REVIEW

Wild Potato Species: Characterization and Biological Potential for Potato Breeding

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Abstract: Wild potato species (genus *Solanum*, section *Petota*) represent a tremendously diverse gene pool which is traditionally utilized as a source of diverse traits for potato breeding. Abiotic and biotic stress tolerance and resistance belong to the most frequently utilized traits of wild species in potato breeding programs. This review provides an introduction to the taxonomy, centre of diversity, genetic characteristics, evolution and important tolerance and resistance traits of wild potatoes and their use for potato breeding. The review has been written for readers who are interested in the problems of finding and utilization of new resistance genes from the wild genetic resources.

Keywords: disease and pest resistance genes; genetic resources; potato resistance breeding; wild potato species

Potatoes seem to have been domesticated at least 7000 years ago (HAWKES 1994), however their introduction into Europe dates back to the 16th-17th century. The first introduced genotypes probably belonged to Solanum tuberosum subsp. andigena Juz. et Buk, which was adapted to short-day conditions and tuberised from December to January in southern Spain (Spanish archives cit. FRUSCIANTE et al. 2000). The European potatoes are considered to be a selection from this genotype (FRUSCIANTE et al. 2000). An alternative theory is that after a European potato blight epidemic new genotypes were introduced, probably S. tuberosum subsp. tuberosum L., originating from Chile (HAWKES 1990). This genotype was better adapted to the long summer day and could spread into northern Europe. The development of the European form of potato was completed between the 18th and 19th century (Frusciante et al. 2000).

In contrast to other crop plants, there is a diverse pool of potato wild species which could be a source of traits for potato breeding – e.g. tolerance to biotic as well as abiotic stress factors (FRUSCIANTE *et al.* 2000; WATANABE 2002; HIJMANS *et al.* 2003). The species used in breeding programmes as donors of tolerance and resistance traits are particularly *S. demissum, S. acaule, S. chacoense, S. spegazinii, S. stoloniferum, S. vernei* (CALIGARI 1992). General information on taxonomy, centre of diversity, genetic characteristics, evolution and important tolerance traits of wild potatoes and their use for potato breeding is discussed in the present review.

Taxonomy of wild potato species

The potato belongs to *Solanaceae*, the family of about 90 genera and 2800 species. The genus *Solanum* consists of about 2000 species (VOLKOV *et al.*

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2003). The wild tuber-bearing Solanum species are divided into two sections: Petota (also known as the section Tuberarium) and Etuberosum. The largest and more important section *Petota* is divided into two subsections (HAWKES 1990): Estolonifera (nine non-tuber-bearing species placed in two series) and Petatoe (1 non-tuber-bearing and 224 tuber-bearing species placed in 19 series). Tuber-bearing species with the "stellata" or "rotata" morphology of the corolla are additionally combined in the corresponding superseries, Stellata or Rotata (VOLKOV et al. 2003). From all the known tuber-bearing Solanum species only seven are cultivated - the worldwide cultivated species Solanum tuberosum L., and six others that are grown only locally in the Andes (HIJMANS & SPOONER 2001).

The classification of the genus Solanum into series is based mainly on corolla shape, fruit shape, leaf shape and dissection, anther form and stigma form (HAWKES 1994); however, because of high morphological similarity and interspecific hybridization the sect. Petota is taxonomically difficult (VOLKOV et al. 2003) - e.g. the Solanum brevicaule complex is a taxonomically confusing group of approximately 30 morphologically similar taxa related to S. tuberosum which differ only in overlapping character states (HUAMÁN & SPOONER 2002). The same is also true of the members of ser. Conicibaccata, Longipedicillata and even ser. Tuberosa and Demissa (VOLKOV et al. 2003). This is the reason why the taxonomy of sect. Petota varies greatly among authors (RAKER & SPOONER 2002). Research is continuing to refine the wild potato taxonomy, and there will likely be a reduction in the number of species and series (VAN DER Berg et al. 1998; Spooner & Hijmans 2001). For example, the chloroplast DNA restriction site data supported only four clades within the sect. Petota, and not the 19 series that were examined (SPOONER & SYTSMA 1992). Other molecular markers such as nuclear RFLP, AFLP and RAPD were also performed (MILLER & SPOONER 1999). These data also fail to support many traditional series (KARDOLUS 1998).

Geographical distribution and centre of diversity

The centres of diversity for wild tuber-bearing *Solanum* species are situated in America, from the south-western United States to central Argentina and Chile. Three geographical areas of wild potato occurrence are traditionally mentioned: an equatorial area with short-day species (ser. Andigena), lowland area of Chile and closely situated islands with long-day species (ser. Tuberosa and Etuberosa) and lowland area of Uruguay (ser. Commersionianna) (HAWKES 1994). According to the latest study of geographical distribution (HIJMANS & SPOONER 2001), the wild potatoes occurred in 16 countries of Americas, but 88% of the observations were from Argentina, Bolivia, Mexico, and Peru. Most of the species (77) were rare and narrowly endemic. Peru had the highest number of species (93). High species richness occurs also in northern Argentina, central Bolivia, central Ecuador and central Mexico. Peru stands out for the high number of rare potato species. This indicates that Peru may still harbour unknown species, as illustrated by the ten new Peruvian wild potatoes described by C.M. Ochoa between 1998 and 1999 (HIJMANS & SPOONER 2001). There is no evidence that wild potatoes are currently being domesticated or their geographic distribution is altered, except for S. chacoense, which is grown as an ornamental plant in Lima, Peru. However, the gene flow between wild and cultivated potato species is taking place in some parts of the Andes (RABINOWITZ et al. 1990).

Genetics of potato species

Tuber-bearing *Solanum* species have unique reproductive characteristics consisting e.g. in: a possibility of both vegetative and sexual reproductive strategy; production of gametes with unreduced chromosome number; existence of different ploidity levels and presence of an endosperm dosage system that regulates interploidy/interspecific crosses (CARPUTO & BARONE 2005). All these traits have been of great importance in breeding as well as in classification and evolutional studies.

The number of ploidy levels of potato species, based on a haploid number of 12, ranges from diploid (2n = 24) to hexaploid (6n = 72), and includes triploids, tetraploids, and pentaploids (WATANABE 2002). Cultivated potatoes are tetrasomic tetraploids (4n = 48), without diploidization. The majority (80%) of the wild species is diploid (CARPUTO & BARONE 2005). It is interesting that few species possess two or more ploidy levels that are morphologically indistinguishable. *S. gourley* possesses diploid and tetraploid cytotypes, *S. oplocense* possesses diploid, tetraploid and hexaploid cytotypes. There is absolutely no idea why this phenomenon should occur only in a small area of southern Bolivia and northern Argentina (HAWKES 1994). The specific ploidy levels are in relation to the phenomenon of unreduced gametes. Next to the normal haploid gametes (*n*), several genotypes produce unreduced gametes (2n) as a result of meiotic anomalies (CARPUTO & BARONE 2005). The frequency of 2*n* pollen production varies from 2% up to 10% (WATANABE 2002). Diploid species of the section *Petota* as well as tetraploid *S. tuberosum* subsp. tuberosum are self-incompatible. The incompatibility is of a gametophytic, multi-allelic nature based on the occurrence of S alleles. In general, potato species are insect-pollinated, cross-breeding species. The other important biological characteristic of the potato is connected with a specific theory called endosperm balance number (EBN) (JOHNSTON & HANNEMAN 1980). This phenomenon has a great importance in breeding programmes and in the potential of interploidy/interspecific crosses. The EBN is a number varying from 1 to 4, expressing the effective ploidy of Solanum species (CARPUTO & BARONE 2005). To make the normal development of the endosperm after fertilization possible, the maternal EBN must be twice higher than the paternal EBN (2:1). The EBN is independent of the ploidity level, and its behaviour is additive. Cultivated S. tuberosum is 4EBN, whereas most of the wild species (either diploid or tetraploid) are 2EBN. Several natural and artificial mechanisms are available to circumvent the EBN incompatibility. The natural occurrence of unreduced gametes makes it possible that species with lower EBN can cross with species with higher EBN. The artificial systems are production of dihaploids or polyploidisation. Despite the EBN system, potatoes of different groups can be combined by somatic fusion in vitro (Carputo & Barone 2005).

Potato species evolution

The tetraploid *S. tuberosum* originated either by a chromosome doubling of diploid cultivated species or by a diploid by diploid cross with chromosome doubling. The likely candidates are *S. stenotomum* and the common weed species *S. sparsipilum* (HAWKES 1994). The evolution of wild potatoes is far more questionable. There are only hypotheses based on the cytological and genetic evidence. Mexico is traditionally (HAWKES 1990) accepted as a place of origin of tuber-bearing potatoes, reflecting the fact that the morphologically most "primitive" species with 1EBN concentrate there. According to HAWKES (1994) the Mexican ancestors migrated (37-40 million years ago) in South America leasing 1EBN (Lignicaulia in Peru; Circaeifolia in Bolivia; Commersoniana in Argentina), creating 2EBN and migrated northwards again (ser. Tuberosa, Megistacroloba, Commersoniana). Finally, the species that arrived in Mexico (ser. Longipedicellata, Demissa) were unable to cross with their 1EBN ancestors. According to this scenario, tuber-bearing species should be closely related with and obviously separated from non-tuber-bearing species. However, the data based on genetic evidence (VOLKOV et al. 2001, 2003) do not support this hypothesis. Comparing the 5S rDNA spacer region a close relationship was found between ser. Etuberosa, South American Stellata and Rotata as well as an isolated position of Mexican Stellata was observed (Volkov et al. 2001). Later, VOLKOV et al. (2003) used also the 5' external transcribed spacer (5' ETS) of nuclearencoded rDNA for phylogenetic analysis. The analysis of ETS shows that "primitive" Rotata originated in South America and contributed to the "advanced" Stellata and Rotata. Therefore, the hypothesis of HAWKES (1990) that "primitive" Stellata returned from Central America should be rejected. Data of Volkov et al. (2003) agree with the analysis of cpDNA, which shows early separation of S. bulbocastanum and S. pinnatisectum from S. commersonii and S. capsicibaccatum together with species of the superser. Rotata (SPOONER & CASTILLO 1997). The origin of polyploid species S. maglia, S. acaule, S. tuberosum and S. demissum is unclear (Volkov et al. 2003).

Wild potatoes and stress resistance

The genus *Solanum*, section *Petota*, offers a tremendously diverse gene pool which can be utilized in potato breeding (WATANABE 2002). The wild potatoes naturally developed in diverse conditions and are adapted to a wide range of environmental stresses (PÉREZ *et al.* 2000). Sequencing of the entire region in both the wild and the cultivated species revealed several active resistance gene (*R* genes) homologues, indicating that the frequent sequence exchange between these tandemly repeated genes created novel *R* gene specificities (PARNISKE *et al.* 1997). Complex loci on chromosome 5 and 12 are important in the case of potato resistance. The cluster on chromosome 5 comprises at least five *R* loci: *R1*, which bestows resistance to Phytophthora infestans (LEONARDS-SHIPPERS et al. 1992); Nb, conferring an HR type of resistance; *Rx2*, conferring extreme resistance to potato virus X (DE JONG et al. 1997) and Gpa and Grp1, conferring extreme resistance to the potato cyst nematode (Rouppe van der Voort et al. 1997). All these loci originated from different genetic backgrounds. A novel R gene cluster was identified on the short arm of chromosome 12 - Gpa, which bestows specific resistance to the potato cyst nematode (Globodera pallida) (ROUPPE VAN DER VOORT et al. 1997) and Rx, which confers extreme resistance to potato virus X (BENDAHMANE et al. 1997). Roupe van der Voort et al. (1999) provided evidence that both genes were physically tightly linked and were introduced into a number of European potato cultivars from a single wild potato clone, S. tuberosum subsp. andigena.

Resistance to viruses

In searching virus resistance, priority is given to potato leafroll virus (PLRV) and potato virus Y(PVY) (MARZEWSKI et al. 2001). Resistance to PLRV is controlled by genetic factors that limit the plant infection by viruliferous aphids or virus multiplication and accumulation. Resistance to aphids has been described as polygenetically controlled; resistance to virus accumulation seems to be under a simple genetic control (BROWN & THOMAS 1994). Quantitative trait locus (QTL) analysis of resistance to virus accumulation revealed one major and two minor QTL. The major QTL is *PLRV1*, situated on chromosome 11; the two minor QTL are mapped to chromosome 5 and 6. PLRV1 is situated close to the RGL locus (MARZEWSKI et al. 2001), which contains a number of R genes (GEBHARDT & VALKONEN 2001). Among these are genes for resistance to potato virus Y (BRIGNETI et al. 1997) and hypersensitive resistance to potato virus A (HÄMÄLÄINEN et al. 2000). A number of wild and cultivated Solanum species possesses genes for resistance to PLVR. S. chacoense seems to be the most promising source for potato breeding (BARKER & WATERHAUSE 1999). Genes for PLRV resistance were also found in S. demissum and S. acaule (SWIEZINSKI et al. 1989) and other species such as S. brevidens, S. etuberosum, S. pinnatisectum and S. verrucosum were also used in PLRV resistance breeding (Рени et al. 1990). Potato virus Y (PVY) strains can be classified at least into three groups, of which PVY⁰ and PVY^N are the most important. Breeding for resistance is easier than in the case of PLVR because markers for the presence of the Ry_{adg} gene were found there (UHRIG *et al.* 1992). These markers are based on a different *N*-like sequence that was mapped to the same resistance location on potato chromosome 6, which includes Ry and PLRV1 (KASAI *et al.* 2000). The species *S. phureja* and *S. stoloniferum* are sources of such genes (ROSS 1986). Sources of PVY resistance became also available from somatic hybrids between *S. brevidens* and *S. tuberosum* (PEHU *et al.* 1990) and this resistance seems active also against PLRV and PVX (UHRIG *et al.* 1992).

Resistance to late blight

Late blight, caused by the pathogen *Phytophthora infestans*, is the most devastating disease for potato cultivation. A disastrous epidemic attack on potatoes in the middle of the 19th century forced the breeders to introduce a new resistant germplasm (UHRIG *et al.* 1992). Previously, wild species from Mexico were used; therefore around 80% of current potato cultivars have late blight resistance genes introduced from the species such as *S. demissum*, *S. chacoense* and *S. phureja* (UHRIG *et al.* 1992; PÉREZ *et al.* 2000).

The qualitative resistance to late blight is based on a series of 11 single dominant R genes, designed R1 to R11 (SHAW 1991). These genes are associated to potato chromosome 5 and cause a hypersensitive type of reaction (GEBHARDT & VALKONEN 2001). Unfortunately, the resistance caused by the R genes appeared not to be durable. More durable is field resistance, which is quantitative and race non-specific (VAN DER VOSSEN et al. 2003). This resistance was firstly found in the Mexican wild species S. demissum and S. stoloniferum (TOXOPEUS 1964) and later also in the species S. phureja and S. tuberosum subsp. andigena (NIEDERHAUSER 1989). However, this type of resistance is difficult to transfer into potato cultivars through crossing and phenotypic selection (VAN DER VOSSEN et al. 2003). Newly the attention is paid to the wild species S. bulbocastanum, which is considered to be highly resistant to all known races of P. infestans, and ploidy manipulation and series of bridge crosses resulted in the germplasm that showed durable and effective resistance (Song et al. 2003). However, breeding efforts with this

genotype have not resulted in the market introduction of resistant cultivars yet. New methods in potato breeding could be a hope for the future. Currently, novel *R* genes have been cloned, including the *S. demissum*- and *S. bulbocastanum*-derived late blight resistance genes *R1*, *RB*, *Rpi-blb1* and *CC-NBS-LRR*. The isolation of resistance genes and subsequent transformation of existing potato cultivars with these genes could be a much quicker way of exploiting late blight resistance in wild *Solanum* species (VAN DER VOSSEN *et al.* 2003).

Recently, a large project of CIP (International Potato Centre) was focused on finding species with both qualitative and quantitative resistance genes. During this project eighteen species that presented both the qualitative and quantitative response were found. The best results were obtained in the species *S. cardiophyllum*, *S. piurae*, *S. circeifolium*, *S. stoloniferum* or *S. polyadenium*. The wild species which were not evaluated for the quantitative resistance before and showed a high level of resistance include: *S. urubambae*, *S. violaceimamoratum*, *S. cantense*, *S. cajamarquense*, *S. orophilum*, *S. velaedei*, which are endemic species (PÉREZ et al. 2000).

Resistance to bacterial diseases

The most important bacterial disease of potato, blackleg of stems and tuber soft rot, are caused by the bacterial species Erwina carotovora subsp. carotovora and E. carotovora subsp. atroseptica. The antecedent sources for resistance to E. carotovora were obtained via somatic fusion between S. tuberosum and the non-tuber-bearing wild species S. brevidens. The fusion hybrids produced highly resistant tubers (UHRIG et al. 1992). New sources of polygenic resistance to E. carotovora subsp. atroseptica were selected in diploid hybrids originating from intercrossing S. tuberosum L. with the wild species S. chacoense and S. yungasense (ZIMNOCH-GUZOVSKA et al. 2000). The F₁ hybrid population was then used to locate QTL for resistance to E. carotovora spp. atroseptica. Genetic factors affecting resistance to E. carotovora were located on all 12 potato chromosomes. Putative QTL for tuber and leaf resistance were identified on chromosome 10. QTL analysis (ZIMNOCH-GUZOVSKA et al. 2000) revealed that the control of resistance to E. carotavora spp. atroseptica was complex and truly polygenic - at least 13 control factors were estimated. The two most significant and reproducible QTL for tuber resistance, *Eca1A* and *Eca6A*, were linked to the RGL loci. This linkage suggests that components for quantitative resistance may be controlled by factors which are similar at the molecular level to the genes encoding qualitative resistance.

Resistance to potato cyst nematode

The most important are endoparasitic sedentary nematodes of the genus Globodera, Heterodera and Melaidogyne (ERNST et al. 2002). G. rostochiensis and G. pallida are the two prevailing potato cyst nematode species. Resistance breeding is complicated by the existence of several pathotypes (five of G. rostochiensis and three of G. pallida) that are distinguished by their ability to multiply on Solanum clones containing different genes for resistance (BRODIE et al. 1988). Several potato cyst nematode resistance genes were genetically characterized within the Solanum species and successfully exploited in potato breeding (Ross 1986). Resistance genes were found in S. tuberosum ssp. andigena (gene H1), S. vernei and S. spegazzinii (gene Fb) (UHRIG et al. 1992). The dominant nematode resistance gene H1 is located on potato chromosome 5 (PINEDA et al. 1993) and has been used to provide a high level of durable resistance against G. rostochiensis pathotypes Ro1 and Ro4 within potato cultivars worldwide (BRODIE et al. 1988). Another nematode resistance gene, Gro1, originating in S. spegazzinii confers resistance to G. rostochiensis pathotypes Ro_{1-5} and was mapped on chromosome 7 (BALLVORA et al. 1995). Difficult is the situation with G. pallida because of the possible polygenic nature of resistance. A number of resistance genes against G. pallida pathotypes (Pa₁, Pa_{2/3}) was characterized from the Solanum species but most of them behave as quantitative ones (PHILLIPS 1994). Recently the Gpa2 gene of potato conferring resistance to a small set of populations of G. pallida was described (VAN DER VOSSEN et al. 2000). The species which may contribute the resistance genes active against G. pallida are S. vernei, S. spegazzinii as well as the wild species S. gourlayi, S. aplocense, S. linguicaule and S. megistacrolobum (BARONE et al. 1990).

Colorado potato beetle resistance

Progress in the development of potato cultivars resistant to the Colorado potato beetle *Leptino*-

tarsa decemlineata has been reviewed extensively (Yencho & Tingey 1994; Pelletier & Tai 2001). Commercial varieties are considered to be equally susceptible to the Colorado potato beetle. Two wild Solanum species, S. chacoense and S. berthaultii, have been used for potato insect resistance breeding (Pelletier et al. 1999). S. chacoense is used for its ability to produce leptine glycoalkaloids. The leptines reduce feeding by adults and increase the preimaginal mortality of Colorado potato beetle. S. berthaultii possesses multiple resistance mechanisms operating in a complementary fashion. This species is used as a source of glandular trichomes (type A and B) on leaves and stems that deter feeding and affect the digestive physiology of the Colorado potato beetle (Kessler & BALDWIN 2002). Since the resistance mechanism is under the control of different loci, the introgression of the whole resistance of S. berthaultii into cultivated potato is complicated because of the strong association with poor yield, poor tuber appearance, late tuberization, etc. (KALAZICH 1989). Except the species S. berthaultii the resistance potential was evaluated in many other species (Pelletier & TAI 2001). PELLETIER and TAI (2001) found that the species S. berthaultii, S. capsicibaccatum, S. jamezii, S. pinnatisectum and S. trifidum demonstrated both antixenosis and antibiosis and expressed different levels of resistance.

Frost resistance

Frost is a major limiting factor in potato production at high altitudes or in mountain areas (HIJMANS & SPOONER 2001). S. tuberosum possesses very low frost resistance, whereas the wild species S. acaule and S. commersonii can survive without frost injury at -4° C, even to -11° C after acclimation (VAYDE 1994). The frost tolerance of wild species is often associated with geographic and ecological factors, suitable for the origin of such adaptation (HIJMANS & SPOONER 2001). Frost tolerance of wild potato species tends to increase with the altitude, while in the other species this relation fails. Associations have been found between the altitude of provenance and the frost tolerance of Solanum acaule (VEGA & BAMBERG 1995). HIJMANS et al. (2003) reported a significant association between frost tolerance and specific species or geographic factors. The highest frost tolerance was found in the case of the species S. acaule (100%), S. albicans (100%),

S. commersonii (99%), S. demissum (92%) and S. paucissectum (92%). Areas with the high level of frost tolerance are the central and southern Peruvian Andes, the lowlands of Argentina and a small area in the central Chilean Andes (HIJMANS et al. 2003). The gene for resistance to low temperature, Scdhn1, was described for the species S. commersonii. The induction of the gene was relatively rapid and maximum amounts of the transcripts were detected already after 1 day and 7 h of treatment with low temperature (BAUDO et al. 1996). Cold acclimation is often associated with numerous biochemical changes including the accumulation of special cryoprotective solutes, changes in the pigment composition and the level of ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco), as well as synthesis of cold regulated (COR) proteins (ZHANG et al. 2002). An increase or a decrease in special cryoprotective matters is genotype specific (BARIENTOS et al. 1993).

Wild species in potato breeding

Potato breeding in the modern sense began in 1807 in England when deliberate hybridization between different varieties was performed by artificial pollination (BRADSHAW & MACKEY 1994). Priorities for modern agriculture are yield stabilization and at the same time a decrease in the use of fertilizers, pesticides and water (EPSO 2005). Potato cultivars with higher levels of disease and pest resistance are highly desirable, but of course further to these properties they must also retain the marketable yield and quality required for a modern cultivar to be successful (BRADSHAW & MACKEY 1994). Plant science is generating major advances in the understanding of strategies that plants use to survive unfavourable environmental conditions and to defend themselves against pathogens and herbivores. The genus Solanum section Petota offers a tremendously diverse gene pool of wild species for enhancing the germplasm of the cultivated potato (WATANABE 2002) and it has been demonstrated many times that resistance genes of wild potatoes could confer durable resistance usable for potato breeding (Song et al. 2003). Few wild tuber-bearing species were involved in the early domestication process in the Andes - probably just several closely related and inter-fertile members of the series Tuberosa. During the 20th century, the genetic base of the European cultivated potatoes was enlarged with

genes conferring high levels of resistance to viruses, cyst nematode and late blight (BRADSHAW & MACKEY 1994) although the classic breeding methods based on the crossing of suitable genotypes are considered not to be sufficient for the utilization of specific properties of the wild potato genotypes. Conventional breeding strategies are too slow because they are essentially based on phenotypic selection, involving crosses between tetraploid varieties and advance clones, and then field evaluation and selection (EPSO 2005). The methods of molecular biology moved the potato breeding forward. This is characterized by a renewed emphasis on single genes for resistance properties studied and manipulated by emerging tools like RFLP or AFLP markers, ploidity manipulating or diploid pre-breeding. Usable could be the methods of genetic engineering -resistance genes could be transferred from wild potato species to related species of cultivated potato, which should dramatically increase the gene pool available for improvement (EPSO 2005).

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