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Review

Potato genetics, genomics, and applications

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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.

I. Potato reproductive biology and genetics

1. Reproductive uniqueness

The diversity of potato species was discussed in a special issue by Machida-Hirano (2015) with respect to geographic distribution and species variation. Common cultivated potato varieties include tetraploid (2n = 4x = 48) with a basic chromosome number of 12, while there are cultivated species at the diploid (2n = 2x = 24) to pentaploid (2n =5x = 60) levels. The triploid and pentaploid cultivated species are grown only on highland plateaus and slopes of the Andes, but diploid cultivated species are grown more widely and also used for breeding tetraploid varieties. Wild and cultivated potato genetic resources provide a variety of reproductive and genetic features associated with species differentiation and breeding applications (**Table 1**). The number of species varies among the taxonomic classifications and around 200 wild species have been identified (Hawkes and Jackson 1992, Hijmans and Spooner 2001, also refer to Machida-Hirano 2015). The majority of the 200 wild species are diploid, and many of these diploids species can be crossed with tetraploids using 2n gametes, which can be easily found in potato genetic resources both in cultivated and wild species (Iwanaga and Peloquin 1982, Watanabe and Peloquin 1989, 1991, Watanabe *et al.* 1991).

Propagation: Potato can be propagated vegetatively by tubers, tissue culture, or even by cuttings (Harris 1978). Usually "seed" implies tuber propagules in the potato community, and true potato seed means botanical seed. Potato species can also produce true potato seeds. Potato fruit looks like a small green tomato. A fertile fruit can contain over 200 true potato seeds in tetraploid cultivars. While diploid wild species are often self-incompatible (Cipar *et al.* 1964, Pal and Nath 1942), the tetraploid cultivars and polyploidy species are self-compatible. Moreover, many polyploidy species are disomic polyploids with a selfing nature, but they have the potential to produce selfed true seed and tubers (Watanabe and Orrillo 1994).

Endosperm Balance Number: Species are sexually separated principally by their ploidy and Endosperm Balance Number (EBN; Hawkes and Jackson 1992). The EBN was hypothesized as a 2 maternal : 1 paternal EBN genic ratio in endosperm and embryo, and a gene dose of the EBN is a prerequisite for successful interspecific crossability based on normal endosperm development to support embryo survival (Johnston *et al.* 1980). The EBN is controlled by a few genes with a variety of alleles (Bamberg 1994). The concept of endosperm development and hybrid embryo success was independently developed originally by two groups: one by the potato group at the University of Wisconsin as the EBN (Johnston *et al.* 1980) and the other by Nishiyama and Yabuno (1978) as polar-nuclei activation indexed by activation/response values (AVs/RVs) on *Avena* and *Ipomoea*. Assignment of EBNs and AVs/RVs depends on plumpness, size, and germinability of hybrid seeds (Katsiotis *et al.* 1995). The applicability of the concept has been proven in

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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 ploidies (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	Hermsen 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)

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

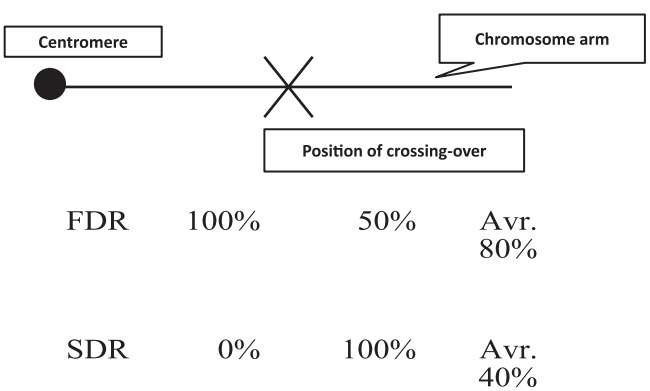

Fig. 1. Percentage of genetic constituents which can be transmitted by alternative genetic modes of 2n gametes. FDR and SDR indicate first division restitution and second division restitution, respectively. Based on one cross-over occurrence at a chromosome arm on potato, FDR 2n gametes can transmit 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 Pelqouin 1958) and also can be introduced by pseudogametic parthenogenesis using special pollinators (Hermsen and Verdeniu 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 F_1 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 S_2 allele consists of two exons and one intron of 117bps with a total size of 786 bps (Kaufmann *et al.* 1991). The *S* locus was identified on chromosome I (Gebhardt *et al.* 1991). A rare self-compatibility-inducing mutant gene, *Sli*, has also been identified, and this unique mutant gene can enable pure genetic lines to be established to study the breeding value 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

Table 2. Comparison of inheritance in tetraploid potatoes and polyploidy wild *Solanum* species

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)

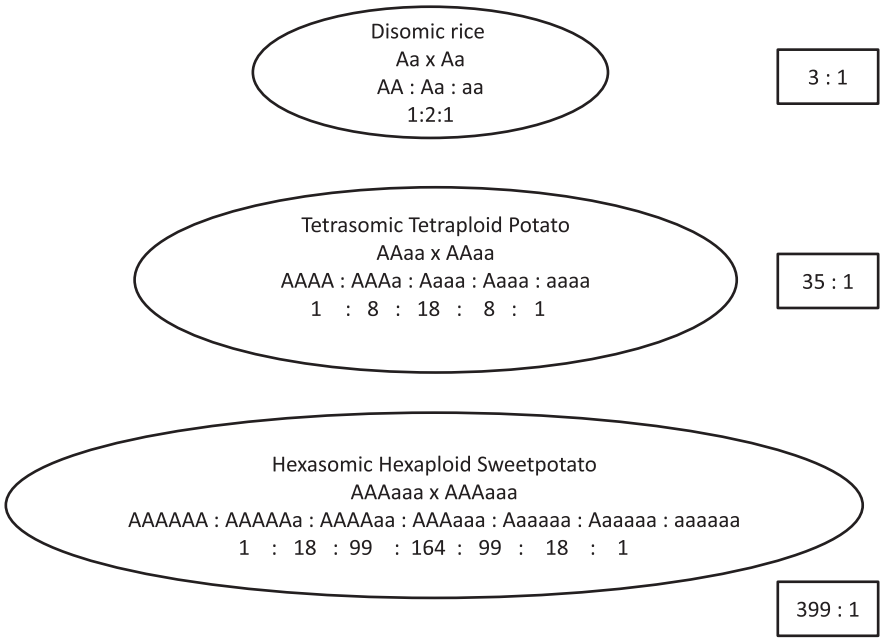

Fig. 2. One variation and complexity of zygotic outputs in polysomic polyploids. Assuming a diallelic model with complete dominant *A* and recessive *a* at a locus, genotypic and phenotypic segregation are displayed in the crosses from heterozygous parental genotypes. Ovals indicate genotypic segregation and squares show phenotypic segregation. Increase of ploidy requires far larger progeny population size for specific phenotypic selection.

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, $a_1a_2a_3$, $a_1a_3a_4$, $a_2a_3a_4$; or tetrallelic $a_1a_2a_3a_4$. 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 *15AA* : 12*Aa* : 1*aa* 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.

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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 ploidies 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 (Hermsen 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 diplopid 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.

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

# loci	FDR			SDR		
	p = 0	p = 0.5	p = 1.0	p = 0	p = 0.5	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

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 to make efficient selection in plant breeding. This theoretical information enabled the generation of multiple resistances to be transferred to 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), Rosaeae (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 poylmorphism) markers (Bonierbale *et al.* 1988). Since potatoes are highly heterozygous, F_1 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

Table 4. Representative potato genetic markers and maps

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) van Eck *et al.* (1995) Rouppe van der Voort *et al.* (1998)	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	Jupe *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

(Rouppe van der Voort *et al.* 1997, 1998). However, Ishidore *et al.* (2003) examined Linkage I with 1,260 loci, and there was a change in *Pst*I-site methylation patterns within a population. The map indicated highly variable recombination frequencies. Although the map indicated that centromeric regions were highly saturated and showed extensive marker clustering, some areas lacked AFLP markers. Currently, there is no miracle marker set to serve all purposes.

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 polymporphic 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 systematical by potato genome information (PGSC 2011).

With further advancement of genome research in plants, many relevant technologies can be applied to potato. DArT (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}, *Solanun tuberosum* Group ANDIGENA (4x); Ry_{sto}, *S. stoloniferum* (4x); Ry_{hou}, *S. hougasii* (6x); Ry_{phu}, Group PHUREJA (2x); Ry_{chc}, *S. chacoense* (2x); and Ry_{brd}, *S. brevidens* (2x). Among potato-related *Solanum* species, the *Ry* gene is always dominant and shows ER expression in F_1 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 (Hämäläinen *et al.* 1997). Ry_{sto} is on chromosome XII (Song *et al.* 2005) and Ry_{chc} 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_{sto} identified by Song *et al.* (2005). Based on sequence analysis, they concluded that the Ry_{sto} 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 pedigree for generating valid selection markers. Ry_{adg}, which came from Gp. ANDIGENA and is widely used in the USA and Europe, provides an example. A resistance gene-like DNA fragment was obtained as a PCR product (310 bp) from potatoes. The RFLP clone, designated as ADG2, co-segregated with the RFLP markers that associate highly with Ry_{adg}. ADG2 was characterized as homologous to the corresponding *R* gene region of several different *R* genes from a wide range of plant species, including kinase 2 and kinase 3a motifs (Hämäläinen *et al.* 1998).

Markers for *Ry* have been generated and validated (**Table 5**). Progress has been made in selection effectiveness and simpler methodology, with faster time and lower costs,

Table 5. Validation history of the selection markers for marker-assisted selection on Ry_{adg} 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 Ry_{adg} phenotype	References
RFLP (GP 125)	30/31 genotypes (96.7%)	Hämäläinen *et al.* (1997)
RFLP (ADG2 probe, 3.5 kb fragment)	77/77 F_1 progeny 112/117 genotypes (95.7%)	Hämäläinen *et al.* (1998) Shiranita *et al.* (1999)
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 *Ry* sources	Shiranita *et al.* (1999)
SCAR (ADG2 fragment with RYSC3 primers)	103/103 genotypes (100%)	Kasai *et al.* (2000)

starting from RFLP, CAPS, and then SCAR. With a SCAR, RYSC3, high association with Ry_{adg} 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 *Ry*s using a wide range of pedigrees and *Ry* 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-Vizcon 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 × 2x and 4x × 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 × 2x and 4x × 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 6. An example of QTL transmission on glandular trichome traits in potato: Frequency of Type A and B glandular trichomes in 4x × 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	Atzimba	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	Atzimba	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	Atzimba	94.106.21	10	100	3	113
Total			357	541	29	927
			(38.5%)	(58.4%)	(3.1%)	

III. Partners, Intellectual Property, and New Technology Assessment for Breeding

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.papaslatinas.org) and APA (African Potato Association, http://www.africanpotatoassociation.org). Multisector 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 (Japan Patent Office), PTO (USA Patent Office), and EPO (European Patent Office)

Patent title	Representative patent or PCT	Date of application (dd/mm/yyyy)	Date of publication of application	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
Lepidopteron 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 *Ryadg* conferring extreme PVY resistance	JP3047022 (24.03.00)	19.04.1999	31.10.2000	19.04.1999	Furusawa, I., 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 biosynthase activity and gene encoding same	PCT/JP2011/069643	30.08.2011	08.03.2012	31.08.2010	Sasaki, K. *et al.*	Kirin Holdings Ltd.

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	Tumer, 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.

licenses. 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 used. 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

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 agriculture 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.

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