorphism (SNP) has been used widely for marker generation in many species and many markers have been generated also in potatoes (Sharma et al. 2013).

3. Use of R gene information from potato genome

Potato and its related species furnish a diversity of resistances to diseases and pests. Classical genetics studies have been conducted on inheritance and R genes have specific gene name designations (Valkonen et al. 1996). These R genes have been mapped to different chromosomal locations. The key class of genes that comprise the vast majority of plant R genes contain a nucleotide-binding site (NBS) and leucine-rich repeat (LLR) domain, and they could be used as a genetic marker set (Leister et al. 1996). Mapping information of R genes and their homologues were integrated by Jupe et al. (2012). Many of the R genes for different pests and diseases are independent. The systematics of the R gene structure was postulated using 438 NB-LRR-encoding sequences. Bakker et al. (2011) linked the existing 82 disease and pest resistance loci using 738 NB-LRR disease resistance gene homologues. Further physical localization of 428 R genes has been achieved (Jupe et al. 2012). These studies have supported the implementation of marker-assisted selection (MAS) for potato breeding (Carrasco et al. 2009).

4. Potato virus Y discussion as an example of validation of markers

Extreme resistances (ERs) to potato virus Y (PVY) are available in various Solanum species, including the following: Ry_adg, Solanum tuberosum Group ANDIGENA (4x); Ry_aco, S. stoloniferum (4x); Ry_CH, S. hougasii (6x); Ry_plas, Group PHUREJA (2x); Ry_chac S. chacoense (2x); and Ry_br, S. brevidens (2x). Among potato-related Solanum species, the Ry gene is always dominant and shows ER expression in F1 hybrids produced by direct crossing between Solanum series Tuberosa and non-tuber-bearing S. brevidens (Series Etuberosa) (Valkonen et al. 1995). ER shows no symptoms with extremely low viral accumulation in inoculated seedlings, and cell death confines the virus (Valkonen et al. 1996). Some of these genes have been used in breeding and they have been mapped using these breeding lines and cultivars. Ry_adg was mapped on chromosome XI (Hårämaläinen et al. 1997). Ry_chc is on chromosome XII (Song et al. 2005) and Ry_chac is on chromosome IX (Sato et al. 2006).

The level of ER is the same among these Ry genes, and the resistance is controlled by a single dominant allele. There is no difference in the level of resistance at the simplex and quadriplex levels for the Ry allele. Thus, a RyRyryry genotype at the tetraploid has the same level of resistance as a RyRyRyRy genotype. Moreover, Ry genes have no additive effect by accumulation of the different Ry loci.

In nature, different genotypes or accessions of a species can furnish the same resistance type, but complete genetic identification, including chromosomal location, is required. Valkonen et al. (2008) compared different accessions of S. stoloniferum that confer ER to PVY. They compared the map positions and markers for Ry_chc identified by Song et al. (2005). Based on sequence analysis, they concluded that the Ry_chc gene from different accessions of S. stoloniferum can be selected with the same marker sets on chromosome XII.

There are also hypersensitive genes to PVY, designated Ny, which also provide some level of resistance (Valkonen et al. 1994). Ry is epistatic to Ny by prohibiting Ny expression. Ny is also valid for resistance breeding in potatoes, but resistance is lowered by high temperatures. Many Ny were obtained from different species and mapped to different chromosomal locations within the potato genome. Szajko et al. (2014) reported that Ny-2, conferring hypersensitive resistance to PVY, was mapped on chromosome XI in cultivar Romula, but this was not at the same genomic position as Ry_adg. The Ny-1 gene was mapped on chromosome IX using the pedigrees from cultivars Albatros and Sekwana.

An R gene is usually identified from a specific potato clone, and pedigree assessment is made on whether the resistance can be identified within the same introgression clone, and pedigree assessment is made on whether the resistance is lowered by high temperatures. Many Ny were obtained from different species and mapped to different chromosomal locations within the potato genome. Szajko et al. (2014) reported that Ny-2, conferring hypersensitive resistance to PVY, was mapped on chromosome XI in cultivar Romula, but this was not at the same genomic position as Ry_adg. The Ny-1 gene was mapped on chromosome IX using the pedigrees from cultivars Albatros and Sekwana.

An R gene is usually identified from a specific potato clone, and pedigree assessment is made on whether the resistance can be identified within the same introgression clone, and pedigree assessment is made on whether the resistance is lowered by high temperatures. Many Ny were obtained from different species and mapped to different chromosomal locations within the potato genome. Szajko et al. (2014) reported that Ny-2, conferring hypersensitive resistance to PVY, was mapped on chromosome XI in cultivar Romula, but this was not at the same genomic position as Ry_adg. The Ny-1 gene was mapped on chromosome IX using the pedigrees from cultivars Albatros and Sekwana.
starting from RFLP, CAPS, and then SCAR. With a SCAR, RYSC3, high association with \( R_y \) was reported (Kasai et al. 2000). This SCAR marker has been widely used in the pedigree programs of North America and Europe. Furthermore, Shiranita et al. (1999) reassessed RFLP markers using ADG2 as a probe, and they have identified general markers for \( R_y \) sources from different species consisting of 117 genotypes with 83% correspondence on ER and non-ER, including susceptibility and hypersensitivity. Validation of this marker set (RYSC3) has been confirmed by different potato breeding groups (Ottoman et al. 2009, Sagredo et al. 2009).

Likewise, several \( R \) genes to potato virus X (PVX) have been reported and they are located at different chromosomal positions (Ritter et al. 1991) but with identical types of resistances, such as ER and hypersensitivity (Tommiska et al. 1998, Valkonen et al. 1996). Furthermore, independence of the virus resistance loci to PVX have been reported (Tiwari et al. 2013).

With the accumulation of independent \( R \) gene information and validation of markers, MAS has enabled the establishment of multiple resistance genotypes (Gebhardt et al. 2006). MAS is effective (Ortega and Lopez-Vizcón 2012) but cost-effectiveness varies depending on how a potato breeding program pursues selection rates of target clones (Slater et al. 2013). There is a need for more coordinated collaboration in the potato research community so that various comparative advantages can be pooled for the overall benefit of potato improvement.

### 5. Example of MAS on quantitative traits

An example of MAS with a combination of molecular markers and graphic genotyping as well as the 2n gamete function is shown in Table 6. Molecular MAS of diploid potato parental lines was tested for quantitative insect resistances conferred by glandular trichomes derived from the diploid wild species \( S. berthaultii \). Diploid potato parental lines were characterized by RFLP, phenotypic trichome expressions, and insect resistances with small insects, such as aphids, potato tuber moths, and mites. Ideotyping of diploid parental lines was performed using the HyperGene computer program (Young and Tanksley 1989) using quantitative trait loci (QTL) information for glandular trichomes (Bonierbale et al. 1994). Progeny testing was conducted on those parents with RFLP-QTL ideotyping by trichome phenotypic observation and insect assays for resistances. Using the selected diploid parents, \( 2x \times 2x \) and \( 4x \times 2x \) crosses were made to test whether the QTL could be transmitted efficiently for glandular trichome expression, and if this could confirm insect resistances. The majority of the progeny in the \( 2x \times 2x \) and \( 4x \times 2x \) crosses showed Type A trichomes and Type A-mediated insect resistances, but Type B trichome expression was low. Thus, QTL information and the corresponding ideotyping on Type A trichomes are effective enough with the same genetic backgrounds on the glandular trichomes, but QTL for Type B trichomes should be elaborated for higher efficiency of obtaining trichome expression and insect-resistant progenies.

### Table 5. Validation history of the selection markers for marker-assisted selection on \( R_y \) that confers extreme resistance to potato virus Y (PVY) located near the proximal end of chromosome XI. Genotype implies representation of cultivars, breeding lines, and clones of wild species from different origins

| Marker type                                      | Correspondence with the target \( R_y \) phenotype | References                     |
|--------------------------------------------------|--------------------------------------------------|--------------------------------|
| RFLP (GP 125)                                    | 30/31 genotypes (96.7%)                          | Hämäläinen et al. (1997)     |
| RFLP (ADG2 probe, 3.5 kb fragment)               | 77/77 F1 progeny 112/117 genotypes (95.7%)       | Hämäläinen et al. (1998)     |
| CAPS (ADG2 fragment)                             | 77/77 genotypes (100%)                           | Sorri et al. (1999)           |
| RFLP (ADG2 probe, 10.5 kb fragment)              | 97/117 genotypes (83%) for different origins of \( R_y \) sources | Shiranita et al. (1999)       |
| SCAR (ADG2 fragment with RYSC3 primers)          | 103/103 genotypes (100%)                         | Kasai et al. (2000)           |

### Table 6. An example of QTL transmission on glandular trichome traits in potato: Frequency of Type A and B glandular trichomes in \( 4x \times 2x \) potato families

| Family | Female parent (4x) without trichomes (4x) | Male parent (2x) with Type A and B trichomes | A trichomes | Also with B trichomes | No trichomes | Total |
|--------|-------------------------------------------|-----------------------------------------------|-------------|----------------------|--------------|-------|
| 95.201 | Atlantic                                  | M200.38                                       | 100         | 8                    | 2            | 110   |
| 94.202 | Atzirba                                   | M200.38                                       | 82          | 35                   | 6            | 123   |
| 94.204 | Serrana.INTA                              | M200.38                                       | 86          | 17                   | 3            | 106   |
| 95.205 | Atlantic                                  | 94.104.37                                     | 30          | 97                   | 3            | 130   |
| 95.206 | Atzirba                                   | 94.104.37                                     | 18          | 99                   | 4            | 121   |
| 95.207 | Serrana.INTA                              | 94.104.37                                     | 15          | 102                  | 5            | 122   |
| 95.208 | Atlantic                                  | 94.106.21                                     | 16          | 83                   | 3            | 102   |
| 95.209 | Atzirba                                   | 94.106.21                                     | 10          | 100                  | 3            | 113   |
| Total  |                                           |                                               | 357         | 541                  | 29           | 927   |

(38.5%) (58.4%) (3.1%)
1. Partners and Industry

Potato is a key crop in global food security. Potato research is supported extensively by two major societies and some regional ones, such as ALAP (La Asociación Latinoamericana de la Papa, Latin America Potato Association, http://www.papaslatin.org) and APA (African Potato Association, http://www.africanpotatoassociation.org). Multi-sector interaction is facilitated by forums, such as the World Potato Congress (http://www.potatocongress.org), by amalgamating the interest of different communities to promote potato production and commercialization of potato products. The potato industry encompasses a wide range of activities. Potato variety development is critical for the seed potato industry, which produces raw potatoes for the fresh food market, processing for industrial materials, such as starch and alcohol, snack foods, frozen fries, and cooked preserved food.

2. Intellectual properties

The potato industry strongly protects intellectual property rights (IPRs) related to industrial applications, such as processing, product development, and trademarks. In addition, inventions from biotechnology and molecular biology are widely covered by intellectual property protection, especially by patents. Seed-tuber production and quality assurance have a strong association with proprietary technology, such as that on virus eradication, pathogen detection, large scale-production by tissue culture, and technical aspects of breeding, especially those related to selection at large plant breeding stations, that may be covered as trade secrets or even by utility patents (Chapman and Watanabe 2007, Watanabe 2011, Watanabe and Komamine 2004).

Specific examples of patents as representation of IPRs claimed on potato biotechnology and breeding applications are shown in Table 7. There are five specific issues. First, a new cultivar can be protected by a patent rather than by plant variety protection laws under the International Union for the Protection of New Varieties of Plants (UPOV) (UPOV, http://www.upov.int/portal/index.html.en). However, what are patentable items is debatable under the main IPR forums, namely, the WTO’s Trade-Related Aspects of Intellectual Property Rights (TRIPS) (http://www.wto.org/english/tratop_e/trips_e/trips_e.htm) and the World Intellectual Property Organization (WIPO) (http://www.wipo.int/portal/en/index.html), and there is no universal recognition of plant variety as a patentable item; thus, this issue has come under the UPOV scheme. Second, the public sector, including state universities, has filed and owns a variety of patents rather than use the UPOV scheme. Third, the Japanese private sector has been somewhat active in patent filing and use, and some key inventions have been covered, such as those by Kirin Co. Ltd.; however, no proactive research publication has been established by the private sector. In addition, these patents have been considered as inappropriate since they appear to have no further application. Fourth, a patent on genetic markers can be made to allow a diversity of free public users of markers. Such patents have been made by Kyoto University and the University of Tsukuba. Fifth, genes and their uses have been protected under the IPR system, and applications for commercial use often have been hindered due to the difficulty of integrating patent

| Table 7. Examples of patents associated with potato biotechnology and breeding applications sorted by the date of application. Sources are JPO (Japanese Patent Office), PTO (US Patent Office), and EPO (European Patent Office) |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Patent title | Representative patent or PCT | Date of application (dd/mm/yyyy) | Date of publication (dd/mm/yyyy) | Priority date | Inventor | Applicant |
| Potato variety ‘‘ND1538-1Russ’’ | US5434343 A | 02.03.1990 | 18.07.1995 | 02.03.1990 | R.H. Johansen | North Dakota State Univ. |
| Potato alpha-amylase gene | PCT/DK1990/000108 | 24.04.1990 | 12.02.1992 | 24.04.1989 | Kirsten Gausing, Jette D. Kreiberg | Danske Spritfabrikker |
| Lepidopteran insect-resistant transgenic potato plants | US 6100456 A | 16.03.1992 | 08.08.2000 | 16.03.1992 | Sticklen, M.B. and J. Cheng | Board of Trustees Operating Michigan State University |
| A novel SCAR marker for the gene Radye conferring extreme PVY resistance | JP3047022 (24.03.00) | 19.04.1999 | 31.10.2000 | 19.04.1999 | Furusawa, L., K. Watanabe and K. Kasai | Kyoto University |
| Gene promoters isolated from potato and use thereof | PCT/US2002/001287 | 18.01.2002 | 01.08.2002 | 23.01.2001 | Z. Dai, B.S. Hooker, L. Shi | Ziyu Dai, Brian S. Hooker, Lifang Shi |
| Novel meloidogyne-resistance gene and utilization thereof | PCT/JP02/12392, JP4320399 | 27.11.2002 | 02.10.2003 | 27.03.2002 | Watanabe, K. and J. Watanabe | Univ. of Tsukuba |
| Comprises transgenic potato which generates starch with modified viscosity and phosphate characteristics; for enhancing quality of paper, cardboard, adhesive, textile, plaster, concrete, fertilizer, medicine, and toothpaste; improving animal feeds | US7897760 B2 | 19.10.2006 | 01.03.2011 | 19.09.1995 | Kossmann, J. and R. Lorberth | BayerBioscience Gmb |
| Protein having glycoalkaloid biosynthese activity and gene encoding same | PCT/JP2011/069643 | 30.08.2011 | 08.03.2012 | 31.08.2010 | Sasaki, K. et al. | Kirin Holdings Ltd. |
licences. Financial resources and/or cross-licensing deals need to be considered for IPR coordination.

On the other hand, some extensive patents have influenced public research, limiting access and activity, such as indicated in Table 8, but many of those patents have now expired. However, private-public cooperation could provide an open arena for initially testing the utility of IPRs before making restrictions and limiting access and use of IPRs (James 2013, Qaim 2009). Key patents have expired or been terminated, making open use possible and helping the research community. This will provide flexibility for the potato breeding community by allowing free IPR platforms for cultivar development.

3. New technology application to breeding: Transgenic potatoes

Potato research has benefitted from transgenic applications. Since two papers in this potato special issue address related content extensively, this section addresses only safety and application for cultivar development. Field trials of transgenic potatoes are not only conducted in developed countries, but also have been conducted in Mexico for virus resistance, and in India and Bangladesh for late blight resistance.

Historical information on field dissemination of transgenic organisms in general can be obtained at Biotrack, maintained by the Organization for Economic Co-operation and Development (OECD) (http://www.oecd.org/science/biotrack/). This evolved functionally into two databases. FAO GM Foods Platform by the Food and Agriculture Organization of the United Nations (http://www.fao.org/food/food-safety-quality/gm-foods-platform/en/) and new testing information and importation decisions for Living Modified Organisms (LMOs), which is a legal term under the Cartagena Protocol on Biosafety (CPB) for the Convention on Biological Diversity (CBD), may be surveyed in the database of the Biosafety Clearing House Mechanism of CPB (http://bch.cbd.int/about/). LMOs are equivalent to transgenic organisms but with a wider coverage of organisms made by modern biotechnology. LMO is defined as a legal term in the CPB. Commercialization data is reported annually by the ISAAA (International Service for the Acquisition of Agri-biotech Applications) (James 2013) and updated by “Biotradestatus” (http://www.biotradestatus.com), supported by the Global Industry Coalition through CropLife International (http://croplife.org) on the regulatory and market status of agricultural biotechnology products.

Products made by new technology must be assessed for risk and relevant management should be established before dissemination for use. This information is essential for deciding whether the products can be used or not. Use of transgenes by genetic engineering enables the use of genetic variation which could not be incorporated by classical breeding methods. Transgene deployment requires the whole process of plant breeding—from selection of parents to release to farmers. Innovative traits from transgenes cannot be disregarded as a source of insect and disease resistances and abiotic stress tolerance if conventional genetic resources cannot be found (Watanabe et al. 1997, 2011).

Risk assessment and management strategies have been conducted on transgenic crops with respect to environmental and food safety (Watanabe and Komamine 2000). Global field assessment and/or importation approval cases of transgenic potato can be found at the Biosafety Clearing House Mechanism homepage of the CPB (https://bch.cbd.int/). Approval of commercial transgenic potatoes can be identified in the GM Approval database (http://www.isaaa.org/gmapprovaldatabase/default.asp) of the ISAAA. Transgenic potato risk assessment procedures can be found in the above databases and also found in the potato biology consensus document (OECD 1997), while geographic location(s) where transgenic potatoes are intended to be used should be examined in those specific locations. Field assessment of transgenic potatoes has also been conducted in the center of origin (Celis et al. 2004). It was reported that there is no harm to many non-target organisms in using nematode-resistant transgenic potato genotypes, but gene flow occurs to wild relatives of potato growing near the transgenic potato crops. The gene flow could increase fitness of wild relatives, but the report suggested that male sterility of the transgenic potatoes drastically reduces the possibility of gene flow out of crop fields and considered it to be a manageable issue.

4. Challenges in the 21st century

Cost-free proprietary technology transfer together with efforts to test new inventions and access their risks has been conducted on potatoes. In the 1990s, the ISAAA mediated between Monsanto and the Mexican public agriculture sector regarding transgenic potato technology on coat-protein virus resistances to PVY and PVX (reviewed in Altman and Watanabe 1995, Watanabe et al. 1997). While commercial varieties were not developed in Mexico, relevant experience on transgenic potatoes with risk assessment and management

Table 8. Examples of patents with an extensive coverage of content on plant biotechnology and breeding applications sorted by the date of application. Sources are PTO (USA Patent Office) and EPO (European Patent Office).

| Patent title | Representative patent, PCT, or notification # | Date of application (dd/mm/yyyy) | Date of publication of application | Priority date | Inventor | Applicant |
|--------------|---------------------------------------------|---------------------------------|-----------------------------------|---------------|----------|-----------|
| Vector for coat proteins for potato virus | US 4970168 A | 27.01.1989 | 13.11.1990 | 27.01.1989 | Turner, N.E. | Monsanto Co. |
| Modification of plant metabolism | EP438904 (GB19890028937) | 21.12.1990 | 11.08.1999 | 21.12.1989 | Burrel, M.M. and K.S. Blundy | Advanced Technologies (Cambridge) Ltd. |
| A method for obtaining plants with reduced susceptibility to plant-parasitic nematodes | WO 1993010251 A1 | 02.11.1992 | 27.05.1993 | 20.11.1991 | Sijmons et al. | Mogen Int. |
strategies was established from this case as well as the issue of IPR sharing.

Agricultural knowledge has to be shared for global food security, but in the past two decades, in the context of agricultural knowledge, including indigenous wisdom, intellectual property has been dealt with under different forums, such as the CBD (http://www.cbd.int) and WIPO (http://www.wipo.int). The paradigm has shifted from philanthropic sharing of agricultural knowledge in the global community to sovereignty rights and to individual protection of indigenous group ownership, especially small holders with no governmental assistance. Ownership must be recognized to avoid infringement of IPRs. However, no comprehensive system has been proposed to monitor, advise, mediate, and solve the potential conflicts of agricultural IPRs sustainably. Even with the modern variety protection under the UPOV, there is insufficient surveillance and identification of the appropriate use of the varieties at a global level. While science and technology must adhere to rigorous standards, global food security demands comprehensive systems to enable needed innovations and research products to reach end users both safely while respecting IPRs.

Acknowledgements

This paper was supported in part by a JST/JICA STREPS project, “Diversity Assessment and Development of Sustainable Use of Mexican Genetic Resources” and by Plant Transgenic Design Initiative at Gene Research Center, University of Tsukuba.

Literature Cited

Allard, R.W. (1960) Chapter 30. Inheritance in autotetraploids. Principles of Plant Breeding. John Wiley & Sons, New York, pp. 385–399.

Allman, D.W. and K.N. Watanabe (1995) (eds.) Plant Biotechnology Transfer to Developing Countries. R. G. Landes Co., Georgetown, Texas, USA, p. 300.

Amador, V., J. Bou, J. Martínez-García, E. Monte, M. Rodriéguez-Falco, E. Russo and S. Prat (2001) Regulation of potato tuberization by daylength and gibberellins. Int. J. Dev. Biol. 45: S37–S38.

Arisumi, T. (1982) Endosperm balance numbers among New Guinea species. J. Hered. 73: 240–242.

Bakker, E., T. Borm, P. Prins, E. van der Vossen, G. Uenk, M. Arens, A. Kozik, W. Howad, P. Arus, A.F. Iezzoni and E. van der Knaap (2009) Development and bin mapping of a Rosaceae Conserved Ortholog Set (COS) of markers. BMC Genomics 10: 562.

Carrasco, A., J.E. Chauvin, B. Trognitz, A. Pawlak, O. Rubio-Covarrubias and E. Zimnoch-Guzowska (2009) Marker-assisted breeding for disease resistance in potato. Potato Res. 52: 245–248.

Castelblanco, W. and M. Fregene (2006) SSCP-SNP-based conserved ortholog set (COS) markers for comparative genomics in cassava (Manihot esculenta Crantz). Plant Mol. Biol. Report. 24: 229–236.

Celim, C., M. Scurrah, S. Cowgill, S. Chumbiauca, J. Green, J. Franco, M. Main, D. Kiezebrink, R.G.F. Visser and H.J. Atkinson (2004) Environmental biosafety and transgenic potato in a centre of diversity for this crop. Nature 432: 222–225.

Chapman, J. and K.N. Watanabe (2007) Chapter 17. 6: Current issues on IP management for health and agriculture in Japan. pp. 1621–1650. In: Krattger, A. et al. (eds.) Mihr-Pipra Handbook of Best Practices for Management of Intellectual Property in Health and Agriculture. Univ. California, Davis, USA.

Cipar, M.S., S.J. Peloquin and R.W. Hougas (1964) Variability in the expression of self-incompatibility in tuber-bearing diplloid Solanum species. Amer. Potato J. 41: 155–162.

de Boer, J.M., T.J.A. Born, T. Jesse, B. Brugman, X. Tang, G.J. Bryan, J. Bakker, H. van Eck, R.G.F. Visser (2011) A hybrid BAC physical map of potato: a framework for sequencing a heterozygous genome. BMC Genomics 12: 594.

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.

Dewitte, A., K. Van Laere and J. Van Huylenbroeck (2012) Use of 2n Gametes in Plant Breeding. In: Abdurakhmonov, I. (ed.) Plant Breeding. In Tech. Riejeka, Croatia, pp. 59–81.

Feingold, S., J. Lloyd, N. Norero, M.W. Bonierbale and J. Lorenzen (2005) Mapping and characterization of new EST-derived microsatellites for potato (Solanum tuberosum L.). Theor. Appl. Genet. 111: 456–466.

Fulton, T. M., R. van der Hoeven, N. Eamnet and S. Danksley (2002) Identification, analysis, and utilization of conserved ortholog set markers for comparative genomics in higher plants. Plant Cell 14: 1457–1467.

Gebhardt, C., E. Ritter, T. Debener, U. Schachtchabel, B. Walkemeier, H. Uhrig and F. Salamini (1989) RFLP analysis and linkage mapping in Solanum tuberosum. Theor. Appl. Genet. 78: 65–75.

Gebhardt, C., E. Ritter, A. Barone, T. Debener, B. Walkemeier, U. Schachtchabel, H. Kaufmann, R.D. Thompson, M.W. Bonierbale, M.W. Galan et al. (1991) RFLP maps of potato and their alignment with the homologous tomato genome. Theor. Appl. Genet. 83: 49–57.

Gebhardt, C., D. Bellin, H. Henselewski, W. Lehmann, J. Schwarzfischer and J.P.T. Valkonen (2006) Marker-assisted combination of major genes for pathogen resistance in potato. Theor. Appl. Genet. 112: 1458–1464.

Ghislain, M., D.M. Spooner, F. Rodriguez, V. Villamón, J. Núñez,
C. Vásquez, R. Waugh and M. Bonierbale (2004) Selection of highly informative and user-friendly microsatellites (SSRs) for genotyping of cultivated potato. Theor. Appl. Genet. 108: 881–890.

Grant, V. (1971) Polyploidy. In: Grant, V. Plant Speciation. Columbia University Press, New York, pp. 283–353.

Grun, P., M. Aubertin and A. Radlow (1962) Multiple differentiation of plasmons of diploid species of Solanum. Genetics 47: 1321–1333.

Hämäläinen, J.H., K.N. Watanabe, J.P.T. Valkonen, A. Arihara, R.L. Piaested, E. Pehu, L. Miller and S.A. Slack (1997) Mapping and marker assisted selection for a gene for extreme resistance to potato virus Y. Theor. Appl. Genet. 94: 192–197.

Hämäläinen, J.H., V.A. Sorri, K.N. Watanabe, C. Gebhardt and J.P.T. Valkonen (1998) Molecular examination of a chromosomes region that contains resistance to potato virus Y and A potyvirus in potato. Theor. Appl. Genet. 96: 1036–1043.

Hanneman, R.E. Jr. (1994) Assignment of Endosperm Balance Numbers to the tuber-bearing Solanums and their close non-tuber-bearing species. Euphytica 74: 19–25.

Harlan, J.R. and J.M.J. De Wet (1975) On Ö. Winge and a prayer: the tenure of triploids in Solanum. Euphytica 15: 183–185.

Harris, P.M. (ed.) (1978) The Potato Crop. The scientific basis for improvement. Chapman & Hall, London, p. 730.

Hawkes, J.G. and M.T. Jackson (1992) Taxonomic and evolutionary implications of the Endosperm Balance Number hypothesis in potatoes. Theor. Appl. Genet. 84: 180–185.

Hermsen, J.G. Th. and J. Verdenius (1973) Selection from Solanum tuberosum group Phureja of genotypes combining high frequency haploid induction with homozygosity for embryo spot. Euphytica 22: 244–259.

Hijmans, R.J. and D.M. Spooner (2001) Geographic distribution of wild potato species. Am. J. Bot. 88: 2101–2112.

Hosaka, K. and R.E. Hanneman, Jr. (1998) 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.

Hougas, R.W. and S.J. Peloquin (1958) The potential of haploids in breeding and genetic research. Am. Potato J. 35: 701–707.

Hussain, S.W. and W.M. Williams (2008) The use of endosperm balance number for predicting gamete selection in complex polyploid interspecific Trifolium repens × T. nigrescens crosses. Plant Breed. 127: 518–523.

Ishidore, E., H. van Os, S. Andrzejewski, J. Bakker, I. Barrena, G.J. van Eck, O. Veldkamp and J. Reuten (2004) A genetic map of potato (Solanum tuberosum) integrating molecular markers, including transposons, and classical markers. Theor. Appl. Genet. 9: 289–300.

James, C. (2013) Global Status of Commercialized Biotech/GM Crops: 2013. ISAAA Brief 46–2013. New York.

Jansky, S. (2000) Breeding for Disease Resistance in Potato. In: Janick, J. (ed.) Plant Breeding Reviews, Volume 19, John Wiley & Sons, Inc., Oxford, UK.

Johnston, S.A., T.P.M. den Nijs, S.J. Peloquin and R.E. Hanneman, Jr. (1980) The significance of genomic balance to endosperm development in interspecific wheats. Theor. Appl. Genet. 57: 5–9.

Johnston, S.A. and R.E. Hanneman, Jr. (1982) Manipulations of Endosperm Balance Number overcome crossing barriers between diploid Solanums species. Science 217: 446–448.

Jupe, F., L. Pritchard, G.J. Etherington, K. Mackenzie, P.J.A. Cook, F. Wright, S.K. Sharma, D. Bolser, G.J. Bryan, J.D.G. Jones et al. (2012) Identification and localization of the NB-LRR gene family within the potato genome. BMC Genomics 13: 75.

Kasai, K., Y. Morikawa, V.A. Sorri, J.P.T. Valkonen, C. Gebhardt and K.N. Watanabe (2000) Development of SCAR markers to the PVY resistance gene Ryadv based on a common feature of plant disease resistance genes. Genome 43: 1–8.

Katsiotis, A., R.E. Hanneman, Jr. and R.A. Forsberg (1995) Endosperm Balance Number and the polar nuclei activation hypotheses for endosperm development in interspecific crosses of Solanaceae and Gramineae, respectively. Theor. Appl. Genet. 91: 848–855.

Kaufmann, H., F. Salamini and R.D. Thompson (1991) Sequence variability and gene structure at the self-incompatibility locus of Solanum tuberosum. Mol. Gen. Genet. 226: 457–466.

Khan, D., D. Livingstone III, D. Main, P. Zheng, C. Sasaki, F.A. Feltus, K. Mockaitis, A.D. Farmer, G.D. May, R.J. Schnell et al. (2012) Identification and mapping of conserved ortholog set (COS) II sequences of cacao and their conversion to SNP markers for marker-assisted selection in Theobroma cacao and comparative genomics studies. Tree Genet. Genomes 8: 97–111.

Kloosterman, B., J. Abelenda, M.M. Gomez, M. Oortwijn, J.M. de Boer, K. Kowitwanich, B.M. Horvath, H.J. van Eck, C. Smaczniai, S. Prat et al. (2013) Naturally occurring allele diversity allows potato cultivation in northern latitudes. Nature 495: 246–250.

Kobayashi, Y., H. Kaya, K. Goto, M. Ibawuchi and T. Araki (1999) A pair of related genes with antagonistic roles in mediating flowering signals. Science 286: 1960–1962.

Leister, D., A. Ballvora, F. Salamini and C. Gebhardt (1996) A PCR-based approach for isolating pathogen resistance genes from potato with potential for wide application in plants. Nat. Genet. 14: 421–429.

Levin, R.A., A. Whelan and J.S. Miller (2009) The utility of nuclear conserved ortholog set II (COSII) genomic regions for species-level phylogenetic inference in Lycium (Solanaceae). Mol. Phylogen. Evol. 53: 881–890.

Lindqvist-Kreuze, H., K. Cho, L. Portal, F. Rodriguez, R. Simon, L.A. Mueller, D.M. Spooner and M. Bonierbale (2013) Linking the potato genome to the conserved ortholog set (COS) markers. BMC Genetics 14: 51.

Machida-Hirano, R. (2015) Diversity of potato genetic resources. Breed. Sci. 65: 26–40.

Mackey, J. (1970) Significance of mating systems for chromosome and gametes in polyploids. Hereditas 66: 165–176.

Marks, G.E. (1966) The enigma of triploid potatoes. Euphytica 15: 285–290.

Matsubayashi, M. (1991) Phylogenetic relationships in the potato and its relatives. In: Gupta, P.K. and T. Tsuchiya (eds.) Chromosome
Engineering in Plants: Genetics, Breeding, Evolution Part B.
Elsevier, pp. 93–118.

McGregor, C.E., C.A. Lambert, M.M. Greyling, J.H. Louw and L. Warnich (2000) A comparative assessment of DNA fingerprinting techniques (RAPD, ISSR, AFLP and SSR) in tetraploid potato (Solanum tuberosum L.) germplasm. Euphytica 113: 135–144.

Meyer, S., A. Nagel and C. Gebhardt (2005) PoMaMo—a comprehensive database for potato genome data. Nucleic Acids Res. 33: D666–D670.

Milbourne, D., R.C. Meyer, A.J. Collins, L.D. Ramsay, C. Gebhardt and R. Waugh (1998) Isolation, characterization and mapping of simple sequence repeat loci in potato. Mol. Genet. Genet. 259: 233–245.

Millam, S., L.A. Payne and G.R. Mackay (1995) The integration of protoplast fusion-derived material into a potato breeding programme—a review of progress and problem. Euphytica 85: 451–455.

Mok, D.W.S. and S.J. Peloquin (1975a) Three mechanism of 2n pollen formation in diploid potatoes. Can. J. Genet. Cytol. 17: 217–225.

Mok, D.W.S. and S.J. Peloquin (1975b) The inheritance of three mechanisms of diploidoid (2n pollen) formation in diploid potatoes. Heredity 35: 295–302.

Mok, D.W.S. and S.J. Peloquin (1975c) Breeding value of 2n pollen (diploidoids) in tetraploid × diploid crosses in potatoes. Theor. Appl. Genet. 46: 307–314.

Mueller, L.A., T.H. Solow, N. Taylor, B. Skwarecki, R. Buels, J. Binns, C. Li, M.H. Wright, R. Ahrens, Y. Wang et al. (2005) The SOL Genomics Network. A comparative resource for Solanaceae biology and beyond. Plant Physiol. 138: 1310–1317.

Navarro, C., J.A. Abelenda, E. Cruz-Oró, C.A. Cuéller, S. Tamaki, J. Silva, K. Shimamoto and S. Prat (2011) Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. Nature 478: 119–122.

Nishiyama, I. and N. Inomata (1966) Embryological studies on cross incompatibility between 2x and 4x in Brassica. Jpn. J. Genet. 41: 27–42.

Nishiyama, I. and T. Yabuno (1978) Interspecific cross-incompatibility due to disturbed activation of the polar nuclei by the male nucleus. Breed. Sci. (Ishushaku zasshi) 28: 71–80.

Nishiyama, I., M. Sarashima and Y. Matsuzawa (1991) Critical discussion on abortive interspecific crosses in Brassica. Plant Breed. 107: 288–302.

OECD (1997) Series on Harmonization of Regulatory Oversight in Biotechnology No. 8. Consensus Document on the Biology of Solanum tuberosum Subsp. tuberosum (Potato). Environment Directorate, Organisation for Economic Co-operation and Development, Paris. p. 38.

Ortega, F. and C. Lopez-Vizcon (2012) Application of molecular marker-assisted selection (MAS) for disease resistance in a practical potato breeding programme. Potato Res. 55: 1–13.

Ortiz, R. and S.J. Peloquin (1994) Use of 24-chromosome potatoes (diploids and dihaploids) for genetic analysis. In: Bradshaw, J.E. and G.R. Mackay (eds.) Potato Genetics. CAB International, Wallingford, UK, pp. 133–154.

Ortiz, R. and K.N. Watanabe (2004) Genetic contributions to breeding polyploid crops. Recent Res. Devl. Genet. Breed. 1: 269–286.

Ottoman, R.J., D.C. Hane, C.R. Brown, S. Yilmaz, S.R. James and A.R. Mosley (2009) Validation and implementation of marker-assisted selection (MAS) for PVY resistance (RVyadm gene) in a tetraploid potato breeding program. Am. J. Potato Res. 86: 304–314.

Pal, B.P. and P. Nath (1942) Genetic nature of self- and cross incompatibility in potatoes. Nature 149: 246–247.

Peloquin, S.J., A.C. Gabert and R. Ortiz (1996) Nature of ‘pollinator’ effect in potato (Solanum tuberosum L.) haploid production. Ann. Bot. 77: 539–542.

Potato Genome Sequencing Consortium (2011) Genome sequence and analysis of the tuber crop potato. Nature 475: 189–195.

Prevost, A. and M.J. Wilkinson (1999) A new system of comparing PCR primers applied to ISSR fingerprinting of potato cultivars. Theor. Appl. Genet. 98: 107–112.

Provan, J., W. Powell and R. Waugh (1996) Microsatellite analysis of relationships within cultivated potato (Solanum tuberosum). Theor. Appl. Genet. 92: 1078–1084.

Pruski, K., P. Duplirissis, T. Lewis, T. Astatkie, J. Novak and P.C. Struik (2001) Jasmonate effect on in vitro tuberization of potato (Solanum tuberosum) cultivars under light and dark conditions. Potato Res. 44: 315–325.

Quim, M. (2009) The economics of genetically modified crops. Ann. Rev. Resour. Econ. 1: 665–693.

Ritter, E., T. Debener, A. Barone, F. Salamini and C. Gebhardt (1991) RFLP mapping on potato chromosome of two genes controlling extreme resistance to potato virus X (PVX). Mol. Gen. Genet. 227: 81–85.

Rodriguez-Falcón, M., J. Bou and S. Prat (2006) Seasonal control of tuberization in potato: Conserved elements with the flowering response. Ann. Rev. Plant Biol. 57: 151–180.

Ross, H. (1986) Potato breeding—Problems and Perspectives. Verlag Paul Parey, Berlin. p. 132.

Roupee van der Voort, J.N.A.M., P. van Zandvoort, H.J. van Eck, R.T. Folktserma, R.C.B. Hutton, J. Draaistra, F.G. Gommers, E. Jacobsen, J. Helder and J. Bakker (1997) Use of allele specificity of comigrating AFLP markers to align genetic maps from different potato genotypes. Mol. Gen. Genet. 255: 438–447.

Roupee van der Voort, J.N.A.M., H.J. Van Eck, J. Draaistra, P.M. van Zandvoort, E. Jacobsen and J. Bakker (1998) An online catalogue of AFLP markers covering the potato genome. Mol. Breed. 4: 73–77.

Sagredo, B., M. Mathias, C. Barriento, I. Acuña, J. Kalazich and J. Santos Rojas (2009) Evaluation of a SCAR RYSC3 marker of the \( R_{Yadm} \) gene to select resistance genotypes to potato virus Y (PVY) in the INIA potato breeding program. Chilean J. Agric. Res. 69: 305–315.

Salaman, R.N. (1910) Male sterility in potatoes, a dominant Mendelian character; with remarks on the shapes of the pollen in wild and domestic varieties. J. Linnean Soc. London, Botany 39: 301–312.

Sato, M., K. Nishikawa, K. Komura and K. Hosaka (2006) Potato virus Y resistance gene, \( R_{Yadm} \), mapped to the distal end of potato chromosome 9. Euphytica 149: 367–372.

Seabrook, J.E.A., S. Coleman and D. Levy (1991) Effect of photoperiod on in vitro tuberization of potato (Solanum tuberosum L.). Plant Cell Tissue Organ Cult. 34: 43–51.

Sharma, S.K., D. Bolser, J. de Boer, W. Amoros, M.F. Carboni, J.M. D’Ambrosio, G. de la Cruz, A. Di Genova, D.S. Douches et al. (2013) Construction of reference chromosome-scale pseudomolecules for potato: integrating the potato genome with genetic and physical maps. G3 (Bethesda) 3: 2031–2047.

Shirinata, A., K. Kasai, J.H. Hämäläinen, J.P.T. Valkonen and K.N. Watanabe (1999) Applicability of the resistance gene-like fragment ADG2 as an RFLP probe in selection of extreme resistance to potato Y potyvirus (PVY). Plant Biotechnol. 16: 361–369.

Slater, A.T., N.O.I. Cogan and J.W. Forster (2013) Cost analysis of the application of marker-assisted selection in potato breeding. Mol. Breed. 32: 299–310.
Song, Y.S., L. Hepting, G. Schweize, L. Hartl, G. Wenzel and A. Schwarzfischer (2005) Mapping of extreme resistance to PVY (RYw) on chromosome XII using anther-culture-derived primary dihaploid potato lines. Theor. Appl. Genet. 111: 879–887.

Sorri, V.A., K.N. Watanabe and J.P.T. Valkonen (1999) Predicted kinase-3a motif of a resistance gene analogue as a unique marker for virus resistance. Theor. Appl. Genet. 99: 164–170.

Stebbins, G.L. Jr. (1950) Variation and Evolution in Plants. Columbia University Press, New York, pp. 298–379.

Struik, P.C., D. Vreugdenhil, H.J. van Eck, C.W. Bachem and R.G.F. Visser (1999) Physiological and genetic control of tuber formation. Potato Res. 42: 313–331.

Swaminathan, M.S. and M.L. Magoon (1961) Origins and cytogenetics of the commercial potato. Advance in Genetics 10: 217–256.

Szajko, K., D. Strzelczyk-Żyta and W. Marczewski (2014) Ny-1 and Ny-2 genes conferring hypersensitive response to potato virus Y (PVY) in cultivated potatoes: mapping and marker-assisted selection validation for PVY resistance in potato breeding. Mol. Breed. 34: 267–271.

Tanksley, S.D., M.W. Ganal, J.P. Prince, M.C. de Vicente, M.W. Bonierbale, P. Broun, T.M. Fulton, J.J. Giovannoni, S. Grandillo and G.B. Martin (1992) High density molecular linkage maps of the tomato and potato. Genetics 132: 1141–1160.

Tiwari, J.K., S.K. Pandey, P. Poonam, S.K. Chakrabarti, J. Gopal and V. Kumar (2013) Molecular markers of Ryadg gene and serological assay reveal potato virus Y (PVY) resistance in the tetraploid Indian potato (Solanum tuberosum) germplasm. Indian J. Agr. Sci. 83: 397–401.

Tommissa, J., J.H. Hämäläinen, K.N. Watanabe and J.P.T. Valkonen (1998) Mapping of the gene Nfpho that controls hypersensitive resistance to potato virus X in Solanum phureja IvP35. Theor. Appl. Genet. 96: 840–843.

Valkonen, J.P.T., S.A. Slack, R.L. Plaisted and K.N. Watanabe (1994) Extreme resistance is epistatic to hypersensitivity resistance to potato Virus Y5 in a Solanum tuberosum subsp. andigena-derived potato genotype. Plant Disease 78: 1177–1180.

Valkonen, J.P.T., S.A. Slack, R.L. Plaisted, M. Orrillo and K.N. Watanabe (1995) Resistances to viruses in F1 hybrids produced by direct crossing between Solanum series Tuberosa and S. brevifrons using S. phureja for rescue pollinations. Plant Breed. 114: 421–426.

Valkonen, J.P.T., R.A.C. Jones, S.A. Slack and K.N. Watanabe (1996) Resistance specificities to viruses in potato: standardization of nomenclature. Plant Breed. 115: 433–438.

Valkonen, J.P.T., K. Wiegmann, J.H. Hämäläinen, W. Marczewski and K.N. Watanabe (2008) Evidence for utility of the same PCR-based markers for selection of extreme resistance to Potato virus Y controlled by Rysto of Solanum stoloniferum derived from different sources. Ann. Appl. Biol. 152: 121–130.

van Eck, H.J., J. Rouppe van der Voort, J. Draaijstra, P. van Zandvoort, E. van Enckevort, B. Segers, J. Peleman, E. Jacobsen, I. Barrera, G.L. Bryan, B. Caromel, B. Ghareeb, E. Isidore, W. de Jong, P. van Koert et al. (2006) Construction of a 10,000-marker ultradense genetic recombinant map of potato: providing a framework for accelerated gene isolation and a genome-wide physical map. Genetics 173: 1075–1087.

Veilleux, R.E. (1999) Anther culture of potato and molecular analysis of anther-derived plants as laboratory exercises for plant breeding courses. Hortotechnology 9: 585–588.

Vo, P., R. Hogers, M. Bleecker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, J. Pot, J. Peleman, M. Kuiper et al. (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res. 23: 4407–4414.

Watanabe, J.A., M. Orrillo and K.N. Watanabe (1999a) Frequency of multiple quantitative pest resistance traits in 4x × 2x crosses of potato. Breed. Sci. 49: 53–61.

Watanabe, J.A., M. Orrillo and K.N. Watanabe (1999b) Resistance to bacterial wilt (Pseudomonas solanacearum) of potato evaluated by survival and yield performance at high temperatures. Breed. Sci. 49: 63–68.

Watanabe, J.A., M. Orrillo and K.N. Watanabe (1999c) Evaluation of in vitro chromosome-doubled regenerates with resistance to potato tuber moth [Phthorimaea operculella (Zeller)]. Plant Biotechnol. 16: 225–230.

Watanabe, J.A. and K.N. Watanabe (2000) Pest resistance traits controlled by quantitative loci and molecular breeding strategies in tuber-bearing Solanum. Plant Biotechnol. 17: 1–16.

Watanabe, K.N. and S.J. Peloquin (1989) Occurrence of 2n pollen and ps gene frequencies in cultivated groups and their related wild species in tuber-bearing Solanums. Theor. Appl. Genet. 78: 329–336.

Watanabe, K.N. and S.J. Peloquin (1991) The occurrence and frequency of 2n pollen in 2x, 4x, and 6x wild, tuber-bearing Solanum species from Mexico, and Central and South America. Theor. Appl. Genet. 82: 621–626.

Watanabe, K.N., S.J. Peloquin and M. Endo (1991) Genetic significance of mode of polyploidization: somatic doubling or 2n gametes? Genome 34: 28–34.

Watanabe, K.N., C. Arbizu and P. Schmiediche. (1992) Potato germplasm enhancement with disomic tetraploid Solanum acaule. I. Efficiency in introgression. Genome 35: 53–57.

Watanabe, K.N. and M. Orrillo (1994) Disomic behavior of polyploid tuber-bearing Solanum species. Jpn. J. Genet. 69: 637–643.

Watanabe, K.N., M. Orrillo, M. Iwanaga, R. Ortiz, R. Freyre and S. Perez (1994) Diploid potato germplasm derived from wild and landrace genetic resources. Am. Potato J. 71: 599–604.

Watanabe, K.N., M. Orrillo and A.M. Golmizraie (1995a) Potato germplasm enhancement for resistance to biotic stresses at CIP. Conventional and biotechnology-assisted approaches using a wide range of Solanum species. Euphytica 85: 457–464.

Watanabe, K.N., M. Orrillo, S. Vega, M. Iwanaga, R. Ortiz, R. Freyre, G. Yerk, S.J. Peloquin and K. Ishiki (1995b) Selection of diploid potato clones from diploid haploid-species F1 families for short day conditions. Breed. Sci. (Ikushugaku zasshi) 45: 341–347.

Watanabe, K.N., M. Orrillo, S. Vega, A. Hurdado, J.P.T. Valkonen, E. Pehu and S.D. Tanksley (1995c) Overcoming crossing barriers between nontuber-bearing and tuber-bearing Solanum species: towards potato germplasm enhancement with a broad spectrum of Solanaceous genetic resources. Genome 38: 27–35.

Watanabe, K.N., M. Orrillo, S. Perez, J. Crusado and J.A. Watanabe (1996a) Testing yield of diploid potato breeding lines for cultivar development. Breed. Sci. (Ikushugaku zasshi) 46: 245–249.

Watanabe, K.N., M. Orrillo, S. Vega, S. Perez, J. Crusado, A.M. Golmizraie and J.A. Watanabe (1996b) Generation of pest resistant, diploid potato germplasm with short day adaptation from diverse range of genetic stocks. Breed. Sci. (Ikushugaku zasshi) 46: 329–336.

Watanabe, K., A.M. Golmizraie and P. Gregory (1997) Chapter 10: Use of Biotechnology Tools in Potato Genetic Resources Management.
and Breeding. In: Watanabe, K.N. and E. Pehu (eds.) Plant Biotechnology and Plant Genetic Resources for Sustainability and Productivity. R.G. Landes Co., Georgetown, Texas, USA, pp. 145–154.
Watanabe, K.N. and A. Komamine (2000) Challenge of Plant and Agricultural Sciences to the Crisis of Biosphere on the Earth in the 21st Century. Landes Bioscience, Austin TX, USA, p. 309.
Watanabe, K.N. and A. Komamine (2004) Issues on Intellectual Property Rights Associated with Agro-Biotechnology in Japan. In: Erbisch, F.H. and K.M. Maredia (eds.) Intellectual Property Rights in Agricultural Biotechnology. 2nd edition. Michigan State University, East Lansing and CAB International, Wallingford, UK, pp. 187–200.
Watanabe, K.N., R. Ortiz and J.A. Watanabe (2005) Chapter 4: Breeding Potential and Transmission of Traits in 4x-2x Crosses. In: Razdan, M.K. and A.K. Mattoo (eds.) Genetic Improvement of Solanaceous Crops, Vol. 2: “Potato”, Science Publishers Inc., USA, pp. 83–99.
Watanabe, K.N. (2011) Challenges for Conservation and Utilization of Plant Genetic Resources. pp. 99–107. Proceedings of NIAS-FAO International Symposium on Plant Genetic Resources for Food and Agriculture in Asia and Pacific: Impacts and future directions. NIAS and FAO RAP Bangkok, RAP Publication 2012/1. p. 118.
Watanabe, K.N., A. Kikuchi, T. Shimazaki and M. Asahina (2011) Salt and drought stress tolerances in transgenic potatoes and wild species. Potato Res. 54: 319–324.
Wenzel, G. and H. Uhrig (1981) Breeding for nematode and virus resistance in potato via anther culture. Theor. Appl. Genet. 59: 333–340.
Wenzel, P., J. Carling, D. Kudrna, D. Jaccoud, E. Huttner, A. Kleinhofs and A. Killian (2004) Diversity arrays technology (DArT) for whole-genome profiling of barley. Proc. Natl. Acad. Sci. USA 101: 9915–9920.
Werner, J.E. and S.J. Peloquin (1991) Occurrence and mechanisms of 2n egg formation in 2x potato. Genome 34: 975–982.
Wu, F., L.A. Muller, D. Crouzillat, V. Petiard and S.D. Tanksley (2006) Combining bioinformatics and phylogenetics to identify large sets of single-copy orthologous genes (COSH) for comparative, evolutionary and systematic studies: a test case in the euaserid plant clade. Genetics 174: 1407–1420.
Xu, B., P. Grun, A. Kheyr-Pour and T.-H. Kao (1990) Identification of pistil-specific protein associated with the self-incompatibility alleles in Solanum chacoense. Sex. Plant Reprod. 3: 54–60.
Yamanaka, Y., E. Suzuki, M. Tanaka, Y. Takeda, J.A. Watanabe and K.N. Watanabe (2003) Assessment of cytochorome P450 sequences offers a useful tool for determining genetic diversity in higher plant species. Theor. Appl. Genet. 108: 1–9.
Yamanaka, S., S. Ikeda, A. Imai, Y. Luan, J.A. Watanabe and K.N. Watanabe (2005) Construction of integrated genetic map between various existing DNA markers and newly developed P450-related PBA markers in diploid potato (Solanum tuberosum). Breed. Sci. 55: 223–230.
Young, N.D. and S.D. Tanksley (1989) Restriction fragment length polymorphism maps and the concept of graphical genotypes. Theor. Appl. Genet. 77: 95–101.