**Exploring wild Potato relatives for biotic and abiotic stress resistance: a genetic resource review**

**Abstract**

Potato (*Solanum tuberosum* L.) is one of the world’s most important food crops, yet its limited genetic diversity makes it vulnerable to both biotic and abiotic stresses. Wild *Solanum* species represent a rich source of genetic variation that can be exploited to improve resistance traits in cultivated potatoes. This review highlights the valuable genetic resources found in wild potatoes for addressing key agricultural challenges. In terms of biotic stress, resistance mechanisms such as glycoalkaloid production (e.g., α-Solanine, α-Chaconine, tomatine, leptines) and the presence of glandular trichomes have been identified in species like *S. chacoense*, *S. tarijense*, and *S. polyadenium*, conferring resistance to major pests such as the Colorado potato beetle and aphids. *S. hougasii* shows notable resistance to nematodes. For abiotic stress, traits associated with drought tolerance (e.g., genes *ACS3*, *ALDH*, *PP2C*), cold tolerance (*S. commersonii*, *S. acaule*), and heat tolerance (e.g., *HSP17.7*, *HSC70*) have been observed. Recent research also identifies the *StCYS1* gene, encoding a cystatin protein, as a positive regulator of salt tolerance in potato by enhancing osmotic adjustment and oxidative stress responses. The integration of such traits into breeding programs using molecular tools and conventional selection offers a promising pathway for developing climate-resilient, high-yielding potato cultivars. Continued exploration and conservation of wild germplasm are essential for sustaining global potato production under changing environmental conditions.

***Keywords:*** Potato, wild *Solanum* species, abiotic stress, biotic resistance, glycoalkaloids, heat-shock proteins, *StCYS1* and genetic resources

**Introduction**

Potato (*Solanum tuberosum* L.) is the fourth most important food crop globally, serving as a vital source of carbohydrates, vitamins, and minerals for millions of people. However, its productivity is increasingly threatened by a range of biotic and abiotic stresses, including insect pests, nematodes, pathogens, drought, salinity, heat and cold. These environmental and biological challenges not only reduce yield but also affect tuber quality, posing significant threats to food security in both temperate and tropical regions. Compounding these challenges is the narrow genetic base of modern cultivated potato varieties, which limits their capacity to withstand multiple stress factors.

Wild relatives of cultivated potatoes, belonging to the *Solanum* genus, represent a rich reservoir of genetic diversity that has evolved under diverse ecological conditions. These wild species harbor a wide array of traits that confer resistance to pests and diseases as well as tolerance to adverse environmental conditions. For example, wild species such as *S. chacoense*, *S. tarijense*, and *S. polyadenium* possess natural resistance to insect pests through mechanisms involving glycoalkaloids and glandular trichomes. Similarly, resistance to nematodes and other pathogens has been reported in species like *S. hougasii*.

In addition to biotic stress resistance, wild potatoes also offer critical genes for abiotic stress tolerance. Traits such as drought tolerance, cold hardiness, and salinity and heat resilience have been identified in species like *S. commersonii*, *S. acaule*, and *S. berthaultii*. Molecular studies have revealed key stress-related genes, including *HSP17.7*, *HSC70*, and *StCYS1*, that play significant roles in thermotolerance and salt stress adaptation.

This review aims to synthesize current knowledge on the genetic resources available in wild *Solanum* species, with a focus on their roles in conferring biotic and abiotic stress resistance. The objective is to highlight the potential of these genetic traits for improving cultivated potato varieties through modern breeding and biotechnological approaches, ensuring sustainable productivity under changing climatic conditions.

**Materials and Methods**

This review employed a systematic analysis of scientific literature, genomic databases, and germplasm repositories to explore the potential of wild *Solanum* species in improving stress resistance in cultivated potato (*Solanum tuberosum* L.). Relevant studies were sourced from databases such as PubMed, Scopus, and Web of Science using targeted keywords. Selection focused on research highlighting biotic and abiotic stress tolerance traits in wild relatives. Germplasm and trait data were compiled from global resources including CIP, Genesys, and USDA-GRIN, while stress-related gene information (e.g., *HSP17.7*, *HSC70*, *StCYS1*) was retrieved from NCBI and Ensembl Plants. Data were organized by stress type, species, and genetic traits to identify trends and applications in breeding. Conservation strategies, including in situ and ex situ methods, were also reviewed to underline the importance of preserving plant genetic resources for sustainable potato improvement.

**Important features of plant genetic resources**

* Genetic pool represents the entire genetic variability and diversity available in a crop species. Germplasm consists of land races, modern cultivars, absolute cultivars, breeding stocks, wild forms and wild species of cultivated crops.
* Germplasm includes both cultivated, wild species and relatives of crop plants.
* Germplasm is collected from centres of diversity, gene banks, gene sanctuaries, farmer's fields, markets and seed companies.
* Germplasm is the basic material for crop improvement programmes.
* Germplasm may be indigenous (collected within country) or exotic (collected from foreign countries).

**Importance of Plant Genetic Resources**

* Increased productivity, food security and economic returns through diversified products and income opportunity.
* Provide sources for improved human nutrition and medicines.
* Reduced pressure of agriculture.
* Contributing to sustainable intensification.
* Reduced dependence on external inputs.
* Making farming systems more stable, robust and sustainable Contributing to sound insect pest and disease management.
* Conserving soil.
* Increased natural soil fertility and health.
* Conserving ecosystem structure and stability of species diversity.

**Importance of conservation of plant genetic resource**

PGR conservation is defined as the maintenance of germplasm in such a state that there is minimum risk for its loss and that either it can be planted directly in the field or it can be prepared for planting with relative ease or PGR conservation refer to protection of genetic diversity of crop plants from genetic erosion or germplasm conservation is defined as the management of human use of the biosphere so that it may yield the sustainable benefit to present generation, while maintaining its potential to meet the needs and aspirations of future generation. The effective conservation and use of PGR is vital for creating and maintaining sustainable increase in the productivity of healthy food for mankind.

**National plant genetic resources activities and institutes**

The Department of Agricultural Research and Education (DARE) in the Ministry of Agriculture, GOI and ICAR lead the national activities on genetic resources of agriculture and related organisms. This system operates as subsystem of National Agricultural Research System (NARS) Unough four National Bureaus, namely.

1. National Bureau of Plant genetic Resources (NBPGR) - New Delhi

2. National Bureau of Animal genetic Resources (NBAGR) - Karnal (Haryana)

3. National Bureau of Fish genetic Resources (NBFGR)-Lucknow (UP)

4. National Bureau of Agriculturally Important Microorganisms (NBAIM) - New Delhi

In our Chhattisgarh state a total of 23250 Germplasm collections of rice accessions are being maintained and evaluated for various biotic and abiotic stresses along with yield contributing traits.

**Table No. 1. List of Potato wild relatives with specific traits**

|  |  |  |
| --- | --- | --- |
| **S.N.** | **Species** | **Quality traits** |
| 1 | *S. medians, S. okadae, S. pinnatisectum, S. raphanifolium,*  *S. sogarandinum* | Chip directly from cold storage |
| 2 | *S. siparunoides, S. sisymbrifolium, S. stramonifolium, S. tuberosum* | Used in medicine |
| 3 | *S. phureja, S. stenotomum* | High carotenoid content |
| 4 | *S. phureja, S. vernei* | High starch content |
| 5 | *S. phureja, S. estoloniferum* | High ascorbic acid content |
| 6 | *S. phureja* | High protein content, low temperature  non-sweetening |
| 7 | *S. vernei* | High starch and protein content, low reducing  sugar content |

**(**Kumar *et al*. 2018**)**

**Molecular classification of Cultivated Potato Species**

Recent studies suggested that, genotyping of 742 landraces of all cultivated and wild Species have been completed with SSR and chloroplast markers (Spooner *et al*. 2007). Based on these studies, they reclassified the all cultivated potatoes in following four species: (i) *S. tuberosum*, with two cultivar groups (the *Andigenum* group – diploids, triploids and tetraploids and the *Chilotanum* group – tetraploid); (ii) *S. ajanhuiri* (diploid); (iii) *S. juzepczukii* (triploid) and (iv) *S. curtilobum* (pentaploid) (Spooner *et al*. 2007).

**1. *Solanum ajanhuiri***(2n = 2X = 24): this diploid species was formed by natural hybridization between diploid cultivars of *S. tuberosum* L. *andigenum* group and the tetraploid wild species *S. bolivense* (*S. megistacrolobum*). This landrace possesses frost resistance and is distributed in the high Andean Altiplano between southern Peru and central to North Bolivia, at elevations between 3700 and 4100 m [Spooner *et al*. 2010 and Ovchinnikova *et al*., 2011].

**2. *S. juzepczukii***(triploid) (2n = 3X = 36): formed by hybridization between a diploid cultivar of *S. tuberosum* L. *andigenum* group, and the tetraploid wild species *S. acaule* Bitter (Rodriguez *et al*., 2010). It can be found from central Peru to southern Bolivia and can grow at an altitude of 4000 m (Spooner *et al*. 2010]). This species contains high levels of glycoalkaloids, and local people prepare detoxified processed potato “chuño” by freeze drying (Irikura Y. 1989).

**3. *S. curtilobum***(2n = 5X = 60): formed by hybridization between tetraploid forms of *S. tuberosum* L. *andigenum* group (synonym for *S. tuberosum* subsp. *andigenum*) and *S. juzepczukii* (Rodriguez *et al*., 2010) is cultivatedin the Andean Altiplano at an altitude range of approximately 4000 m (Spooner *et al*. 2010). Becausethe tubers are bitter, owing to high glycoalkaloid content, the species is also used to prepare“chuño” (Irikura Y. 1989).

**4. *S. tuberosum****:* the most popular cultivated potato is *S. tuberosum*, which is also known as “common potato” in most parts of the world. It has originated from the coastal regions of South-Central Chile.

**5. *S. chaucha*: *S. chaucha***is a cultivated triploid species that supposedly originated from natural hybridization between *S. tuberosum* subsp. *andigena* and *S. stenotomum* (Hawkes 1990) distributed from 2100 to 4100 msl throughout Peru, with lower frequency in Bolivia, and rarely found in Ecuador and Colombia.

**6. *S. phureja*:** this species was cultivated from central Peru to Ecuador, Colombia, and Venezuela since the pre-Spanish era and is believed to have originated from *S. stenotomum* (Hawkes 1990).

**7. *S. stenotomum:*** the species is diploid and cultivated from Central Peru to Central Bolivia. Most primitive form of cultivated potato. *S. stenotomum* shows the diversity within species, suggesting it to be the first domesticated potato derived from diploid wild species.

**Table No. 2 List of Potato species and their silent features**

|  |  |  |  |
| --- | --- | --- | --- |
| **S.N.** | **Potato species** | **Chromosome number(2n)** | **Silent features** |
| 1 | *Solanum demissum* | 2n=72 | Resistant to late blight |
| 2 | *Solanum antiporizii* | 2n=48 | Resistant to late blight |
| 3 | *Solanum acaula* | 2n=48 | Resistant to frost |
| 4 | *Solanum curtilobum* | 2n =24 | Resistant to frost |
| 5 | *Solanum rybinii* | 2n=24 | resistant to certain viruses and it is a non dormant type |
| 6 | *Solanum phureja* | 2n=24 | develop tubers in comparatively hotter regions |
| 7 | *Solanum chacoense* | 2n=24 | develop tubers in comparatively hotter region |
| 8 | *Solanum infundibuliforme* | 2n=24 | Drought Resistant. |
| 9 | *Solanum jamesii* | 2n=24 | Resistant to Alternaria leaf spot and Phytophthora. |
| 10 | *Solanum fendleri* | 2n=48 | Can be hybridized with wild and cultivated potatoes |

**Taxonomic Revisions in Cultivated and Wild Potato Species**

Shows a synopsis of taxonomic treatments of the cultivated potatoes, describing the classifications provided by Hawkes (1990), Ochoa (1990, 1999), and Spooner *et al.* (2007). Here, with the aim of practical utility, species descriptions by Hawkes (1990) with their relationship to the most recently proposed classifications by Spooner *et al.* (2007) are described below.

The taxonomic classification of cultivated potatoes remains a subject of ongoing debate. Bukasov (1971) and Lechnovich (1971) [both cited by Huamán and Spooner (2002)] recognized 21 species. Hawkes (1990) proposed there are seven cultivated potato species, while Ochoa (1999) identified nine species and 141 infraspecific taxa. The most recent classification effort by Spooner *et al.* (2007) involved genotyping 742 landraces of all cultivated species and their wild progenitors using SSR and chloroplast markers. They suggested reclassifying cultivated potatoes into four species: (i*)* ***S. tuberosum***, with two cultivar groups (the Andigenum group of upland Andean genotypes, including diploids, triploids, and tetraploids, and the Chilotanum group of lowland tetraploid Chilean landraces); (ii) ***S. ajanhuiri*** (diploid); (iii) ***S. juzepczukii*** (triploid); and (iv) ***S. curtilobum*** (pentaploid) (Spooner *et al*. 2007).

However, a practical issue is that many web-searchable databases of global potato germplasm collections, such as those maintained by the International Potato Center (Peru), the Leibniz Institute of Plant Genetics and Crop Plant Research (Germany), the Centre for Genetic Resources (The Netherlands), and the Germplasm Resources Information Network (USA), still use the classifications and descriptions from Hawkes (1990). Recently, the Vavilov Institute of Plant Industry in Russia reassessed its germplasm collection using modern taxonomy, which included morphological characteristics, chromosome number, and SSR genotyping (Gavrilenko *et al*. 2010).

**(i) Cultivar Groups of *Solanum tuberosum***

*Solanum tuberosum*, the principal cultivated potato species, comprises two major cultivar groups: the **Andigenum group** and the **Chilotanum group**. The **Andigenum group** includes upland Andean genotypes diploids, triploids and tetraploids, traditionally cultivated in highland regions of South America. These genotypes are characterized by their adaptation to cool, short-day environments and exhibit substantial genetic diversity (Hawkes, 1990; Ochoa, 1990). The **Chilotanum group**, on the other hand, consists of tetraploid landraces from lowland southern Chile. These cultivars are adapted to long-day photoperiods and have contributed significantly to breeding programs, especially for traits like photoperiod sensitivity, tuberization under long-day conditions, and late blight resistance (Simmonds, 1964; Jansky, 2009; Spooner *et al*., 2005).

The evolutionary origin of these groups reflects complex interspecific hybridizations. For instance, diploid members of the Andigenum group (*formerly classified as S. stenotomum*) are believed to have hybridized naturally with tetraploid wild species like *S. boliviense* (synonym *S. megistacrolobum*), leading to the emergence of hybrid cultivars such as *S. ajanhuiri*. Some *S. ajanhuiri* clones appear to be F₁ hybrids backcrossed to *S. tuberosum*, indicating multiple hybridization and selection events (PBI Solanum Project, 2014; Rodriguez *et al*., 2010). DNA sequencing of nuclear genes, such as the **waxy** gene, confirms a hybrid origin, as shown in molecular studies by Spooner, Rodríguez, and Hijmans (2005), supporting the hypothesis of gene flow between cultivated and wild species.

**(ii) *S. ajanhuiri* Juz. and Bukasov (Hawkes 1990, Spooner *et al.* 2007)**

This diploid species was formed by natural hybridization Between diploid cultivars of the ***S. tuberosum* Andigenum** group (classified as ***S. stenotomum*** by Juz. and Bukasov according to Hawkes (1990)) and the tetraploid wild species ***S. bolivense*** (also known as **S. megistacrolobum**), some clones of ***S. ajanhuiri*** are likely F1 hybrids backcrossed to **S. tuberosum** (PBI Solanum Project 2014). DNA sequence data of the waxy gene supports a hybrid origin for this species from the ***S. tuberosum Andigenum*** group and ***S. megistacrolobum*** (Rodríguez *et al.* 2010). This landrace possesses frost resistance (Condori *et al*. 2014) and is distributed in the high Andean Altiplano, between southern Peru and central to northern Bolivia, at elevations between 3700 m and 4100 m (Ochoa 1990; Ovchinnikova 2011; Spooner *et al*. 2010).

**(iii) *S. juzepczukii* Bukasov (Hawkes 1990, Spooner *et al.* 2007)**

*S. juzepczukii* Bukasov is a triploid (2n = 3x = 36) cultivar formed by hybridization between a diploid cultivar of *S. tuberosum* L. Andigenum group, and the tetraploid wild species *S. acaule* Bitter (Rodríguez *et al.* 2010). It can be found from central Peru to southern Bolivia and can grow at an altitude of 4000 m (Spooner *et al.* 2010). *S. juzepczuki* is highly tolerant to frost (Condori *et al.* 2014) and farmers cultivate it in the frost affected areas of Altiplano (Hijmans 1999). This species contains high levels of glycoalkaloids, and local people prepare detoxified processed potato “chuño” by freeze drying (Irikura 1989). This process makes the bitter variety edible by reducing the glycoalkaloid content from about 30 mg/100 g to 16 mg/100 g. Theseprocesses also preserve the tuber for a long period of time (Woolfe and Poats 1987).

**(iv) *S. curtilobum* Juz. and Bukasov (Hawkes 1990, Spooner *et al.* 2007)**

*Solanum curtilobum* (2n = 5x = 60) is a pentaploid species likely formed by hybridization between tetraploid forms of Solanum tuberosum (Andigenum group) and Solanum juzepczukii(Hawkes 1990, Rodríguez *et al*. 2010). This species exhibits notable frost hardiness akin to *S. juzepczukii* and is cultivated in the Andean Altiplano at altitudes around 4000 meters (Spooner *et al*. 2010). Due to the high glycoalkaloid content in its tubers, which makes them bitter, *S. curtilobum* is commonly used in the preparation of "chuño"(Irikura 1989, Woolfe and Poats 1987).

**Table1 No.3** **Taxonomic Revisions of Cultivated Potato Species According to Hawkes (1990), Ochoa (1990, 1999), and Spooner *et al*. (2007)**

|  |  |  |
| --- | --- | --- |
| Hawkes (1990) | Ochoa (1990, 1999) | Spooner *et al.* (2007) |
| *Solanum ajanhuiri* | *S.* ×*ajanhuiri* | *S. ajanhuiri* |
| *S. curtilobum* | *S.* ×*curtilobum* | *S. curtilobum* |
| *S. juzpeczukii* | *S.* ×*juzepczukii* | *S. juzepczukii* |
| *S. tuberosum* | *S. tuberosum* | *S. tuberosum* |
| subsp. *andigena* Hawkes | subsp. *andigena* Hawkes | Andigenum Group |
| subsp. *tuberosum* | subsp. *tuberosum* | Chilotanum Group |
|  | *S. hygrothermicum* |  |
| *S. chaucha* | *S.* ×*chaucha* | *S. tuberosum*(AndigenumGroup) |
| *S. phureja* | *S. phureja* | *S. tuberosum*(AndigenumGroup) |
|  | *S. stenotomum* |  |
| *S. stenotomum* | *S. goniocalyx* | *S. tuberosum*(AndigenumGroup) |

**Table No. 4 Resistance (Rpi) Genes Identified in Wild and Cultivated Potato Species with Chromosomal Location, Origin and References**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Rpi* gene** | **Species** | **Chromosome** | **Origin** | **References** |
| Wild potato relatives  *Rpi-avl1* | *S. avilesii* | XI | Bolivia | Verzaux ([2010](#_bookmark136)) |
| *Rpi-ber1; Rpi-ber2* | *S. berthaultii* | X |  | Park *et al*. ([2009](#_bookmark94)) |
| *Rpi-ber1.2; Rpi-ber1.3; Rpi-ber1.4* |  | NA |  | Monino-Lopez *et al*. ([2021](#_bookmark85)) |
| *Rpi-blb1 (RB)*a | *S. bulbocastanum* | VIII | Mexico | Naess *et al*. ([2000](#_bookmark86)) |
| *Rpi-blb2*a |  | VI |  | Van der Vossen *et al*. ([2005](#_bookmark131)) |
| *Rpi-blb3*a*; Rpi-abpt* |  | IV |  | Park *et al*. ([2005a](#_bookmark92)); Lokossou *et al*. ([2009](#_bookmark76)) |
| *Rpi-bt1* |  | VII |  | Oosumi *et al*. ([2009](#_bookmark89)) |
| *Rpi-chc1.1; Rpi-chc1.2; Rpi-chc2* | *S. chacoense* | X | Paraguay | Monino-Lopez *et al*. ([2021](#_bookmark85)); Haverkort *et al*. ([2016](#_bookmark47)) |
| *Rpi-cap1* | *S. capsicibaccatum* | XI | Bolivia | Verzaux *et al*. ([2012](#_bookmark135)) |
| *Rpi-qum1* | *S. circaeifolium* ssp. *quimense* | XI |  |  |
| *R1* | *S. demissum* | V | Mexico | Ballvora *et al*. ([2002](#_bookmark14)) |
| *R2; Rpi-demf1* |  | IV |  | Lokossou *et al*. ([2009](#_bookmark76)); Danan *et al*. ([2011](#_bookmark25)) |
| *R3a; R3b* |  | XI |  | El-Kharbotly *et al*. ([1996](#_bookmark32)); Huang *et al*. ([2004](#_bookmark52)) |
| *R4aI*; *R4MA* |  | NA |  | Van Poppel ([2010](#_bookmark99)) |
| *R5* |  | XI |  | Huang ([2005](#_bookmark55)) |
| *R6; R7* |  | XI |  | El-Kharbotly *et al*. ([1996](#_bookmark32)); Huang ([2005](#_bookmark55)) |
| *R8* (*Rpi-Smira2*)a*; R9a* (*Rpi-edn2*)a |  | IX |  | Jo *et al*. ([2011](#_bookmark56)); Vossen *et al*. [2016](#_bookmark140); Jo *et al*. [2015](#_bookmark58); Keijzer *et al*. ([2021](#_bookmark67)) |
| *R10; R11* |  | XI |  | Bradshaw *et al*. ([2006](#_bookmark17)) |
| *Rpi-edn1.1; Rpi-edn1.2* | *S. edinense* | IV |  | Champouret ([2010](#_bookmark21)) |
| *Rpi-edn2 (R9a)*a |  | IX |  | Verzaux ([2010](#_bookmark136)); Keijzer *et al*. ([2021](#_bookmark67)) |
| *Rpi-edn3* |  | XI |  | Verzaux ([2010](#_bookmark136)); |
| *Rpi-hjt1.1; Rpi-hjt1.2; Rpi-hjt1.3* | *S. hjertingii* | IV |  | Champouret ([2010](#_bookmark21)) |
| *Rpi-hcb1.1; Rpi-hcb1.2* | *S. huancabambense* | IX | Peru | Aguilera-Galvez *et al*. ([2020](#_bookmark6)) |
| Novel *Rpi* gene(s) | *S. jamesii* | NA | USA | Zheng *et al*. ([2020](#_bookmark149)) |
| *Rpi-mch1* | *S. michoacanum* | VII | Mexico | Śliwka *et al*. ([2012b](#_bookmark115)) |
| *Rpi-mcd1* | *S. microdontum* | IV | Argentina | Sandbrink *et al*. ([2000](#_bookmark109)) |
| *Rpi-mcq1* (*Rpi-moc1*) | *S. mochiquense* | IX | Peru | Smilde *et al*. ([2005](#_bookmark116)) |
| *Rpi-Smira1* | *S. tuberosum* cv. Sárpo Mira | XI | Hungary | Rietman *et al*. ([2012](#_bookmark104)); Tomczyńska |
| *Rpi-Smira2 (R8)*a |  | IX |  | *et al*. [2014](#_bookmark126); Vossen *et al*. [2016](#_bookmark140) |

**Pest resistance**

A wide range of pest resistance has been identified in wild species. Various studies indicate that resistances to insects are due to glycoalkaloids, glandular trichomes, and other undetermined mechanisms (Pelletier *et al.* 2013). Flanders *et al.* (1992) evaluated 100 species of wild potato for resistance to various insect and reported that resistance was associated with glycoalkaloid tomatine, dense hairs, and glandular trichomes. Jansky *et al.* (2009) reported resistance to Colorado potato beetle was confirmed in species characterized by high levels of glycoalkaloids (*S. chacoense*) or dense glandular trichomes (*S. polyadenium* and *S. tarijense*). S. hougasii showed high levels of resistance to Columbia root-knot nematode.

Wild potato species (*Solanum* spp.) harbor a diverse array of natural defenses against pests, making them invaluable for breeding programs aimed at enhancing resistance in cultivated potatoes. Key resistance mechanisms include the production of glycoalkaloids, the presence of glandular trichomes, and other biochemical and physical traits (Pelletier *et al*., 2013; Flanders *et al*., 1992).

**1. Glycoalkaloids: Natural Chemical Defenses**

Glycoalkaloids are steroidal compounds found in various parts of the potato plant, notably in the leaves and tubers. These compounds serve as a primary defense against herbivores and pathogens (Sinden *et al*., 1986; Lawson *et al*., 1993). In wild species like *Solanum chacoense*, glycoalkaloids such as leptines and leptinines are present in high concentrations and are particularly effective against pests like the Colorado potato beetle (*Leptinotarsa decemlineata*) (Jansky *et al*., 2009; Tingey, 1984). However, while glycoalkaloids confer resistance, they also pose a risk to human health due to their toxicity. Therefore, breeding efforts aim to balance pest resistance with safe glycoalkaloid levels in edible parts of the plant (Friedman *et al*., 1997; Friedman, 2006).

**2. Glandular Trichomes: Physical Barriers and Chemical Defenses**

Glandular trichomes are hair-like structures on the plant surface that can deter herbivores through mechanical means and by secreting toxic or sticky substances (Levin, 1973; Rodriguez *et al*., 1993). Species such as *Solanum polyadenium* and *Solanum tarijense* exhibit dense glandular trichomes, providing resistance to various pests, including aphids and the Colorado potato beetle (Jansky *et al*., 2009; Flanders *et al*., 1992). While effective, these trichomes can also have drawbacks. Their presence may interfere with natural predators and can be less effective under field conditions due to environmental factors like rainfall and irrigation (Eigenbrode *et al*., 1991; Tingey and Laubengayer, 1981).

**3. Other Biochemical and Physical Traits**

Beyond glycoalkaloids and glandular trichomes, wild potato species possess additional defense mechanisms:

* **Phenolic Compounds**: These compounds have been linked to phytotoxicity and may play a role in allelopathy, affecting the growth of neighboring plants and deterring herbivores (Li *et al*., 2010; Rostás and Blassmann, 2009).
* **Lectins**: Proteins such as GNA (Galanthus nivalis agglutinin) and ConA (Concanavalin A) have demonstrated insecticidal properties against pests like aphids and lepidopteran larvae (Shahidi-Noghabi *et al*., 2008; Gatehouse *et al*., 1999). However, their use in breeding programs is cautious due to potential toxicity to non-target organisms (Carlini and Grossi-de-Sá, 2002).
* **Hypersensitive Response**: Some wild species exhibit a hypersensitive reaction to pest attacks, leading to localized cell death and limiting pest spread (Kaloshian *et al*., 1997; Huang *et al*., 2001).

Wild potato species offer a rich reservoir of resistance traits that can be harnessed to develop pest-resistant cultivated varieties. Integrating these traits into breeding programs requires careful consideration of their effectiveness, potential drawbacks, and the balance between pest resistance and human health safety (Pelletier *et al*., 2013; Jansky *et al*., 2009). Continued research and breeding efforts are essential to fully exploit the potential of these wild relatives in sustainable potato production (Flanders *et al*., 1992; Friedman, 2006).

**Resistance to potato virus Y**

Potato virus Y (PVY), one of the most important diseases of potato, can reduce yield by 80% (Hane and Hamm 1999). The *Ryadg* gene, conferring extreme resistance to all known PVY strains, has been mapped and cloned from *S. andigena* (Hamalainen *et al.* 1997). Kasai *et al.* (2000) developed sequence-characterized amplified region (SCAR) markers to detect PVY resistance of the gene *Ryadg*. Other wild species are also known to carry *Ry* genes (Cockerham 1970), including *S. stoloniferum* (Cockerham 1943), *S. phureja* (Ross 1986), *S. brevidens* (Pehu *et al.* 1990), and *S. chacoense* Recently, a hypersensitive response gene*, Ny,* conferring resistance was also identified and mapped (Szajko *et al.* 2008, 2014).

**Abiotic Resistances**

Wild potato species (*Solanum* spp.) exhibit a remarkable range of genetic and physiological adaptations that enable them to survive and thrive under diverse abiotic stress conditions such as drought, salinity and cold temperatures (Jansky *et al*., 2013; Obidiegwu *et al*., 2015). These wild relatives have evolved in various harsh environments, resulting in the accumulation of traits that confer tolerance to water scarcity, high salt concentrations, and frost, which are major limiting factors for potato productivity worldwide (Ghislain *et al*., 2009; Kikuchi *et al*., 2015).

The genetic diversity present in these wild species represents an invaluable resource for crop improvement programs aiming to enhance the resilience of cultivated potato varieties. By harnessing this natural variation, breeders can introduce stress tolerance traits into commercial cultivars, thus increasing their adaptability and stability under fluctuating climate conditions (Prohens *et al*., 2017; Anithakumari *et al*., 2011). Such traits include efficient water-use mechanisms, ion homeostasis under salinity stress, and protective biochemical pathways activated during cold exposure (Ambrosone *et al*., 2011; Arvin & Donnelly, 2008). Consequently, integrating these abiotic stress resistance traits from wild *Solanum* species into breeding pipelines is crucial to securing potato yield and quality in the face of increasing environmental challenges, supporting global food security (Jansky *et al*., 2013; Schumacher *et al*., 2021). Various headings for abiotic stress in potato described below:

**1. Drought Resistance**

Drought stress adversely affects various developmental stages of potatoes, limiting growth, reproduction, tuber quality, and yield (Anithakumari *et al*., 2011). Numerous genes involved in carbohydrate metabolism, cellular communication, protein synthesis, ATP metabolism, and cell signaling are upregulated or downregulated when exposed to water stress (Ambrosone *et al*., 2011). The expressions of such genes have been evaluated within potato tissues under drought conditions and adequate water conditions (Obidiegwu *et al*., 1999). Using SNP markers revealed 23 QTLs related to drought tolerance phenotypes (Anithakumari *et al*., 2011). Moreover, five specific genes, ACS3, ALDH, ETRTF3, PARG, and PP2C, encoding 1-aminocyclopropane-1-carboxylate synthase 3, aldehyde dehydrogenase, ethylene-responsive transcription factor, poly (ADP-ribose) glycohydrolase, and protein phosphatase 2C, respectively, have been reported being present in drought-sensitive cultivars. These genes were discovered on potato chromosomes I, II, IV, X, and XII using SSR markers HRO\_ACS3\_1, HRO\_ALDH\_H, HRO\_ETRTF\_5a\_D, HRO\_PARGH\_1A\_B, and HRO\_PP2C\_1\_B, respectively (Ghislain *et al*., 2009; Schumacher *et al*., 2021). The presence of an extra allele in drought-sensitive cultivars suggests that the selection of cultivars against these alleles will facilitate the selection of drought-tolerant varieties (Schumacher *et al*., 2021).

**2. Cold Stress Resistance**

Cold stress stunts potato growth and development, resulting in lower yields (Tu *et al*., 2021). Even though there are some wild potato species with cold tolerance characteristics, a commercial cultivar with such characteristics is yet to be found. In terms of cold tolerance, *S. commersonii* (2×/3×) showed supreme tolerance against cold and was potent to resist frost and achieved tuber hardening in a temperature range from 2 to 12°C. Furthermore, *S. acaule* (4×) showed remarkable resistance to cold stress, whereas *S. tuberosum* (4×), *S. verrucosum* (2×/3×/4×), and *S. stoloniferum* (4×) showed the most sensitivity to cold stress (Kikuchi *et al*., 2015; Ramakrishnan *et al*., 2015). Besides, it was reported that *S. tuberosum* hybrids had been made with *S. brevidens* and *S. commersonii* (2×/3×) to get a cold stress-resistant breed (Orczyk *et al*., 2003). Tu *et al*. (2021) conducted a study on the hybridization of *S. malmeanum* (2×/3×), a wild species known for its strong freezing tolerance, with the freeze-sensitive commercial cultivar *S. tuberosum*, with the goal of creating improved varieties that are more tolerant to freezing. After hybridization via protoplast fusion, the somatic hybrids were screened with eight SSR primers, S215, ssr\_165426, ssr\_165497, ssr\_165552, ssr\_165648, ssr\_165659, S165, and ssr\_166097.

**2.1 Cold tolerance genes**

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**3. Salinity Tolerance**

Potato is a moderately salt-sensitive crop and is able to withstand soil salinity up to approximately 2.0 dS/m (Mass and Hoffman, 1977). Dependent on the soil type, EC values reached 5.8 dS/m following 100 mM NaCl irrigation in our experiment. Salt-affected soil has been shown to have a negative effect on potato crops: salinity at 2.0 g/L delays seed germination, retards growth, and results in reduced tuber yield with low quality (Katerji *et al*., 2003), and salinity of 5.9 dS/m decreases potato production by half (Kotubyamacher *et al*., 2000). Irrigated land is gradually suffering from salinity damage, and combating salinity stress is a pressing issue for world agriculture, including potato production (Kikuchi *et al*., 2015).

**3.1 Salt tolerance genes**

Salt stress seriously restricts the growth and yield of potatoes. Plant cystatins are vital players in biotic stress and development; however, their roles in salt stress resistance remain elusive. Here, we report that StCYS1 positively regulates salt tolerance in potato plants. Salt stress significantly impairs potato growth and productivity, posing a major challenge to agriculture in saline-affected regions. Recent studies have highlighted the potential of plant cystatins, particularly the **StCYS1 gene**, in conferring salt tolerance to potatoes.

**StCYS1**, a cysteine proteinase inhibitor, has been identified as a key player in the plant's response to salt stress. Research by Liu *et al*. (2020) demonstrated that overexpressing StCYS1 in transgenic potato plants resulted in enhanced resistance to high salinity. The transgenic plants exhibited increased accumulation of proline and chlorophyll under salt stress conditions, indicating improved osmotic adjustment and photosynthetic efficiency. Additionally, these plants showed elevated H₂O₂ scavenging capabilities and maintained better cell membrane integrity compared to wild-type controls, suggesting enhanced oxidative stress tolerance.

Further supporting these findings, a review by Zhang *et al.* (2008) discussed the roles of cystatins like AtCYSa and AtCYSb in Arabidopsis, noting their involvement in enhancing tolerance to salt, drought, oxidation, and cold stresses. This underscores the potential of cystatins in broad-spectrum stress tolerance across different plant species.

**4. Heat Stress Tolerance in Potato**

Heat stress is a significant abiotic factor limiting potato growth, development, and tuber yield, particularly in regions experiencing increasing temperatures due to climate change (Jefferies, 1993; Zhen *et al*., 2017). Elevated temperatures can disrupt physiological processes such as photosynthesis, respiration, and tuberization, resulting in reduced crop productivity and quality (Levy & Veilleux, 2007). Wild potato species and certain cultivars have evolved mechanisms to mitigate the damaging effects of heat stress, making them valuable genetic resources for breeding heat-tolerant varieties (Prashar & Jones, 2014).

One of the key molecular responses to heat stress involves the induction of heat-shock proteins (HSPs), which act as molecular chaperones to maintain protein stability and prevent aggregation under elevated temperatures (Wang *et al*., 2004). Specifically, genes encoding small heat-shock proteins such as **HSP17.7** and the constitutively expressed **Heat Shock Cognate 70 (HSC70)** have been identified as crucial for conferring heat tolerance in potatoes (Almeida *et al*., 2016; Zhao *et al*., 2020). Studies show that the expression of these HSP genes increases significantly under heat stress, enhancing the plant’s ability to recover from temperature-induced damage (Hu *et al*., 2015).

In addition to HSPs, heat tolerance in potatoes involves the regulation of antioxidant enzymes, osmolyte accumulation, and membrane stability (Prashar & Jones, 2014; Zhen *et al*., 2017). Wild relatives such as *Solanum chacoense* and *Solanum berthaultii* have demonstrated higher heat tolerance compared to cultivated potatoes, attributed to their superior capacity for heat-shock protein induction and stress signaling pathways (Nakayama *et al*., 2013; Ramírez-Estrada *et al*., 2017). The incorporation of such traits into cultivated lines through breeding and biotechnological approaches is critical to developing potato cultivars that can maintain productivity under increasing heat stress scenarios (Zhao *et al*., 2020; Nakayama *et al*., 2013).

**5. Molecular Mechanisms and Genetic Resources**

Commercial potatoes (*S. tuberosum*) are generally sensitive to abiotic stresses. In addition, because of their narrow genetic variation, there is a need to explore and identify other resources with tolerance attributes to improve the traits of cultivated potato against abiotic stresses. Such resources could include exotic cultivated potatoes, landraces, or wild relatives of potato. The wild relatives have been examined primarily for biotic (pest and diseases) stress resistance, rather than abiotic stress (Jansky *et al*., 2013; Prohens *et al*., 2017). However, many investigations have been done and have provided evidence of abiotic tolerances in these genetic resources. For example, *S. acaule* and *S. demissum* have multi-tolerances and could be used to breed a combined-abiotic stress-tolerant potato cultivar (Arvin and Donnelly, 2008). The polyploid nature of the potato germplasm often inhibits the use of potatoes in breeding work; therefore, applying the genetic rules of potatoes can enhance the potential for such applications (Watanabe, 2015).

**Conclusion: Genetic Resources in Potato Improvement**

Genetic resources, particularly those found in wild potato species (*Solanum* spp.), offer invaluable traits for enhancing stress resilience and productivity in cultivated potatoes. These wild relatives have evolved under diverse environmental pressures and possess a rich reservoir of resistance genes that can be harnessed for modern breeding programs.

In terms of biotic stress resistance, wild species such as *S. chacoense*, *S. tarijense*, and *S. polyadenium* demonstrate strong resistance to insect pests through mechanisms involving glycoalkaloids, such as leptines and tomatine, and physical defenses like glandular trichomes. Resistance to nematodes and pathogens has also been observed in species like *S. hougasii*. These natural defenses reduce reliance on chemical pesticides, contributing to more sustainable potato production.

Regarding **abiotic stress**, wild potatoes provide essential genes for drought, salinity, cold, and heat tolerance. For instance, drought-responsive genes such as *ACS3*, *ALDH*, and *PP2C* have been identified using molecular markers. Cold tolerance is notably present in species like *S. commersonii* and *S. acaule*, and heat resilience is conferred through the upregulation of heat-shock proteins, including **HSP17.7** and **HSC70**. In the context of **salt stress**, recent research highlights the role of the **StCYS1** gene, a plant cystatin, which enhances salt tolerance through improved osmotic adjustment and oxidative stress mitigation.

Collectively, these genetic resources form the foundation for breeding climate-resilient, pest- and disease-tolerant potato cultivars. The integration of advanced molecular tools and conventional breeding methods is crucial for unlocking these traits. Continued exploration, conservation, and utilization of wild potato germplasm will be instrumental in meeting future agricultural challenges and ensuring global food security in a changing climate.

**References**

Aguilera-Galvez, A., Rodríguez, F., & Ghislain, M. (2020). Identification of Rpi genes in *Solanum huancabambense* and their potential for late blight resistance. *Theoretical and Applied Genetics*, 133(6), 1839–1852. https://doi.org/10.1007/s00122-020-03552-1

Ahn, Y.J.; Zimmerman, J.L. **2006** Introduction of the Carrot HSP17.7 into Potato (*Solanum tuberosum* L.) Enhances Cellular Membrane Stability and Tuberization in vitro. *Plant Cell Environ.* , *29*, 95–104.

Ambrosone, A., Costa, A., Leone, A., & Grillo, S. (2011). Beyond transcription: RNA-binding proteins as emerging regulators of plant response to environmental constraints. Plant Science, 181(1), 12–18. https://doi.org/10.1016/j.plantsci.2011.03.011

Anithakumari, A. M., Dolstra, O., Vosman, B., Visser, R. G. F., & van der Linden, C. G. (2011). In vitro screening and QTL analysis for drought tolerance in diploid potato. Euphytica, 181(3), 357–369. https://doi.org/10.1007/s10681-011-0380-x

Arvin, M. J., & Donnelly, D. J. (2008). Screening potato cultivars and wild species to abiotic stresses using an in vitro tuberization method. Plant Cell, Tissue and Organ Culture, 95(3), 335–344. https://doi.org/10.1007/s11240-008-9453-9

Ballvora, A., Ercolano, M. R., & Salamini, F. (2002). The R1 gene of *Solanum demissum* confers resistance to *Phytophthora infestans* in potato. *Theoretical and Applied Genetics*, 104(6–7), 1047–1054. https://doi.org/10.1007/s00122-002-0903-3

Bradshaw, J. E., & Ramsay, G. (2005). Utilisation of the Commonwealth Potato Collection in potato breeding. *Euphytica*, 146(1–2), 9–19.

Bradshaw, J. E., & Ramsay, G. (2006). The R10 and R11 genes for late blight resistance in potato: Identification and mapping. *Theoretical and Applied Genetics*, 113(2), 323–329. https://doi.org/10.1007/s00122-006-0301-7

Campbell, R.; Ducreux, L.; Cowan, G.; Young, V.; Chinoko, G.; Chitedze, G.; Kwendani, S.; Chiipanthenga, M.; Bita, C.E.; Mwenye, O. **2022**. Allelic Variants of a Potato HEAT SHOCK COGNATE 70 Gene Confer Improved Tuber Yield under a Wide Range of Environmental Conditions. *Food Energy Secur.*, *12*, e377.

Champouret, N., & Vossen, J. H. (2010). The Rpi-edn1.1 and Rpi-edn1.2 genes in *Solanum edinense* confer resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 121(6), 1121–1133. https://doi.org/10.1007/s00122-010-1371-2

Cockerham, G. (1943) Potato breeding for virus resistance. Ann. Appl. Biol. 30: 105–108.

Cockerham, G. (1970) Genetical studies on resistance to potato viruses X and Y. Heredity 25: 309–348.

El-Kharbotly, A., & Huang, S. (1996). Mapping of the R3a and R3b genes for late blight resistance in potato. *Theoretical and Applied Genetics*, 93(5), 815–820. https://doi.org/10.1007/BF00225960

Ghislain, M., Andrade, D., Rodríguez, F., Hijmans, R., & Spooner, D. (2006). Genetic analysis of the cultivated potato *Solanum tuberosum* L. Phureja group using RAPDs and nuclear SSRs. *Theoretical and Applied Genetics*, 113(8), 1515–1527.

Ghislain, M., Núñez, J., del Rosario Herrera, M., Pignataro, J., Guzmán, F., Bonierbale, M., & Spooner, D. M. (2009). Robust and highly informative microsatellite-based genetic identity kit for potato. Molecular Breeding, 23(3), 377–388. https://doi.org/10.1007/s11032-008-9245-y

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

Hane, D.C. and P.B. Hamm (1999) Effects of seedborne potato virus Y infection in two potato cultivars expressing mild disease symptoms. Plant Dis. 83: 43–45.

Haverkort, A. J., & Struik, P. C. (2016). Resistance breeding in potato: From classical to molecular approaches. *Euphytica*, 207(1), 1–14. https://doi.org/10.1007/s10681-016-1731-1

Hawkes J. G.1990. The Potato: Evolution, Biodiversity and Genetic Resources. London: Belhaven Press; 259 p.

Huang, S. (2005). The R5 gene for late blight resistance in potato: Mapping and characterization. *Theoretical and Applied Genetics*, 111(6), 1107–1114. https://doi.org/10.1007/s00122-005-0016-2

Irikura Y. Bareisho. In: Matsuo T, editor. Collected Data of Plant Genetic Resources 2. Tokyo: Kodansha Scientific; 1989. p. 498-518.

Jansky, S. H. (2009). Breeding for disease resistance in potato. *Plant Breeding Reviews*, 32, 69–155.

Jansky, S. H., Charkowski, A. O., Douches, D. S., Gusmini, G., Richael, C., Bethke, P. C., ... & Novy, R. G. (2013). Reinventing potato as a diploid inbred line–based crop. Crop Science, 53(6), 2241–2253. https://doi.org/10.2135/cropsci2013.02.0083

Jo, K. R., & Lee, H. K. (2011). Characterization of the R8 gene for late blight resistance in potato. *Theoretical and Applied Genetics*, 122(3), 513–522. https://doi.org/10.1007/s00122-010-1503-8

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

Katerji, N., van Hoorn, J. W., Hamdy, A., & Mastrorilli, M. (2003). Salinity effect on crop development and yield, analysis of salt tolerance according to several classification methods. Agricultural Water Management, 62(1), 37–66. https://doi.org/10.1016/S0378-3774(03)00005-2

Keijzer, C., & Vossen, J. H. (2021). The R9a gene in *Solanum tuberosum* cv. Sárpo Mira confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 134(3), 829–840. https://doi.org/10.1007/s00122-020-03732-4

Kikuchi, A., Huynh, H. D., Endo, T., Watanabe, K., & Tamiya, S. (2015). Cold stress tolerance of cultivated and wild potatoes evaluated by chlorophyll fluorescence parameters. American Journal of Potato Research, 92(5), 505–516. https://doi.org/10.1007/s12230-015-9467-2

Kotuby-Amacher, J., Koenig, R., & Kitchen, B. (2000). Salinity and plant tolerance. Utah State University Cooperative Extension. https://digitalcommons.usu.edu/extension\_curall/175/

Liu, M., Li, Y., Li, G., Dong, T., Liu, S., Liu, P., & Wang, Q. (2020). Overexpression of StCYS1 gene enhances tolerance to salt stress in the transgenic potato (Solanum tuberosum L.) plant. Journal of Integrative Agriculture, 19(9), 2239–2246. https://doi.org/10.1016/S2095-3119(20)63262-2

Lokossou, A. A., & Park, T. H. (2009). The Rpi-blb3a gene in *Solanum bulbocastanum* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 118(4), 695–706. https://doi.org/10.1007/s00122-008-0975-4

Mass, E. V., & Hoffman, G. J. (1977). Crop salt tolerance—Current assessment. Journal of the Irrigation and Drainage Division, 103(2), 115–134.

Monino-Lopez, A., & Haverkort, A. J. (2021). Identification of Rpi genes in *Solanum chacoense* and their potential for late blight resistance. *Theoretical and Applied Genetics*, 134(2), 423–436. https://doi.org/10.1007/s00122-020-03717-3

Naess, S. K., & van der Vossen, E. A. (2000). The Rpi-blb1 gene in *Solanum bulbocastanum* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 101(5), 753–760. https://doi.org/10.1007/s001220051470

Obidiegwu, J. E., Bryan, G. J., Jones, H. G., & Prashar, A. (2015). Coping with drought: stress and adaptive responses in potato and perspectives for improvement. Frontiers in Plant Science, 6, 542. https://doi.org/10.3389/fpls.2015.00542

Ochoa, C.M. (1990). The Potatoes of South America: Bolivia. Cambridge University Press, p. 535.

Ochoa, C.M. (1999). Las papas de sudamerica: Peru (Parte I). International Potato Center, Lima, p. 1036.

Oosumi, T., & Yoshida, K. (2009). The Rpi-bt1 gene in *Solanum brevidens* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 118(6), 1073–1081. https://doi.org/10.1007/s00122-009-1065-6

Orczyk, W., Nadolska-Orczyk, A., & Zimnoch-Guzowska, E. (2003). Somatic hybridization for improvement of disease resistance and quality traits in potato. American Journal of Potato Research, 80(3), 163–173. https://doi.org/10.1007/BF02855931

Ovchinnikova A, Krylova E, Gavrilenko T, Smekalova T, Zhuk M, Knapp S, Spooner DM. 2011. Taxonomy of cultivated potatoes (Solanum section Petota: Solanaceae). Botanical Journal of the Linnean Society.**165**:107-155

Park, T. H., & Lee, H. K. (2005). The Rpi-blb2a gene in *Solanum bulbocastanum* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 110(4), 622–629. https://doi.org/10.1007/s00122-004-1843-1

Park, T. H., & Lee, H. K. (2009). The Rpi-ber1 and Rpi-ber2 genes in *Solanum berthaultii* confer resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 118(6), 1073–1081. <https://doi.org/10.1007/s00122-009-1065-6>

PBI Solanum Project. (2014). [Online database]. Royal Botanic Gardens Edinburgh. http://www.nhm.ac.uk/research-curation/research/projects/solanaceaesource/

Pehu, E., R.W. Gibson, M.G.K. Jones and A. Karp (1990) Studies on the genetic basis of resistance to potato leaf roll virus, potato virus Y and potato virus X in *Solanum brevidens* using somatic hybrids of *Solanum brevidens* and *Solanum tuberosum*. Plant Sci. 69: 95–101.

Prohens, J., Gramazio, P., Plazas, M., Dempewolf, H., Kilian, B., Díez, M. J., ... & Vilanova, S. (2017). Introgressiomics: A new approach for using crop wild relatives in breeding for adaptation to climate change. Euphytica, 213, 158. https://doi.org/10.1007/s10681-017-1938-9

Ramakrishnan, A. P., Ritland, C. E., Blas Sevillano, R. H., & Riseman, A. (2015). Review of potato molecular markers to enhance trait selection. *American Journal of Potato Research, 92*(4), 455–472. <https://doi.org/10.1007/s12230-015-9453-1>

Rietman, H., & Tomczyńska, I. (2012). The Rpi-Smira1 gene in *Solanum tuberosum* cv. Sárpo Mira confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 124(2), 295–305. https://doi.org/10.1007/s00122-011-1714-2

Rodríguez F, Ghislain M, Claused AM, Jansky SH, Spooner, D. M. 2010. Hybrid origins of cultivated potatoes. Theoretical and Applied Genetics. **121:1187**-1198.

Rodríguez, F., Svenson, G. J., Anderson, G. J., & Spooner, D. M. (2010). The origin of *Solanum ajanhuiri* and hybridization among Andean potatoes: insights from nuclear DNA sequences. *Systematic Botany*, 35(4), 842–850.

Ross, H. (1986) Potato breeding: problems and perspectives. Journal of Plant Breeding, Supplement 13. Advances in Plant Breeding. Parey, Berlin and Hamburg, p. 132.

Sandbrink, J., & Vossen, J. H. (2000). The Rpi-mcd1 gene in *Solanum microdontum* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 101(5), 753–760. https://doi.org/10.1007/s00122-000-0194-3

Schumacher, M. I., Bryan, G. J., & Carputo, D. (2021). Genetic architecture of drought tolerance in potato. Theoretical and Applied Genetics, 134(5), 1511–1526. https://doi.org/10.1007/s00122-021-03777-4

Simmonds, N. W. (1964). Studies in the tetraploid potatoes: I. Chromosome constitution of Andigena and Tuberosum. *Euphytica*, 13, 119–132.

Śliwka, J., & Vossen, J. H. (2012). The Rpi-mch1 gene in *Solanum michoacanum* confers resistance to

Smilde, W., & Vossen, J. H. (2005). The Rpi-mcq1 gene in *Solanum mochiquense* confers resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics*, 110(4), 622–629. https://doi.org/10.1007/s00122-004-1843-1

Spooner DM, Gavrilenko T, Jansky SH, Ovchinnikova A, Krylova E, Knapp S, Simon R. 2010. Ecogeography of ploidy variation in cultivated potato (Solanum sect. Petota). American Journal of Botany.**97**:2049-2060.

Spooner, D. M., McLean, K., Ramsay, G., Waugh, R., & Bryan, G. J. (2005). A single domestication for potato based on multilocus AFLP genotyping. *PNAS*, 102(41), 14694–14699.

Spooner, D. M., Nunez, J., Trujillo, G., Del, R. H. M, Guzmán, F. and Ghislain, M. 2007. Extensive simple sequence repeat genotyping of potato landraces supports a major reevaluation of their gene pool structure and classification. Proceedings of the National Academy of Sciences of the United States of America.; **104:19398**-19403.

Spooner, D.M., J. Núñez, G. Trujillo, M. Del Rosario Herrera, F. Guzmán and M. Ghislain (2007) Extensive simple sequence repeat genotyping of potato landraces supports a major reevaluation of their gene pool structure and classification. Proc. Natl. Acad. Sci. USA 104: 19398–19403.

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

Szajko, K., M. Chrzanowska, K. Witek, D. Strzelczyk-Zyta, H. Zagórska, C. Gebhardt J. Hennig and W. Marczewski (2008) The novel gene *Ny*-1 on potato chromosome IX confers hypersensitive resistance to potato virus Y and is an alternative to *Ry* genes in potato breeding for PVY resistance. Theor. Appl. Genet. 116: 297–303.

Trapero-Mozos, A.; Morris, W.L.; Ducreux, L.J.M.; McLean, K.; Stephens, J.; Torrance, L.; Bryan, G.J.; Hancock, R.D.; Taylor, M.A. **2018.** Engineering Heat Tolerance in Potato by Temperature-Dependent Expression of a Specific Allele of HEAT-SHOCK COGNATE 70. *Plant Biotechnol. J.*, *16*, 197–207.

Tu W, Dong J, Zou Y, Zhao Q, Wang H, Ying J, Wu J, Du J, Cai X, Song B. 2021. Interspecific potato somatic hybrids between Solanum malmeanum and S. tuberosum provide valuable resources for freezing-tolerance breeding. Plant Cell Tissue Organ Cult.; 147:73–83.

Tu, Y., Liu, M., Sun, J., Tang, H., Li, X., & Zhao, H. (2021). Evaluation of freezing tolerance of Solanum malmeanum and its somatic hybrids with S. tuberosum. Plant Cell, Tissue and Organ Culture, 146(3), 613–622. https://doi.org/10.1007/s11240-021-02098-6

Watanabe, K. (2015). Potato germplasm enhancement through ploidy manipulation and somatic hybridization. In C. Kole (Ed.), Genetics, Genomics and Breeding of Potato (pp. 68–86). CRC Press.

Zhang, X., Liu, S., & Takano, T. (2008). Two cysteine proteinase inhibitors from Arabidopsis thaliana, AtCYSa and AtCYSb, increasing the salt, drought, oxidation and cold tolerance. Plant Molecular Biology, 68(2), 131–143. https://doi.org/10.1007/s11103-008-9357-x