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REVIEW

Progress in somatic hybridization research in potato during the past 40 years

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Abstract Somatic hybridization has been used in potato to overcome the sexual barriers between the cultivated (*Solanum tuberosum* L.) and wild species. To date hundreds of inter/intra-specific somatic hybrids have been produced via protoplast fusions using 23 *Solanum* species and characterized for multiple traits such as agronomic, disease/pest resistance, salinity, frost and others. With increasing success in recovery of fusion products, somatic hybrids have been exploited in potato genetics, breeding and genomics studies. Here, we report on progress in somatic hybridization research in potato during the past 40 years.

Keywords Breeding · Genetics · Genomics · Potato · *Solanum* species · Somatic hybrid

Introduction

A huge genetic diversity is available in *Solanum* species for various desirable traits. Wild *Solanum* species have been used in potato breeding but they represent only a small fraction to the total *Solanum* diversity (Bradshaw et al. 2006). Huge efforts are involved in successful utilization of wild species to widen the narrow genetic base of the cultivated potato. Many useful genes of wild sources cannot be transferred to common potato through conventional breeding because of sexual barriers caused by the differences in ploidy level and endosperm balance number (EBN) (Spooner and Salas 2006). However, it is now possible to overcome the sexual barriers using methods such as manipulation of ploidy and EBN, bridge crosses, mentor pollination, embryo rescue, hormone treatment, reciprocal crosses, and somatic hybridization (reviewed by Jansky 2006).

Somatic hybridization aims to strengthen the potato gene pool by introducing genes from wild species (Helgeson et al. 1993). This technique allows several advantages over conventional breeding and transgenic methods, such as: (i) produces fertile somatic hybrids with target traits of wild *Solanum* species, (ii) provides access to basic pre-breeding material for effective utilization in breeding, (iii) enables easy transfer of monogenic and polygenic traits in one step, (iv) results recombination of nuclear and cytoplasmic genomes, and (v) avoids biosafety regulatory issues associated with transgenics. In the past, a few researchers discussed protoplast fusion in *Solanum* species (Orczyk et al. 2003), plant species (Waara and Glimelius 1995; Davey et al. 2005; Eeckhaut et al. 2013), citrus (Guo et al. 2013), asymmetric fusion (Lakshmanan et al. 2013), asymmetric fusion in wheat (Liu and Xia 2014), integeneric fusion (Liu et al. 2005) and crop improvement in China (Wang et al. 2013).

During the past 40 years, hundreds of symmetric somatic hybrids were produced, while limited number of asymmetric somatic hybrids. More than a decade back, Orczyk et al. (2003) reviewed application of potato somatic hybrids in genetics and breeding, and since then several progresses have been achieved in this area. Hence, this review aims to progress in somatic hybridization research in potato and their application to genetics, breeding and genomics studies.

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Production of potato somatic hybrids

Protoplast fusion and culture

Protoplast isolation was first reported by Cocking (1960) and after a decade successful regeneration of plants from tobacco protoplasts was obtained (Takebe et al. 1971). With the development of electrofusion method, reports on recovery of somatic hybrid regenerants were more prevalent (Fish et al. 1988; Bates et al. 1987) might be due to easy control of fusion parameters than the chemical method using polyethylene glycol (Wallin et al. 1974). In food crops, electrofusion was first reported in potato between *Solanum tuberosum* and semi-cultivated (*S. phureja*) (Puite et al. 1986). Leaf-mesophyll cells of in vitro-grown plants were used largely to isolate protoplasts in protoplast-digestion-medium (Binding et al. 1978), then culture of fused products in the VKM medium (Binding and Nehls 1977) followed by shoot development on the $MS_{13}K$ medium (Behnke 1975). Recently, selection of somatic hybrids (*S. tuberosum* + *S. chacoense*) based on callus growth tagged with green fluorescent protein has been observed (Rakosy-Tican and Aurori 2015). Over the 40 years, many fusion experiments were executed and hundreds of potato somatic hybrids were produced and characterized, as summarized in Table 1.

Confirmation of somatic hybrids

A large number of potato somatic hybrids have been produced via protoplast fusion between the common and the wild species *S. acaule, S. berthaultii, S. brevidens, S. bulbocastanum, S. cardiophyllum, S. chacoense, S. circaefolium, S. commersonii, S. etuberosum, S.* × *michoacanum, S. melongena, S. nigrum*, S. *phureja, S. pinnatisectum, S. tuberosum, S. sanctae-rosae, S. spegazzinii, S. stenotomum, S. tarnii, S. torvum, S. vernei, S. verrucosum*, and *S. villosum* (Table 1). Following regeneration, somatic hybrids are characterized through various methods such as cytological (flow cytometry, chromosome count, guard cell count, FISH-fluorescence in situ hybridization and GISH-genomic in situ hybridization), isozyme, molecular markers (e.g. RAPD-random amplified polymorphic DNA, RFLP-restriction fragment length polymorphism, ISSR-inter simple sequence repeat, SSR-simple sequence repeat, AFLP-amplified fragment length polymorphism, and DArT-diversity array technology), phenotypes (e.g. foliage, stem, leaf, flower and tuber traits) and pollen fertility. Somatic hybrids are also analyzed for cytoplasm types (W/α, T/β, W/γ, W/δ and S/ε: Lössl et al. 1999) based on organelle (chloroplast and mitochondria) genomes-specific markers as described by Lössl et al. (2000). Finally, somatic hybrids are examined for the presence of target traits under field or controlled conditions and for many other traits (Table 1).

Application of potato somatic hybrids

Genetics

Genetics of potato somatic hybrids and their segregating progenies has been studied in nuclear genome to dissect the recombination patterns. Chromosomal segregation pattern was analyzed in hexaploid somatic hybrid (*S. brevidens* + *S. tuberosum*) and their progenies with *S. tuberosum* using RFLP (Williams et al. 1993) and RAPD markers (McGrath et al. 1996). Study suggests that *S. brevidens* ribosomal (r) DNA loci are primarily contributed to isochromosome formation in the hybrids and progenies (McGrath and Helgeson 1998). Further, a chromosome substitution line was developed in *S. breviden*-somatic hybrids and progenies (BC_1, BC_2 and BC_3) with *S. tuberosum*. Study demonstrates that a single copy of chromosome 8 from *S. brevidens* replaced the same in the BC_3 clone and has significant impact on transferring resistance to tuber soft rot and early blight (Tek et al. 2004). The importance of combining GISH and DNA markers was also suggested to study chromosomal behaviours in potato (Dong et al. 1999). Poor chromosomal pairing was observed in somatic hybrid (*S. etuberosum* + *S. tuberosum*) and progenies (BC_1 and BC_2), and further suggests that genome dosage affects tuber formation but has less effect on potato virus Y (PVY) resistance (Gavrilenko et al. 2003). Evidence of tetrasomic inheritance was investigated in a tetraploid somatic hybrid (*S. commersonii* + *S. tuberosum*) and F_2 progeny (90 individuals) using RAPD and AFLP markers. Segregation pattern was investigated by RFLP markers in a progeny of hexaploid somatic hybrids (*S. acaule* + *S. tuberosum*) crossed with *S. tuberosum*. Study concludes that somatic hybridization allows the effective use of *S. acaule* genes into cultivated potato (Yamada et al. 1998). Recently, somatic hybrid (*S. chacoense* + *S. tuberosum*) exhibited tetrasomic or disomic segregation ratio using SSR markers and suggested that pentaploid hybrid exhibits tetraploid inheritance pattern (Chen et al. 2016).

Interaction between nuclear and cytoplasmic genes can affects fertility and agronomic traits of somatic hybrids and progenies (Lössl et al. 1994). Segregation and recombination patterns of organelle genomes were investigated in potato (Frei et al. 1998) and analyzed variations (Tiwari et al. 2014, 2016). Majority of somatic hybrids follow recombination of mitochondrial genome from both parents, and chloroplast pattern from only one parent (e.g. *S. bulbocastanum*: Iovene et al. 2007; *S. pinnaticetum*: Sarkar et al. 2011; *S. chacoense*: Chen et al. 2013) except recombination of chloroplast genome was observed only once in *S. vernei*-somatic hybrid (Trabelsi et al. 2005). Loss of male sterility was observed in nuclear-mitochondrial genomes re-arrangement in *S. commersonii*-somatic hybrids and BC_1 progeny (Cardi et al. 1999). Study suggests possibility of exploitation of novel cytoplasm

Table 1 Summary of production and characterization of potato somatic hybrids developed using *Solanum* species

Somatic hybrid/fusion parents		Target trait	Characterization	References
1. *S. acaule* (+) *S. tuberosum*				
S. acaule dihaploid (2*x*)	*S. tuberosum* (4*x*) dihaploid (2*x*)	Potato virus X (PVX) resistance	Chromosome counting, RFLP, segregation pattern and BC_1 family	Yamada et al. (1997, 1998)
S. acaule (4*x*) and dihaploid (2*x*)	*S. tuberosum* (4*x*) and dihaploid (2*x*)	Resistance to bacterial ring rot (*Clavibacter* spp.) and potato leaf roll virus (PLRV)	RAPD, flow cytometry, phenotypes, glycoalkaloid aglycone content, anther culture and BC_1 family	Rokka et al. (1998, 2005)
S. acaule dihaploid (2*x*)	*S. tuberosum* (4*x*)	Glycolkaloids	Phenotypes	Kozukue et al. (1999)
2. *S. berthaultii* (+) *S. tuberosum*				
S. berthaultii (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to insects, PVY, soil-borne pathogens (*Fusarium, Pythium* and *Rhizoctonia* spp.) and salinity tolerance	Isozyme, cytology, ISSR, cytoplasmic DNA analysis, flow cytometry, phenotypes, nutrients content (Na, Cl and K) and tuber traits	Serraf et al. (1991), Bidani et al. (2007), Nouri-Ellouz et al. (2016)
3. *S. brevidens* (+) *S. tuberosum*				
S. brevidens (2*x*)	*S. tuberosum* (4*x*)/dihaploid (2*x*)	PVY, PLRV, late blight, early blight, bacterial soft rot (*Erwini* spp.) and frost resistance	Chromosome counting, isozyme analysis, RFLP, phenotypes, RAPD analysis, back cross progenies (BC_1, BC_2 and BC_3), RFLP and FISH analyses and field trials	Austin et al. (1985a, b, 1986, 1988), Gibson et al. (1988), Fish et al. (1988), Rokka et al. (1994), Polgar et al. (1999), Chen et al. (1999b), Tek et al. (2004)
S. brevidens (2*x*)	*S. tuberosum* (4*x*)	PLRV and cold-stress resistance	Isozyme analysis, chromosome staining, phenotypes, multivariate analysis, X-ray irradiation, southern hybridization and phenotypes	Preiszner et al. (1991), Fehér et al. (1992), Xu et al. (1993)
S. brevidens (2*x*)	*S. tuberosum* (4*x*)	Bacterial soft rot (*Erwini* spp.) resistance	Segregation analysis, back-cross progenies (BC_1, BC_2 and BC_3), and fluorescence in situ hybridization (FISH) analyses	McGrath et al. (1996, 2002), McGrath and Helgeson (1998)
S. brevidens (2*x*)	*S. tuberosum* (4*x*)	Common scab (*Streptomyces* spp.) resistance	Chromosome counting, BC_1 and BC_2 progenies, and phenotypes	Ahn and Park (2013)
S. brevidens (2*x*)	*S. tuberosum* (4*x*)	Glycoalkaloids	GISH and Gas chromatography-mass spectrometry (GC-MS) analyses and genomic composition of somatic hybrids	Laurila et al. (2001)
4. *S. bulbocastanum* (+) *S. tuberosum*				
S. bulbocastanum (2*x*)	*S. tuberosum* (4*x*)	Nematode (*Meloidogyne* spp.) resistance	Chromosome counting, isozyme analysis, phenotypes, crossability and tuber traits	Austin et al. (1993), Mojtahedi et al. (1995)
S. bulbocastanum (2*x*)	*S. tuberosum* haploids (2*x*)	Late blight resistance	X-ray irradiation, flow cytometry and RFLP analyses	Oberwalder et al. (1997, 1998)
S. bulbocastanum (2*x*)	*S. tuberosum* (4*x*)	Late blight resistance	RFLP, RAPD, and back cross progenies (BC_1 and BC_2) and gene mapping analyses	Helgeson et al. (1998), Naess et al. (2000, 2001)

Table 1 (continued)

Somatic hybrid/fusion parents			Target trait	Characterization	References
	S. bulbocastanum (2*x*)	*S. tuberosum* (4*x*)	Late blight resistance	Cytology (chromosome counting and GISH), flow cytometry, AFLP and SSR analyses, fertility, phenotypes and hybridization	Rakosy-Tican et al. (2015)
	S. bulbocastanum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Plant regeneration, RAPD, flow cytometry and phenotypes	Szezerbakowa et al. (2000, 2001, 2003a), Bołtowicz et al. (2005), Greplová et al. (2008)
	S. bulbocastanum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	ISSR, cytoplasmic DNA, genomic in situ hybridization (GISH), ploidy analysis and anther culture	Iovene et al. (2007, 2012), Aversano et al. (2009)
5.	*S. cardiophyllum* (+) *S. tuberosum*				
	S. cardiophyllum (2*x*)	*S. tuberosum* (4*x*)	Late blight resistance	RAPD, chromosome counting and phenotypes	Shi et al. (2006)
	S. cardiophyllum (2*x*)	*S. tuberosum* (4*x*)	Late blight, PVY and Colorado potato beetle resistance	SSR, AFLP, flow cytometry, phenotypes and fertility of hybrids	Thieme et al. (2004, 2010)
	S. cardiophyllum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	RAPD, ISSR, SSR, AFLP, cytoplasm type (chloroplast and mitochondrial genomes), flow cytometry, phenotypes and fertility of hybrids	Chandel et al. (2015)
6.	*S. chcoense* (+) *S. tuberosum*				
	S. chcoense (2*x*)	*S. tuberosum* dihaploid (2*x*)	Colorado potato beetle resistance	Morphological, biochemical (anthocyanin pigment) and isozyme markers	Cheng et al. (1995)
	S. chcoense (2*x*)	*S. tuberosum* (4*x*)	Bacterial wilt (*Ralstonia* spp.) resistance	RAPD, flow cytometry, nuclear and cytoplasmic genomes, genomic stability, meiotic behaviour of pollen mother cells and SSR analysis	Cai et al. (2004), Guo et al. (2010), Chen et al. (2013)
7.	*S. circaefolium* (+) *S. tuberosum*				
	S. circaefolium (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Flow cytometer, RFLP analyses and fertility of hybrids	Oberwalder et al. (1997, 2000)
8.	*S. commersonii* (+) *S. tuberosum*				
	S. commersonii (2*x*)	*S. tuberosum* dihaploid (2*x*)	Verticillium wilt, tuber soft rot (*Erwinia* spp.) and frost resistance	RAPD, ploidy (chloroplast count in stomata guard cell, chromosome counts and flow cytometer), phenotypes, fertility, cell sorting, southern analysis and organelle DNA, BC_1 and F_2 progenies, multivariate analysis, AFLP and organelles DNA analyses	Cardi et al. (1993, 1999, 2002), Cardi (1998); Nyman and Waara (1997), Waara et al. (1998), Bastia et al. (2000, 2001), Carputo et al. (2000), Barone et al. (2002), Scotti et al. (2003, 2004)

Table 1 (continued)

Somatic hybrid/fusion parents		Target trait	Characterization	References
S. commersonii (2*x*)	*S. tuberosum* dihaploid (2*x*)	Bacterial wilt resistance and cold-stress/freezing tolerance	RAPD, isozyme, chromosome counting, selfing/crossing, back cross progenies (BC_1 and BC_2) and phenotypes	Kim et al. (1993), Laferriere et al. (1999), Kim-Lee et al. (2005), Chen et al. (1999a, c)
9. *S. etuberosum* (+) *S. tuberosum*				
S. etuberosum (2*x*)	*S. tuberosum* dihaploid (2*x*)	PVY, PLRV and green peach aphid resistance	Genomic and chloroplast DNA, RFLP, GISH, cytology, phenotypes, tuber characteristics, back cross progenies (BC_1, BC_2 and BC_3) and field trials	Novy and Helgeson (1994a, b), Dong et al. (1999), Novy et al. (2002, 2007), Gillen and Novy (2007)
S. etuberosum (2*x*)	*S. tuberosum* dihaploid (2*x*)	PVY resistance	Isozyme, SSR markers, GISH and back-cross progenies (BC_1 and BC_2) and flow cytometry	Thieme et al. (1999, 2004), Gavrilenko et al. (2003)
S. etuberosum (2*x*)	*S. tuberosum* dihaploid (2*x*)	PVY resistance	RAPD, SSR, flow cytometry, cytoplasm type and phenotypes	Tiwari et al. (2010, 2015c)
10. *S. melongena* (+) *S. tuberosum*				
S. melongena (2x)	*S. tuberosum* dihaploid (2*x*)	Bacterial wilt resistance	Ploidy level (chromosome count and flow cytometry), SSR, GISH karyotypes and cytoplasmic DNA analysis	Yu et al. (2013)
11. *S.* × *michoacanum* (+) *S. tuberosum*				
S. × *michoacanum* (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	RAPD, SSR, CAPS, ploidy level (guard cell count and flow cytometry), phenotypes, fertility, and F_1 and BC_1 progenies	Szczerbakowa et al. (2010), Smyda et al. (2013), Smyda-Dajmund et al. (2017)
12. *S. nigrum* (+) *S. tuberosum*				
S. nigrum (6*x*) (non-tuberous)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Plant regeneration, RAPD, flow cytometry, phenotypes and crossing	Szczerbakowa et al. (2000, 2001, 2003b, 2011), Zimnoch-Guzowska et al. (2003)
S. nigrum (6*x*)	*S. tuberosum* (4*x*)	Atrazine resistance	Chromosome counting and phenotypes	Binding et al. (1982)
S. nigrum (6*x*) complex species	*S. tuberosum* (4*x*) and dihaploid (2*x*)	–	Isozyme, flow cytometry, selectable markers and phenotypes	Horsman et al. (1997)
13. *S. phureja* (+) *S. tuberosum*				
S. phureja (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Fluorescein diacetate staining, cytology, chromosome number and phenotypes	Puite et al. (1986), Mattheij and Puite (1992)
S. phureja (2*x*)	*S. tuberosum* dihaploid (2*x*)	Bacterial wilt resistance	Isozyme, RAPD, SSR, flow cytometry, chloroplast genome and phenotypes	Fock et al. (2000)

Table 1 (continued)

Somatic hybrid/fusion parents		Target trait	Characterization	References
S. phureja monoploids (1*x*)	*S. phureja* monoploids (1*x*)	Long photoperiods	SSR, flow cytometry, field evaluations, sequence-specific amplification polymorphism (S-SAP) and retrotransposon-based markers analyses	Lightbourn and Veilleux (2007), Lightbourn et al. (2007)
14. *S. pinnatisectum* (+) *S. tuberosum*				
S. pinnatisectum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Flow cytometry, RFLP, phenotypes and tuber traits	Menke et al. (1996)
S. pinnatisectum (2*x*)	*S. tuberosum* dihaploid (2*x*) and *S. phureja* (2*x*)	Late blight resistance	γ-Irradiation, isozyme analysis, chromosome counting and chloroplast DNA analyses	Sidorov et al. (1987)
S. pinnatisectum (2*x*) and Hybrid clone (*S. pinnatisectum* × *S. bulbocastanum*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Isozyme, RAPD, flow cytometry, cytological, phenotypes, crossability and fertility	Thieme et al. (1997)
S. pinnatisectum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	RAPD, cytological and phenotypes	Szczerbakowa et al. (2005)
S. pinnatisectum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	RAPD, flow cytometry and phenotypes	Greplová et al. (2008)
S. pinnatisectum (2*x*)	*S. tuberosum* (4*x*)	Late blight resistance	SSR, organelle DNA analysis and phenotypes	Polzerová et al. (2011)
S. pinnatisectum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	Efficient electrofusion system, RAPD, SSR, cytoplasm type, flow cytometry, phenotypes, field trial, breeding potential and crossing (BC_1 progeny)	Sharma et al. (2011), Sarkar et al. (2011), Tiwari et al. (2013a), Luthra et al. (2016)
15. *S. tuberosum* (+) *S. tuberosum*				
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	PVX and PVY resistance	Chromosome counting, isozyme and phenotypes	Austin et al. (1985b), Thach et al. (1993)
S. tuberosum (4*x*)	*S. tuberosum* (4*x*)	Cytoplasmic male sterility	Phenotypes, flower morphology and true potato seed	Perl et al. (1990)
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to *Globodera* spp. and metribuzin herbicide	Isozyme and phenotypic markers	Möllers and Wenzel (1992)
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to potato cyst nematode and late blight	Phenotypic markers, chromosome counting, flower morphology and RAPD analyses	Cooper-Bland et al. (1994), Rasmussen et al. (1996, 1998)
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	–	Isozyme, chromosome counting, RAPD analysis and phenotypes	Gavrilenko et al. (1999), Przetakiewicz et al. (2007)
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to PLRV, PVY, late blight and soft rot (*Erwiniai* spp.)	RAPD analysis, chromosome counting, flow cytometry, phenotypes, fertility and back crossing	Rokka et al. (1994, 2000), Valkonen and Rokka (1998)

Table 1 (continued)

Somatic hybrid/fusion parents		Target trait	Characterization	References
S. tuberosum dihaploid (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to PVY and storage rot (*Pythium aphanidermatum*)	Isoenzyme analysis, chromosome counting, microtuberization, SSR, ISSR and organelle DNA analyses	Nouri-Ellouz et al. (2006)
16. *S. sanctae-rosae* (+) *S. tuberosum*				
S. sanctae-rosae (2*x*)	*S. tuberosum* (4*x*)	Potato cyst nematode resistance	SSR, RFLP mitochondrial profiles and organelle genomes analyses	Harding and Millam (2000)
17. *S. spegazzinii* (+) *S. tuberosum*				
S. spegazzinii (2*x*) and Hybrid clone (2*x*) (*S. microdontum* x *S. vernei*)	*S. tuberosum* (4*x*) and dihaploid (2*x*)		X-ray irradiation, micromanipulation, fluorescence-activated cell sorting (FACS), cytoplasmic genomes and RAPD analyses	Rasmussen et al. (1997, 2000)
18. *S. stenotomum* (+) *S. tuberosum*				
S. stenotomum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Bacterial wilt resistance	Ploidy level, pollen viability, isozyme, SSR, chloroplast DNA, protein extraction, carboxylase assays, Western blot analysis, microtuberization and biochemical (sucrose and glucose) analyses	Fock et al. (2001)
19. *S. tarnii* (+) *S. tuberosum*				
S. tarnii (2*x*)	*S. tuberosum* (4*x*)	Late blight, Colorado potato beetle and PVY resistance	Flow cytometric, SSR, AFLP and BC_1 progenies analyses	Thieme et al. (2004, 2008)
20. *S. torvum* (+) *S. tuberosum*				
S. torvum (2*x*)	*S. tuberosum* dihaploid (2*x*)	*Verticillium* wilt resistance	Isozyme, morphological markers and phenotypes	Jadari et al. (1992)
21. *S. vernei* (+) *S. tuberosum*				
S. vernei (2*x*)	*S. tuberosum* dihaploid (2*x*)	Salt tolerance	Isoenzyme, RAPD, ISSR, organelle DNA, flow cytometry and phenotypes	Trabelsi et al. (2005)
22. *S. verrucosum* (+) *S. tuberosum*				
S. verrucosum (2*x*)	*S. tuberosum* dihaploid (2*x*)	Resistance to PLRV	RAPD, chloroplast counting, phenotypes and field trials	Carrasco et al. (2000)
23. *S. villosum* (+) *S. tuberosum*				
S. villosum (4*x*)	*S. tuberosum* dihaploid (2*x*)	Late blight resistance	RAPD, GISH and reactive oxygen species (ROS) production by pathogen analyses	Tarwacka et al. (2013)

S. brevidens, S. commersonii, S. etuberosum and *S. villosum* are non-tuberous wild potato species. Cytoplasm types are described as: (i) ALC1/ALC3: 381 bp (T/β), 622 bp (W/α and W/γ); (ii) ALM1/ALM3: 1.2 kb (W/α and W/γ); (iii) ALM4/ALM5: 1.6 kb (T/β), 2.4 kb (W/α); and (iv) ALM6/ALM7: 2.4 kb (W/γ) (Lössl et al. 2000) in potato breeding (Scotti et al. 2003), especially variation in a hot spot mitochondrial region (*rpl5–rps14*) (Scotti et al. 2004). Recently, random and non-random segregations of organelle genomes were observed in somatic hybrid (*S.* × *michoacanum* + *S. tuberosum*) using DArT markers (Smyda-Dajmund et al. 2016).

In search of new genes, a few potato somatic hybrids and their progenies were exploited in linkage mapping studies. The *RB* gene (*Rpi-blb1*) originates from diploid wild species *S. bulbocastanum* of somatic hybrid (*S. bulbocastanum* + *S. tuberosum*) and confers durable resistance to late blight (Helgeson et al. 1998; Song et al. 2003). The *RB* gene was mapped to potato chromosome 8 through analysis of somatic hybrid progenies (BC_1 and BC_2) (Naess et al. 2000, 2001). Besides, genetic stability of in vitro plants of somatic hybrids (*S. tuberosum* dihaploid 'C-13' + *S. pinnatisectum*, and 'C-13' + *S. etuberosum*) was confirmed using methylation-sensitive amplified polymorphism (MSAP) and AFLP markers (Tiwari et al. 2013b, 2015d, e).

Breeding

Improvement of somatic hybrids is essential for desirable agronomic traits through breeding methods to decrease the undesirable effects of wild species. In addition, transfer of disease/pest resistance traits from somatic hybrids to progenies is also important. Assessment of genetic and phenotypic variation among somatic hybrids (Gavrilenko et al. 1999) and development of their advanced progenies such as F_2, BC_1, BC_2 and BC_3 led to the effective utilization somatic hybrids in potato breeding (Table 1). Somatic hybrids performed better in field trials in terms of tuber traits and phenotypes (Carrasco et al. 2000), and a few hybrid produced higher yield, tuber number and weight than parents (Möllers et al. 1994). Tuber yield per plant of backcrossed progenies of somatic hybrid improved considerably to that of parents (Carputo et al. 2000). Recently, potential *S. pinnatisectum*-somatic hybrids (P4, P8 and P10) were selected for adaptability, tuber traits, late blight resistance and keeping quality traits in the sub-tropical plains of India, where nearly 90% of potato is grown (Luthra et al. 2016). Further, hybrid progeny (BC_1) was also generated that can be utilized in potato breeding (Luthra et al. 2016). Good tuber yield and quality were observed in *S. tarnii*-somatic hybrids derived BC_1 progenies in the field trials (Thieme et al. 2008). Further, study confirmed that somatic hybrid had resistance to both PVY and late blight, of which only PVY resistance was transferred to BC_1 progeny. Multiple years of field evaluations of *S. etuberosum*-somatic hybrids and progenies showed stable transmission and expression of PLRV and PVY resistances in three (BC_1, BC_2 and BC_3) and two (BC_1 and BC_2) generations, respectively (Novy et al. 2007). Besides, resistances to PVY, potato leaf roll virus (PLRV), and Green peach aphid in BC_2 progeny were also observed (Novy et al. 2002). Another study demonstrates that late blight resistance can be transferred successfully through breeding from tetraploid somatic hybrids (*S.* × *michoacanum* + *S. tuberosum* and autofused *S.* × *michoacanum*) to common varieties (Smyda-Dajmund et al. 2017). Bacterial wilt resistance was transferred to advanced progenies of *S. commersonii*-somatic hybrids, and three highly resistant clones (BC_1 and BC_2) were selected as breeding materials (Kim-Lee et al. 2005). The effect of genetic constitution of *S. tuberosum* was investigated in *S. bulbocastanum*-somatic hybrids and progenies (BC_1 and BC_2) (Rakosy-Tican et al. 2015). Field performance for foliage maturity and tuber traits (tuber yield, tuber number, tuber weight and specific gravity) was observed in somatic hybrids (*S. brevidens*/*S. commersonii* + *S. tuberosum*) progenies and implicated to breeding for freezing tolerance (Chen et al. 1999a, b, c). Somatic hybrids (*S. commersonii* + *S. tuberosum*) were observed more similar to cultivated potato for phenotypes in field evaluations and developed F_2 progeny, and suggested to fast transfer of useful traits from *S. commersonii* into cultivated background (Cardi 1998; Cardi et al. 2002). Recently, SSR alleles were identified for bacterial wilt resistance breeding in *S. chacoense*-somatic hybrids and backcross progenies (Chen et al. 2016). To our knowledge, there are investigations up to BC_3 generation and all attempts to exploit somatic hybrid material so far have not resulted in registration of a potato cultivar.

Genomics

Somatic hybrids and their parents have been exploited to a limited extent in genomics studies. Whole genome sequences of chloroplast genome of wild potato species (*S. commersonii*), a commonly used fusion parent, was deciphered and identified two Indel markers for application in chloroplast genotyping (Cho et al. 2016). High-throughput genotyping of somatic hybrids (*S.* × *michoacanum* + *S. tuberosum*) showed presence of both parental chromosomes and loss of some markers (13.9–29.6%) in the hybrids using 5358 DArT markers analysis (Smyda-Dajmund et al. 2016). In functional genomics, genes controlling potato tuberization in tuber-bearing somatic hybrids (*S. tuberosum* + *S. etuberosum*) vs. control parent (*S. etuberosum*-non tuberous) were identified using microarray. Findings suggest candidate genes expression in leaf tissue of somatic hybrid are implicated to tuber growth and development process such as transport, carbohydrate metabolism, phytohormones and transcription/translation/binding functions (Tiwari et al. 2015a, b). In another study, late light resistance genes were identified in somatic hybrid (*S. tuberosum* + *S. pinnatisectum*) by microarrays and study suggests a broad spectrum of candidate genes involved in late blight resistance in the hybrid (Singh et al. 2016a).

Further, recent identification of eight miRNAs (miR395, 821, 1030, 1510, 2673, 3979, 5021 and 5213) in *S. pinnatisectum*-somatic hybrid for late blight resistance genes and their targets has led a new insight in potato biology (Singh et al. 2016b). Most of the predicted target genes are associated with different biological processes such as disease resistance proteins and transcription factors families. These miRNAs could be manipulated through RNAi technique for transgenic development (Singh et al. 2016b). Thus, with the advancement in next-generation sequencing technologies, there is a huge scope to deploy these novel tools in somatic hybrids to study potato biology and improvement.

Conclusions

Limited utilization of *Solanum* species and therefore narrow genetic base of the cultivated potato is the cause of concern of yield stagnation. Development of potato somatic hybrids using wild *Solanum* species with desirable attributes could be helpful to address this issue. Analyzing breeding potential of somatic hybrids, development of advanced progenies by hybridization with common varieties and identification of linked molecular markers are important for their successful applications in potato breeding. Further, information on nuclear-cytoplasmic interaction between cultivated and wild species could also be useful while exploitation of somatic hybrids in breeding. Novel genomics tools like whole genome sequencing, DArT markers based genotyping, microRNAs, microarrays and many others could strengthen the somatic hybridization research in potato. Moreover, access to the next-generation sequencing technologies and the potato genome sequences are essential for application of genome-enabled breeding strategies and critical investigation of complex biological processes like heat tolerance, tuberization, yield, disease-pest resistance and other traits. The sequence data could be extensively deployed for gene discovery, marker development, phylogeny, comparative genomics, breeding, and engineering of new genotypes/phenotypes. Taken together, above studies would provide a myriad of useful information available in somatic hybrids for potato genetics, breeding and genomics improvement.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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