



Introgressive Hybridization in Potato Revealed by Novel Cytogenetic and Genomic Technologies

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Abstract

Potato is the third most important food crop in the world and is crucial to ensure food security. However, increasing biotic and abiotic stresses jeopardize its stable production. Fortunately, breeders count on a rich pool of wild relatives that provide sources for disease resistance and tolerance to environmental stresses. To use such traits effectively, breeders require tools that facilitate exploration and exploitation of the genetic diversity of potato wild relatives. Introgression programs to incorporate such alien chromatin into the crop have so far relied on cytogenetic and genetic studies to tap desired traits from these wild resources. The available genetic and cytogenetic tools, supplemented with more recent genomic technologies, can assist in the use of potato relatives in pre-breeding. This information can also facilitate cisgenesis and genome editing to improve potato cultivars. Despite the abundant and rapidly growing genomic information of potato, that of its wild relatives is still limited.

Resumen

La papa es el tercer alimento más importante en el mundo y es crucial para garantizar la seguridad alimentaria. No obstante, el aumento de los factores adversos bióticos y abióticos pone en riesgo la estabilidad de la producción. Afortunadamente, los mejoradores cuentan con rico acervo de parientes silvestres que suministran fuentes de resistencia a enfermedades y tolerancia a factores ambientales adversos. Para utilizar tales caracteres efectivamente, los mejoradores requieren de herramientas que faciliten la exploración y explotación de la diversidad genética de los parientes silvestres de la papa. Los programas de introgresión para incorporar tal cromatina ajena al cultivo hasta ahora han recurrido a estudios citogenéticos y genéticos para captar caracteres deseables de esas fuentes silvestres. Las herramientas genéticas y citogenéticas disponibles, suplementadas con tecnologías genómicas más recientes, pueden asistir en el uso de los parientes de la papa en pre-mejoramiento. Esta información también puede facilitar la cisgénesis y la edición genómica para mejorar las variedades de papa. A pesar del abundante y rápido crecimiento de la información genómica de la papa, la de los parientes silvestres es aún limitada.

Keywords Potato wild relatives · Introgression · Comparative genomics · Pre-breeding

The Use of Wild Relatives in Potato Breeding

Potato is one of the major crops in the world and is viewed as a key source to ensure food security of its fast-growing population. The crop can produce high yields with limited inputs, and

supplies at the same time a good source of energy and health-promoting nutrients (Birch et al. 2012). However, increasing biotic and abiotic stresses represent a serious and constant risk for food security and so jeopardize stable production (Bradshaw 2007a). The genetic diversity of cultivated potato that may provide allelic resources for controlling such stresses has been substantially reduced in the process of domestication and selection. Only a few clones of tetraploid cultivated *Solanum tuberosum* from the Andes were introduced to Europe and though they must have contained a lot of genetic variation, the available biodiversity was only partially captured (Hawkes 1990; Spooner et al. 2005; Ríos et al. 2007; J.M. Bradeen and Haynes 2011; Ramsay and Bryan 2011; Birch et al. 2012; Kloosterman et al. 2013). This limited

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genetic diversity was further reduced due to genetic bottlenecks during photoperiod adaptation and losses resulting from viruses and the late blight epidemics of 1845–1846 (Bethke et al. 2017). However, cultivated potato and its wild relatives signify a more diverse (Fig. 1) and accessible germplasm resource than that of any other crop (Ross 1986; Hanneman 1989; Peloquin et al. 1989; Hawkes 1990). Their value as breeding material is given by their wide geographical distribution and great range of ecological adaptation (Fig. 1) (Hawkes 1994), together with their availability through the Inter-genebank Potato Database (IPD) (<http://germplasmbd.cip.cgiar.org>) established by the CIP (International Potato Centre) and the Association for Potato Intergenebank Collaboration. To use potato wild relatives (WR) efficiently to expand its genetic base, breeders require tools that facilitate exploration and exploitation of their genetic diversity.

This diversity coming from potato WR can transfer specific traits to potato by introgressive hybridization. It involves the introduction of alien chromatin carrying a gene of interest from a wild relative to the crop genome. After the interspecific hybridization and repeated backcrossings, the selected gene(s) of interest are incorporated into the crop chromosomes by homoeologous recombination. The offspring are then selected for the desired trait while the wild genetic background is removed by selection in consecutive backcross generations as far as possible. Linkage drag may occur when the introgressed chromatin still contains tightly linked wild traits from the ancestral donor that cannot be removed by recombination (Ramsay and Bryan 2011). An alternative approach is genetic base

broadening (Bradshaw 2016), which favours allelic variation besides incorporating genes of interest, and thus maximizes the heterozygosity and epistasis required for yield improvement (Mendoza and Haynes 1974), but completely loses the genetic background of the original cultivar. Base broadening, which is often the underlying objective of breeders (Bradshaw 2007b), uses the broadest possible starting material and depends on recombination between the parental genomes in the hybrid. It is then followed by weak selection in target environments but requires enough time to produce advanced backcrosses of improved material that can be crossed with elite germplasm without negative effects on yield and agronomic performance. This process results in improved genotypes that can be used as parents in breeding programmes (Bradshaw 2016).

Determining Existing Introgression Events in Potato Cultivars

Several reports of natural hybrids suggest that potato WR readily hybridize in the wild (Spooner and Hijmans 2001; Camadro 2012; Spooner et al. 2014). Examples of such events include the triploid hybrids between *Solanum commersonii* and *S. chacoense*, or *S. commersonii* and *S. gourlayi* (Masuelli and Camadro 1992; Ortiz 1998). When samples are collected from natural populations, these may carry introgressions from other wild species (Camadro 2012; Spooner et al. 2014; Bethke et al. 2017). Such introgressed segments represent a source of variability through new allele



Fig. 1 Diversity in flowers, fruits, tubers, plants and habitats of sympatric potato wild relatives. **a** Typical diploid *Solanum malmeanum* **b** Typical diploid *S. commersonii*. **c** Intermediate morphotype, possibly a triploid hybrid between *S. commersonii* and *S. chacoense*, **d** Typical diploid *S. chacoense*

combinations but also a challenge for the ex situ conservation and utilization of potato WR.

Potato wild relatives like diploid *Solanum bulbocastanum*, *S. stoloniferum* and *S. chacoense* or hexaploid *S. demissum* (Pavek and Corsini 2001) have been extensively used in potato introgressive hybridization breeding (Hanneman 1989; Peloquin et al. 1989; Watanabe et al. 1994; Jansky 2000; Pavek and Corsini 2001; Bradshaw et al. 2006; Bradshaw 2007a; Bradshaw 2007b; Bradshaw and Ramsay 2009; Jansky 2009a; Bradshaw and Bonierbale 2010; Ramsay and Bryan 2011). Such taxa not only display various advantages over cultivated germplasm (Jansky and Peloquin 2006), such as resistance to the late potato blight, caused by *Phytophthora infestans* and other diseases caused by bacteria and viruses (Jansky 2000; Simko et al. 2009), they also provide the genetic basis for tolerance to cold, frost and other environmental stresses. It is widely accepted that many modern cultivars have wild species donors in their pedigrees (Love 1999). Andean farmers allow wild populations of potato species to grow on their fields, so wild germplasm is introduced into both diploid and tetraploid cultigens (Ugent 1970). Moreover, the use of potato WR in introgressive hybridization breeding before the existence of common pedigree records implies that the original introgression events have not been documented and that the sources of certain desirable traits are unknown (Love 1999; Leisner et al. 2018).

One of the direct methods to demonstrate introgressed alien chromatin in the crop chromosomes is comparative chromosome painting by Fluorescent in situ Hybridization, that establishes the structural and numerical comparisons of chromosome sets between species of the genus *Solanum* (Tang et al. 2008; Iovene et al. 2008; Szinay et al. 2008; Szinay et al. 2010; Lou et al. 2010; Verlaan et al. 2011; Szinay et al. 2012). Under low stringency conditions, it is possible to use tomato or potato probes in these experiments to perform cross-species chromosome painting and to display homoeologous chromosomal positions in related *Solanum* species. In this way, many hitherto unknown inversions could be described (Tang et al. 2008; Lou et al. 2010; Szinay et al. 2010; Peters et al. 2012; Szinay et al. 2012). BAC-FISH also allowed the accurate mapping of the *Ty-1* gene introgressed from *S. chilense* into cultivated tomato and provided an explanation for observed linkage drag resulting from suppression of recombination (Verlaan et al. 2011). There are no such studies in potato cultivars, although there are many reports of introgressions based on molecular markers (Hosaka 1995; Bryan et al. 1999; Provan et al. 1999; van der Voort et al. 1999; Gebhardt et al. 2004; Flis et al. 2005; Sokolova et al. 2011).

Resequencing studies in tomato have identified polymorphisms related to introgressions (Causse et al. 2013), while in potato, these have been shown in some diploid and tetraploid landraces as well as in cultivars (Hardigan et al. 2017). Bioinformatic tools like *iBrowser* (Aflitos et al. 2015) have been developed to use SNPs identified from the increasing

genome sequence data available to pinpoint past undescribed introgressions from wild relatives in the genomes of cultivated *Solanum* species. These approaches together with other modern technologies will also prove useful when designing new introgressive hybridization schemes.

Tools for Establishing Introgressive Hybridizations

In spite of the widely available diversity in germplasm collections worldwide, only 10% of the potato species have been explored for use in breeding programmes (Bradshaw 2007a). This is a rather low percentage, bearing in mind that by manipulation of ploidy and other biotechnological interventions, virtually any potato species can be used in introgressive hybridization breeding (Ortiz 1998; Jansky 2006; Ortiz et al. 2009). Moreover, the few species that have been employed in breeding programs to provide specific traits have not been investigated systematically.

Knowledge of genome organization and divergence between potato and its wild relatives is most helpful to create new introgressive hybridization schemes. Before choosing a wild relative as donor, it is important to know if there are inversions or translocations that will impede introgression or cause linkage drag (Fig. 2). Another key aspect is to always take into account hybridization barriers that have been thoroughly reviewed elsewhere (Camadro et al. 2004; Jansky 2009b; Bethke et al. 2017). The great potential recognized in these wild relatives encouraged scientists to develop strategies for overcoming such barriers (Jansky 2006; Bradshaw and Bonierbale 2010; Bethke et al. 2017). Once the crossing barriers are overcome, stabilizing the introgression in the potato genotypes still represents a challenge due to its tetraploid inheritance. Additionally, inbreeding depression forces breeders to use different genotypes as recurrent parents for backcross progenies. Despite all these obstacles to recover a superior cultivated background after hybridization with a wild species, the value of these potato WR makes it worth the effort. A wide variety of cytogenetic, genetic and genomic tools can be used to assist in these efforts.

Classical Cytogenetics Tools

Classical cytogenetics should be the first tool to study potato WR to be used as donors and their hybrids with potato. It helps to establish ploidy levels and Endosperm Balance Number (EBN) of the interspecific hybrids (Peloquin et al. 1989; Jansky 2009; Ono and Hosaka 2010) and to assess the effects of ploidy changes in the parental species and their hybrids (Mok and Peloquin 1975; Adiwilaga and Brown 1991; Carputo et al. 1997; Ortiz 1998; Carputo et al. 2000; Jansky 2006; Lightbourn and Veilleux 2007; Jansky 2009; Ortiz et al.

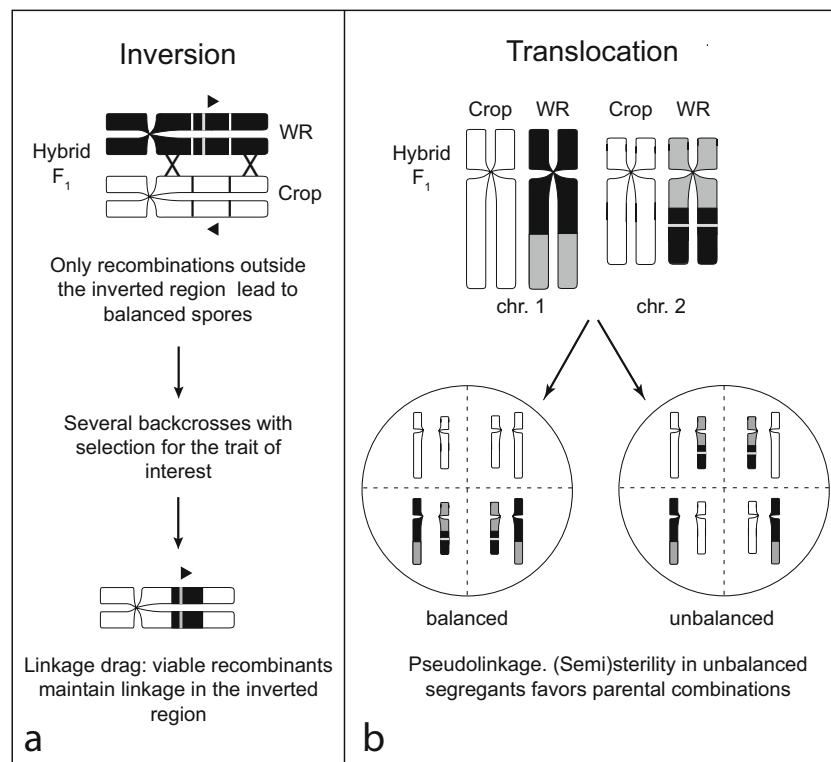


Fig. 2 shows two simplified examples of structural chromosome rearrangements and the consequences they may have for plant genetics and breeding. Both examples represent a hybrid F_1 , which carries chromosomes from the crop (white) and the wild relative (WR, black). a) In the case of a (paracentric) inversion a distal region of the long arm is inverted in the WR (black). In the hybrid in which one chromosome contains the inversion, chromosomes fail to pair in this region or form a loop structure. Crossovers in this region result in a sterile spore so viable spores pass only the non-recombined region to the next generation. If the trait of interest is located in the inverted region, after several backcrosses with selection for this trait, the genetic background of the crop (white) will be recovered but the inverted region will be maintained as a block containing the selected trait together with undesired wild chromatin, a

genetic phenomenon known as linkage drag. b) In the case of a reciprocal translocation, fragments of two non-homologous chromosomes are swapped in the chromosomes originating from the wild relative. In meiosis of the hybrid F_1 , two outcomes can be considered: a balanced segregation in which the two non-translocated chromosomes and the two translocated chromosomes go to opposite poles, resulting in balanced viable spores. In the second case, a non-translocated and a translocated chromosome are included in the same daughter cell, which contains a duplicated fragment of one chromosome and a deletion of a fragment of the other chromosome and hence results in a sterile spore. Reduced fertility of the unbalanced products favors the maintenance of the parental combinations causing the apparent linkage of loci in the chromosomes involved in the translocation

2009). Direct cytogenetic analysis is also the most direct approach to observe meiotic chromosome pairing behaviour in interspecific hybrids and their progenies (de Jong et al. 1993; Carpato et al. 1995; Masuelli and Tanimoto 1995; Barone et al. 1999; Carpato 2003; Chen et al. 2004; Gaiero et al. 2017).

Genome differentiation between wild potato species is assumed to play a minor role as an isolation mechanism (Dvorak 1983; Camadro et al. 2004). For potato and its relatives, genomic formulas were proposed by Matsubayashi (1991) who distinguished five genomes in Section *Petota* (A, B, C, D and P) through classical genome analysis of meiotic behaviour and pollen fertility in interspecific hybrids. Genomes identified with different letters show little or no pairing in the meiosis of their amphidiploid hybrids, which display pollen sterility. The most common genome is type A, which presents different degrees of structural variants depending on the scale of the chromosomal rearrangements. Genome E is proposed for the closely related non-tuber-bearing species of the

Section *Etuberosum*. For potato breeders, homoeologous pairing and crossovers in their hybrids with cultivated potatoes is of more interest than their phylogenetic relationships because it predicts their success for breeding via crossing. The most stringent test for pairing between homoeologous chromosomes is the analysis of meiosis of triploid hybrids. If the chromosomes form trivalents in the meiosis of triploids, then introgression is possible (Jansky 2006). The chances of alien chromatin introgression are greater as homoeologous pairings are more likely to occur in the triploid compared to the meiotic pairing in tetraploids in which potentially there is always a homolog for each chromosome which may pair preferentially (Sybenga 1996; Jansky 2006). Although the factors that determine homeologous pairing are not clear yet, homology in repetitive sequences seems to play an important role. Genome divergences caused by repeats have been assessed within and between the potato and tomato clades, characterizing the abundance and dynamics of the repetitive fractions of their

genomes (Gaiero et al. in prep). These can have significant consequences in genome homology, genome expansion and in the occurrence and impact of structural rearrangements.

Molecular Cytogenetics Tools

Molecular cytogenetics has been one of the major instruments in tracing the course of alien chromosomes in introgressive hybridization breeding. It has been applied for most major crop species (Benavente et al. 2008), including potato (Yeh and Peloquin 1965; Mok et al. 1974; Pijnacker and Ferwerda 1984; Visser and Hoekstra 1988; Mohanty et al. 2004; Gavrilenko 2007). It allows identification of whole chromosome sets or of specific chromosome pairs and it also enables comparisons of the chromosomal positions of markers or regions of interest across related species.

Genome painting or GISH (Genomic in situ hybridization) is a powerful FISH technique used for tracing homoeologous chromosome pairing, recombination and transmission. It consists in labelling genomic DNAs from one or both parental species as probe(s) to hybridize on chromosome slides of the interspecific hybrid and its progeny (Fig. 3a). If the genomes of the parental species (especially their dispersed and tandem repeats) have diverged sufficiently, chromosomes of the two species can be easily discriminated in the hybrid nuclei through different fluorescent dyes. In nuclei from interspecific

(sexual or somatic) hybrids between potato (genome A) and non-tuber bearing relatives (genomes E, B or P) GISH has been successful in discriminating chromosomes (Dong et al. 1999; Dong et al. 2001; Gavrilenko et al. 2002; Gavrilenko et al. 2003; Dong et al. 2005). In wider hybrids such as *S. nigrum* (+) *S. tuberosum* and its backcrosses (Horsman et al. 2001), alien chromosomes are easily distinguishable. These studies provide further evidence of genome differentiation, in the sense that genomes identified with different letters not only do not pair in the meiosis of their hybrids but also can be discriminated by GISH. When divergence is not so high, contrast in the hybridization differentiation can be improved by adjusting washing stringency and proportion of blocking (unlabelled) DNA in the FISH experiments (Jiang and Gill 1994). However, there is a technical limit to what can be discriminated by GISH. As an example, the technology has not been successful in studies of hybrids between potato and its closer A-genome tuber-bearing wild relatives, with the exception of *S. bulbocastanum*, a diploid (1EBN, A^b genome) Mexican species (Iovene et al. 2007). Hybrids between *S. commersonii* and *S. tuberosum* Group Phureja behaved as near autopolyploids during male meiosis and it was not possible to discriminate the chromosomes coming from each parental species through GISH (Gaiero et al. 2017). These results suggest that repetitive sequences have not diverged much among the genomes of cultivated and wild potatoes.

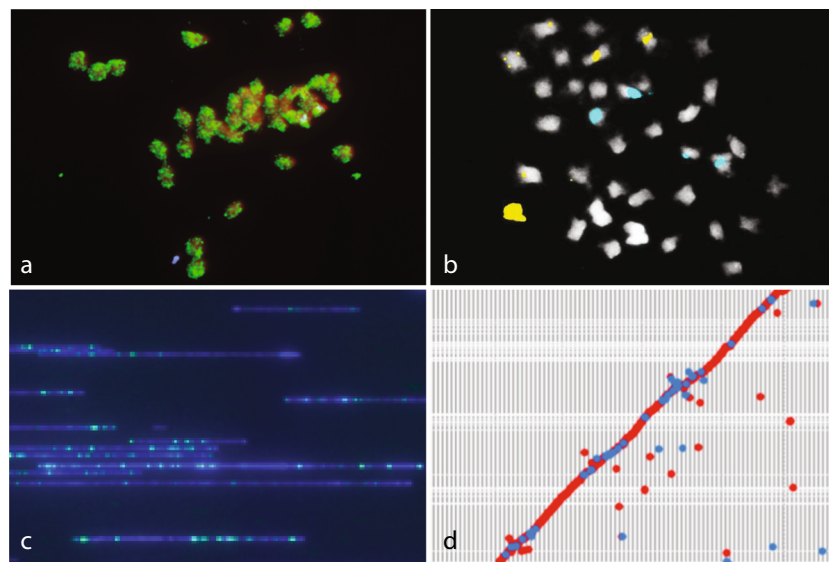


Fig. 3 Examples of the various technologies available to assist in introgressive hybridization breeding. a) genome painting (GISH) with *S. commersonii* genomic DNA probe (green) on the chromosomes of a triploid interspecific hybrid (*S. commersonii* x *S. tuberosum* Group Phureja) in a meiotic cell complement. Notice that all chromosomes are hybridized with the probe. b) Chromosome identification through BAC-FISH on the chromosomes of a triploid interspecific hybrid (*S. commersonii* x *S. tuberosum* Group Phureja) in a meiotic cell complement. Three chromosomes from pair 1 are identified with a yellow probe and three chromosomes from pair 2 are identified with a blue probe.

c) Example of optical mapping in which high-molecular weight *Solanum* DNA molecules are stained with YOYO (blue) showing sequence-specific single strand nicks (green), and then stretched by moving along a nanochannel array. Millions of such images are integrated to build a consensus genome map. d) Dot-plot comparison of the genome assemblies of *Solanum commersonii* and *S. tuberosum* (DM) obtained through the software MUMmer. It shows a high degree of collinearity with only few small inversions (inverted stretches of dots across the diagonal)

Chromosome rearrangements between related species can cause specific problems at different meiotic stages of their interspecific hybrids (Fig. 2). Typical examples are heterozygosity for paracentric inversions which can cause anaphase I (and or II) bridges and hence sterility or aneuploidy (Fig. 2a) or reciprocal translocations, which can lead to semi-sterility or aneuploidy (Fig. 2b). Such rearrangements between the homoeologues represent an important limitation in introgressive breeding due to the unintended retention of large blocks of DNA surrounding a gene of interest (Fig. 2a), genetically described as linkage drag (Jacobsen and Schouten 2007). There are no reports of large scale chromosome rearrangements in potato and its wild relatives, in contrast to some detailed descriptions of rearrangements among Solanaceous crops (Iovene et al. 2008; Tang et al. 2008; Lou et al. 2010; Peters et al. 2012; Szinay et al. 2012). Linkage drag represents a limitation for introgressive hybridization breeding because blocks of alien chromatin surrounding the gene of interest can be retained even after many generations of backcrossing. The impact of genetic drag is even greater when the linked regions have a negative effect on agronomic performance (Fig. 2a). Selection against such undesired blocks can be simplified by marker-assisted breeding and genomic selection, but these approaches are still challenging (Warschefsky et al. 2014), especially in autotetraploid genotypes. While the literature on comparative FISH analysis in *Solanum* is vast, there are only a few studies that have utilized sufficient high-quality sequence data needed to reveal fine-scale structural differences related to introgression barriers (Datema et al. 2008; Peters et al. 2012; Causse et al. 2013; Aflitos et al. 2014; Aflitos et al. 2015; de Boer et al. 2015).

A considerable body of literature on FISH applications for breeding is available for tomato as reviewed by Szinay et al. (2010), with reports of many structural rearrangements among tomato and its wild relatives that have significant impacts on breeding (Anderson et al. 2010; Verlaan et al. 2011; Szinay et al. 2012). With multi-colour fluorescence microscopy it is possible to hybridize many probes each labelled with a different fluorescent dye in a single experiment, reducing the examination of any chromosome set to only a few experiments (Tang et al. 2009; Szinay et al. 2010). For potato, a set of chromosome-specific cytogenetic DNA markers (CSCDM) made from DNA probes selected from a *S. bulbocastanum* library was developed to associate all twelve linkage groups to potato chromosomes and build a reference karyotype (Dong et al. 2000; Song et al. 2000). The RHPOTKEY BAC library was developed for the diploid potato clone RH89–039-16 (Borm 2008). The positions of the BACs in this library were anchored to AFLP markers in the ultrahigh density (UHD) genetic map (van Os et al. 2006). From this library, a set of 60 BACs with known positions in the Ultra High Density (UHD) linkage map were selected for localization on pachytene chromosomes, thus providing a useful tool

to study collinearity between potato and its wild relatives (Tang et al. 2009; Achenbach et al. 2010; de Boer et al. 2011). Gaiero et al. (2016) used this BAC set to build cytogenetic maps for *S. commersonii* and *S. chacoense* and to compare them to that of cultivated potato. Their results indicate a high collinearity at the chromosomal scale between the three species which makes them promising donors in introgressive hybridization schemes. They also used them to identify specific chromosome pairs in triploid hybrids between *S. commersonii* and *S. tuberosum* Group Phureja (Fig. 3b).

Using a higher number of BAC probes which are located closer together in linkage maps, high resolution cytogenetic mapping has been employed to describe rearrangements in chromosome 6 coming from potato and tomato (Iovene et al. 2008; Tang et al. 2008). Such fine mapping has also been useful to design strategies for the sequencing projects of these crops (Xu et al. 2011; The Tomato Genome Consortium 2012). They have helped by identifying the boundaries between the highly condensed heterochromatin and euchromatin, which is easier to sequence and assemble (Szinay et al. 2008; Tang et al. 2009; Szinay 2010; Tang et al. 2014). Thus, the sequencing and assembly efforts could be better directed to the euchromatic regions. Because these crops were sequenced using BAC libraries, cytogenetic maps have also been used to construct the backbone for sequence assembly of tomato (Szinay et al. 2008) and potato (Visser et al. 2009). The seed BAC clones that were chosen to start the assembly were confirmed through BAC-FISH, the BAC positions on genetic and physical maps were verified and gaps in the assembly were identified and sized (Iovene et al. 2008; Szinay et al. 2008; Tang et al. 2008; Tang et al. 2009). The use of a very large number of BAC-FISH probes, coupled with information from physical maps (restriction and optical maps) allowed for the correction of miss-assemblies in the tomato genome and identification of scaffolds that were not in the correct order or orientation, or both (Shearer et al. 2014). The potato assembly was similarly improved using information from physical and genetic maps to achieve a reference genome at the level of pseudomolecules (equivalent to chromosomes) (Sharma et al. 2013; Hardigan et al. 2016). Such integration of technologies has only been applied to date for *S. chacoense* among the potato WR (Leisner et al. 2018).

Mapping Tools

The cutting edge technology of genome mapping through nanochannels (Lam et al. 2012; Cao et al. 2014) is the ideal tool for completing genome assemblies and even identifying, spanning and assembling repeated sequences. In addition to assisting in genome assembly, genome mapping can assess structural variation among related species or genotypes within a species (Cao et al. 2014). This technology uses nicking enzymes to create DNA sequence-specific nicks that are

subsequently labelled by a fluorescent nucleotide analogue (Xiao et al. 2007). The DNA is linearized by confinement in a nanochannel array (Das et al. 2010) and then photographed (Fig. 3c). The DNA loading and imaging cycle can be automatically repeated many times, so data can be obtained at high throughput and high resolution (Hastie et al. 2013). Genome mapping using nanochannels has been used only recently for genome assembly in higher plants such as spinach (Xu et al. 2017), subterranean clover (Kaur et al. 2017), maize (Jiao et al. 2017), quinoa (Jarvis et al. 2017) and bread wheat (Staňková et al. 2016). In the genus *Solanum*, the related method known as optical mapping (Zhou et al. 2004) was used for whole genome analysis in tomato (Shearer et al. 2014) and also in other crops like rice (Zhou et al. 2007), maize (Zhou et al. 2009) and for crop relatives such as *Medicago truncatula* (Young et al. 2011). One of the limitations for its use in the higher plant genomics community, is the challenge of obtaining sufficient amounts of high molecular weight nuclear DNA (HMW DNA) due to the thick cell walls and cytoplasmic polyphenols and polysaccharides.

Moving from physical to genetic mapping, considerable effort has been put into mapping traits of interest on the genetic maps of the few potato WR that have been used in potato breeding. Understandably, most attention has been devoted to mapping resistance to late blight (*Phytophthora infestans*), the most important potato disease and responsible for the infamous Irish Potato Famine in 1845–46. The most remarkable source for resistance to *P. infestans* is *S. bulbocastanum* (Naess et al. 2001; Lokossou et al. 2010). Resistance to *P. infestans* was also mapped in *Solanum demissum* (Jo et al. 2011), *S. venturii* (Pel et al. 2009), *S. pinnatisectum* (Kuhl et al. 2001), *S. avilesii* (Verzaux et al. 2011), *S. paucisectum* (Villamon et al. 2005) and in *S. phureja* x *S. stenotomum* (Costanzo et al. 2005; Simko et al. 2006). Different alleles from a single locus on chromosome 8 from *S. bulbocastanum*, which carries resistance to late blight, have been the subject of physical mapping and positional cloning (Bradeen et al. 2003; Song et al. 2003; Van Der Vossen et al. 2003). Resistance to important potato viruses like PVX and PVY has also been the focus of mapping efforts (Cockerham 1970; Solomon-Blackburn and Barker 2001; Flis et al. 2005; Y.-S. Song et al. 2005; Sato et al. 2006; Simko et al. 2009), together with other traits of interest (Anithakumari et al. 2011) and with pyramiding of resistance genes (Tan 2008). Genome-wide association studies (GWAS) have been particularly useful for complex traits in cultivated potato (Ewing et al. 2004; Gebhardt et al. 2004; Simko 2004; Simko et al. 2004; Simko et al. 2006; Visser et al. 2015), but only one study includes the use of wild relatives (Hardigan et al. 2017). All these efforts have allowed the use of tightly linked molecular markers to select resistant genotypes or to select against donor genome in backcross progenies from an introgression scheme, in the so-called marker-assisted breeding (reviewed by Barone

(2004); Tiwari et al. (2013)). Most literature on selection against wild genome comes from studies on the introgression of *S. commersonii* into a *S. tuberosum* tetraploid background (Barone et al. 2001; Carputo et al. 2002; Barone 2004; Iovene et al. 2004). The greatest impact of these molecular breeding technologies has been on pre-breeding and parental development (De Koeeyer et al. 2011) and also on the exploration of germplasm resource (Bamberg and del Rio 2013; Carputo et al. 2013; Manrique-Carpintero et al. 2014; Warschefsky et al. 2014).

Genomics Tools

The available genomic knowledge on wild potatoes is relatively limited compared to that of tomato WR (Szinay et al. 2012; Aflitos et al. 2014; Bolger et al. 2014). The tendency now is to slowly move to more sophisticated genomics of WR, elucidating the available diversity and desirable traits (Bradeen and Haynes 2011; Ramsay and Bryan 2011). The increasing number of molecular markers and DNA sequence data to be generated will allow for faster progress in breeding by simultaneously selecting genes/QTLs while selecting against wild species genome content (Bradshaw 2007b).

With the development of high-throughput DNA sequencing, genome assemblies for tomato (The Tomato Genome Consortium 2012), potato (Xu et al. 2011) and several of their WR (Aflitos et al. 2014; Bolger et al. 2014; Aversano et al. 2015; Leisner et al. 2018) have become available. Concerted genomics and bioinformatics efforts have improved genome assemblies (Sharma et al. 2013; Shearer et al. 2014; Hardigan et al. 2016). However, only a few studies have utilized sufficient high-quality physical maps needed to reveal structural differences (Fig. 3d) related to introgression barriers (Peters et al. 2012; Aflitos et al. 2014; Aflitos et al. 2015; de Boer et al. 2015). Although sequence data for some wild species are available (e.g., *S. chacoense*, *S. commersonii*), the only comparative structural analysis performed so far used DArT markers, finding microscale genome sequence variation (Traini et al. 2013). A vast survey of genome-wide sequence variation across a diversity panel of cultivated and wild potato species was performed by Hardigan et al. (2017), finding more variation than in any other crop resequencing project. In most cases of crop wild relatives (CWR) only a draft genome is available and it is of limited use, depending on the quality of the assembly (Pérez-de-Castro et al. 2012). Such is the case of the whole genome draft sequence available for *Solanum commersonii* (Aversano et al. 2015). Assembly to the level of pseudomolecules is achieved when mapping against the reference potato genome. This approach does not cater for structural variation between the two species. In the case of *S. chacoense*, the genotype that was sequenced (M6) was an inbred clone, so increased homozygosity facilitated genome assembly. The construction of pseudomolecules was achieved

including information from genetic maps using M6 as parent of the segregating population, so it does not assume collinearity with a reference genome (Leisner et al. 2018). Ideally, breeders should count on fully assembled and well annotated reference genomes for potato WR to assist in gene discovery and dissection of the genetic basis of a trait.

Making the Most of Biotechnological Approaches through Wild Relatives

One might argue that resorting to potato WR as donors of desirable traits through introgressive hybridization seems no longer necessary with modern technologies such as cisgenesis or the CRISPR-Cas9 genome editing, as it allows researchers to transfer directly the gene of interest or to change the native sequence into a tailor-made version, respectively. Nevertheless, it is first necessary to identify the original genes conferring the trait of interest and to mine their allele diversity in order to isolate them, clone them and accurately modify them or transfer them into targeted cultivars. This is possible through newly developed genetic and genomic tools (Cardi 2016).

Knowledge on the physical position of the genes of interest is useful to isolate them and transfer them to cultivated potato. The identification, mapping, cloning and the techniques to use resistance genes against *Phytophthora infestans* coming from potato WR was reviewed by (Park et al. 2009). Most mapped and cloned genes come from *S. demissum* (Jo et al. 2011) or *S. bulbocastanum* (Naess et al. 2000; Naess et al. 2001; Bradeen et al. 2003; J. Song et al. 2003; Lokossou et al. 2010), although using an interspecific candidate gene approach, Pel et al. (2009) were able to map and clone a dominant from an alternative donor (*S. venturii*). These genes have already been used or are in the pipeline for cisgenesis into cultivated potato backgrounds (Haverkort et al. 2008; Park et al. 2009; Zhu et al. 2015).

Recently, all known major *R* genes in potato have been sequenced and an ‘omics’ approach was used to recognize the genes responsible for late blight resistance (Van Weymers et al. 2016). The previously developed SolRgene database provides easy access to the sequences of *R* genes across *Solanum* section Petota, allowing the cloning of many of those genes for downstream biotechnological uses (Vleeshouwers et al. 2011). New sources of resistance have been identified and their genes cloned using the latest third generation sequencing technologies. These new variants are now available for biotechnological applications (Witek et al. 2016). The genome sequence and transcriptomes of potato WR like *S. commersonii* and *S. chacoense* have allowed the identification of pathogen-receptor genes and to describe non-acclimated and cold-acclimated gene expression as well as to get insights on tuberization and glycoalkaloid production (Narancio et al.

2013; Aversano et al. 2015; Leisner et al. 2018). A large resequencing effort across potato cultivars and landraces together with potato WR shed light on the kinds of traits and genes that were under selection during the domestication process and provided a useful catalogue of genomic variation within the potato gene pool (Hardigan et al. 2017). Microsatellite markers (SSR) transferred from potato to its wild relatives can be used to screen for genetic variability. An example of this is the evaluation of 10 accessions from *S. chacoense* using 15 SSR markers developed for potato, which showed high levels of heterozygosity in the collection (Haynes et al. 2017). Using sequence data, new SSR markers can be specifically devised for wild species, increasing their amplification success and polymorphic information content. This is what happened for a diversity panel of *S. commersonii* accessions and for a biparental population both screened with SSR markers developed from short read sequence data (Sandro et al. 2016). Adding value to collected samples in gene banks through all this genetic and genomic information and mining allele variation from natural populations or ex situ collections will be critical for the efficient use of potato WR in the genomics era.

Breeders can use potato WR to introduce new genes in a commercial cultivar or to select superior alleles to replace their cultivated counterparts through cisgenesis. They can also use structural and functional genomic information on potato WR to adopt as templates to target specific sites and edit gene sequences in elite cultivars. In the case of genome editing, knowing the target genome sequence is essential to prevent targeting of repeated sequences dispersed throughout the genome and to respond to regulatory demands (Cardi 2016). However, most of the time breeders do not aim at transferring only one gene of interest but to broaden the genetic base of a potato cultivar (Bradshaw 2007b; Bradshaw 2016) and to introduce adaptability and hardiness from potato WR usually growing in a wide variety of environments (Bethke et al. 2017). Such a time-consuming process depends on many backcrosses to recover the cultivated background that was lost with the initial hybridization. It is also claimed that the undesirable traits that come from the potato WR are hard to remove, especially in a tetraploid potato background. An idea that is gaining popularity is the use of diploid inbred lines in potato breeding (Lindhout et al. 2011; Endelman and Jansky 2016; Jansky et al. 2016). These allow for easier genetic mapping with increased resolution and simplify genetic analysis because of their disomic inheritance (Endelman and Jansky 2016). In breeding, they can be used to create F_1 hybrid seed with enhanced heterosis that can be propagated through true potato seed (Lindhout et al. 2011; Jansky et al. 2016). Potato WR have a role to play both in the development of diploid inbred lines and in their use as breeding material. One of the most frequently used strategies to achieve diploid inbred lines is through the crossing with a *S. chacoense* genotype carrying

a dominant self-incompatibility inhibitor allele called *SlI* (Hosaka and Hanneman Jr 1998; Phumichai et al. 2005; Lindhout et al. 2011; Jansky et al. 2016). After the diploid inbred lines are obtained, they can generally be crossed directly with diploid potato WR facilitating introgression at the diploid level (Jansky 2006; Jansky et al. 2016).

Many of the limitations in introgressive hybridization breeding can be overcome by an efficient use of new genomic technologies and approaches. These will allow prediction of homology and collinearity to anticipate the degree of pairing, recombination and linkage drag expected in any interspecific cross, together with mining of existing variation in natural populations and optimal choice of the genotypes to start introgression schemes. Genomics will not only facilitate marker-assisted selection for the traits of interest but also against the wild donor chromatin. To the question posed by (Bethke et al. 2017) in their review paper: Are we getting better at using Wild Potato Species in Light of New Tools? The answer is clearly Yes, but the possibilities are still endless. The approaches we are now developing may still seem expensive and difficult to apply to routine breeding; however, information is accumulating fast. At the current rate of technological advance in the automation of data acquisition and analysis, it does not seem impossible to envision the fulfillment of the promises of the use of potato WR in the near future, as long as we keep going in that direction.

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