Genetic Resources

SHORT COMMUNICATION

Genetic Resources (2022), 3 (6), 64–73
DOI: 10.46265/genresj.PSES6766
https://www.genresj.org
ISSN: 2708-3764

The role of tomato wild relatives in breeding disease-free varieties

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Abstract: Cultivated tomato (*Solanum lycopersicum*) is one of the most economically important and widely grown vegetable crops worldwide. However, tomato plants are often affected by biotic and abiotic stresses that reduce yield and affect fruit quality. Phenotypic diversity is evident in cultivated tomatoes, particularly for horticultural traits, but genetic diversity is rather narrow. Major disease resistance genes for different pathogens such as viruses, fungi, bacteria and nematodes are mainly derived from wild tomato species and introgressed into cultivated tomatoes. Here, we list the major disease and insect-pest resistance genes identified in *S. pimpinellifolium*, *S. habrochaites*, *S. peruvianum*, *S. chilense*, *S. pennellii*, *S. galapagense*, *S. arcanum* and *S. neorickii* with perspective on the gap between current knowledge on tomato wild relatives and the knowledge that is needed.

Keywords: Tomato, crop wild relatives, disease resistance, genomics, plant genetic resources, plant breeding

Citation: Khazaei, H., Madduri, A. (2022). **The role of tomato wild relatives in breeding disease-free varieties**. *Genetic Resources* 3 (6), 64–73. doi: 10.46265/genresj.PSES6766.

Tomato wild relatives

Crop wild relatives (CWRs) are potential sources of allelic variation useful to overcome biotic and abiotic stresses as they often grow and reproduce in marginal habitats (Ortiz, 2015; Bohra *et al*, 2021). Tomato wild relatives are native to South America, distributed from the coastal region of Ecuador to northern Chile, including the Galápagos Islands (Darwin *et al*, 2003). These regions have extremely varied environments within short distances due to differences in altitude (Andean geography) and diverse ecological habitats, which led to local adaptation and generation of large genetic diversity among (Figure 1) and within wild tomato species. *Solanum section Lycopersicon* (Mill.) Wettst. consists of cultivated tomato (*S. lycopersicum*) and 12 wild relatives (Ramírez-Ojeda *et al*, 2021). The Tomato Genetics Resource Center (C.M. Rick TGRC, University of California-Davis, USA, https://tgrc.ucdavis.edu/) hosts the largest genetic stocks of wild tomato collections, with over 900 accessions. The largest collection belongs to accessions of *S. pimpinellifolium* (~300) followed by *S. habrochaites* (~120), *S. peruvianum* (~100), *S. chilense* (~100), and *S. pennellii* (~50), respectively (Table 1). The World Vegetable Center (WorldVeg, Taiwan https://genebank.worldveg.org/#/) and the United States Department of Agriculture, Agricultural Research Service (USDA-ARS, https://www.ars-grin.gov/) genebanks also maintain the second and third largest wild tomato collections, respectively (Table 1). However, the majority of their wild tomato collection was originally obtained from the TGRC collection. Furthermore, these genebanks harbour an extensive collection of introgression lines derived from different tomato wild species (Ebert and Schafleitner, 2015).

Utilization of tomato wild relatives for biotic stress breeding

Domestication has increased the phenotypic diversity of cultivated tomatoes but may have narrowed their resistance to biotic and abiotic constraints as selection ensued (Vu *et al*, 2020). Tomato wild relatives germplasm harbour natural resistance to various diseases and insect pests. Sources of genetic resistance to many of the biotic stresses faced by cultivated toma-

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Received: 05.07.2022 | Accepted: 08.08.2022 | Published online: 22.09.2022

Figure 1. Diversity in fruit colour and leaf shape of some tomato wild relatives. From left to right: *S. pimpinellifolium* (LA1269), *S. peruvianum* (L00887-3), *S. chilense* (LA2737B) and *S. galapagense* (VI063177). The size of the marker is 14cm × 1cm. Photo credit: Hamid Khazaei

Table 1. Genetic resources of tomato wild relatives maintained by the Tomato Genetics Resource Center (C.M. Rick TGRC), World Vegetable Center (WorldVeg), and the United States Department of Agriculture, Agricultural Research Service (USDA-ARS) genebanks (data accessed on June 23, 2022).

Species	**No. of accessions per genebank**		
	TGRC	**WorldVeg**	**USDA-ARS**
S. pimpinellifolium	290	342	338
S. habrochaites	120	139	49
S. peruvianum	69	116	11
S. chilense	115	46	1
S. pennellii	47	59	5
S. corneliomulleri	53	10	12
S. neorickii	47	12	8
S. galapagense	28	27	4
S. arcanum	45	4	3
S. cheesmaniae	12	17	5
S. chmielewskii	16	11	0
S. lycopersicoides	23	5	0
S. sitiens	13	5	2
S. huaylasense	16	0	0
S. ochranthum	7	0	2
S. juglandifolium	5	1	0

toes have been identified in some accessions of wild tomato species that have been historically used to introduce resistance (R) genes into cultivated tomato varieties. It should be noticed that there is genetic diversity for biotic resistance response within tomato wild species, and only a few accessions within each species have been identified as sources of resistance (Ebert and Schafleitner (2015) and references). We list major R genes found in and introgressed from wild tomato species into cultivated tomatoes in Table 2, along with information about their causal pathogens as footnotes. For example, the R genes/alleles conferring resistance to the begomoviruses that cause tomato yellow leaf curl diseases (called *Ty* genes), were found in wild tomato species. Most tomato advanced lines grown in tropical and subtropical regions of the world carry at least one source of *Ty* resistance genes (*Ty-1*/*Ty-3*) or multiple *Ty* genes (*Ty-2*, *ty-5*, *Ty-6*). The pyramiding of *Ty* genes into one line leads to broad and probably more durable resistance to begomoviruses. Likewise, R genes for late blight (caused by *Phytophthora infestans*, *Ph* genes) and fusarium wilt (caused by *Fusarium oxysporum*, *I* genes) also originated from wild tomatoes (Table 2). These genes are also frequently present in the modern tomato lines worldwide. Some important major QTLs (quantitative trait locus) such as *Bwr* and *EB*, conferring bacterial wilt (caused by *Ralstonia* spp.) and early blight (caused by *Alternaria linariae*) resistance, were first introgressed to adapted cultivated tomato cultivars from *S. pimpinellifolium* and later uncovered and genetically mapped. Some R genes (*Rx-1*, *-2* and *-3*) for bacterial spot resistance (caused by several species of gram-negative bacteria in the genus *Xanthomonas*) were also derived from *S. pimpinellifolium* via cultivated tomato. Several R genes against important pathogens in tomato have mainly been introgressed, from the wild species *S. pimpinellifolium*, *S. habrochaites*, *S. peruvianum*, *S. chilense* and *S. pennellii*, into modern tomato varieties (Table 2). However, most tomato breeding programmes focus on *S. pimpinellifolium* due to its red fruit colour (Figure 1) and its close relationship to cultivated tomato, which allows breeders to easily obtain interspecific crosses. That is probably why most of the R genes have already been identified in this species.

Table 2. List of major biotic resistance genes incorporated into cultivated tomatoes (*Solanum lycopersicum*) from wild relatives of tomato and *S. lycopersicum* var. *cerasiforme*. Causative agents for the listed diseases are included in footnotes.

Species	R-genes' contribution	Disease/Insect pest	References
S. pimpinellifolium L.	*I* and *I-2*	Fusarium wilt[1]	Stall and Walter (1965); reviewed in Chitwood-Brown *et al* (2021)
	Ph-1, *Ph-2*, *Ph-3* and *Ph-5*	Late blight[2]	Bonde and Murphy (1952); Gallegly and Marvel (1955); AVRDC (1994); Foolad *et al* (2006)
	EB-5 and *EB-9*	Early blight[3*]	Anderson *et al* (2021)
	Bwr-6 and *Bwr-12*	Bacterial wilt[4*]	Wang *et al* (2013)
	Rx-1, *Rx-2* and *Rx-3*	Bacterial spot[5*]	Yu *et al* (1995); reviewed in Adhikari *et al* (2020)
	Rx-4	Bacterial spot	Robbins *et al* (2009)
	Sm	Gray leaf spot[6]	Parlevliet (2002)
	Cf genes (except *Cf-4* and *Cf-5*)	Leaf mold[7]	Bailey (1950); reviewed in Scott and Gardner (2007)
	Sw-1(*a* and *b*), *Sw-2*, *Sw-3* and *Sw-4*	TSWV[8]	Finlay (1953); Roselló *et al* (1998); Zhu *et al* (2017); reviewed in Qi *et al* (2021)
	Pto	Bacterial speck[9]	Pitblado and Kerr (1980)
	Cmm genes	Bacterial canker[10]	Forster and Echandi (1972); Sotirova *et al* (1994); Sen *et al* (2021)
S. habrochaites S. Knapp and D. M. Spooner	*Ph-4*	Late blight	Lough (2003)
	Cf-4	Leaf mold	Stevens and Rick (1986)
	Ty-2	TYLCV[11]	Hanson *et al* (2006)
	Tm-1	ToMV[12]	Pelham (1966)
	Ol-1/*Ol-3*, and *Ol-5*	Powdery mildew[13]	van der Beek *et al* (1994); Huang *et al* (2000); Bai *et al* (2005)
	Cmm genes	Bacterial canker	Forster and Echandi (1972); Francis *et al* (2001); Coaker and Francis (2004); Sotirova *et al* (1994)
	Rbcq genes	Gray mould[14]	ten Have *et al* (2007); Finkers *et al* (2007a,b)
S. peruvianum L.	*ty-5*	TYLCV	Hutton *et al* (2012)
	Sw-5 and *Sw-6*	TSWV	Giordano *et al* (2000); Rosello *et al* (2001)
	Mi genes	Root-knot nematodes[15]	Smith (1944); reviewed in El-Sappah *et al* (2019)
	Tm-2, *Tm-2*^{2} and *Tm-2a*	ToMV	Soost (1963); Ganal and Tanksley (1996) and Tanksley and Nelson (1996)
	Ve	Verticillium wilt[16]	Diwan *et al* (1999)
	Frl	Fusarium crown[17]	Vakalounakis *et al* (1997)
S. chilense (Dunal) Reiche	*Ty-1*/*Ty-3a*, *Ty-4*, and *Ty-6*	TYLCV	Zamir *et al* (1994); Ji *et al* (2007); Ji *et al* (2009); Gill *et al* (2019)
	Sw-7	TSWV	Stevens *et al* (1994)
	Cmm genes	Bacterial canker	Sotirova *et al* (1994)
	Lv	Powdery mildew	Yordanov *et al* (1975); Chunwongse *et al* (1997)
	-	Gray mould	ten Have *et al* (2007)

Continued on next page

Table 2 continued

Species	**R-genes' contribution**	**Disease/Insect pest**	**References**
S. pennellii Correll	*I-3* and *I-7*	Fusarium wilt	Catanzariti *et al* (2015); Gonzalez-Cendales *et al* (2016)
	Asc	Alternaria stem canker[18]	Scott and Gardner (2007)
	Xv-4	Bacterial spot	Astua-Monge *et al* (2000)
	Acylsugar-related genes	A wide range of insects	Leckie *et al* (2012, 2016); Schilmiller *et al* (2012)
S. galapagense S. C. Darwin and Peralta	*Wf-1* and *Wf-2*	Whiteflies[19]	Firdaus *et al* (2013); Santegoets *et al* (2021)
S. arcanum Peralta	*Ol-4*	Powdery mildew	Bai *et al* (2005)
	Cmm genes	Bacterial canker	Crinò *et al* (1995); Sotirova *et al* (1994); Sen *et al* (2013)
S. neorickii D. M. Spooner, G. J. Anderson and R. K. Jansen	*V2*	Verticillium wilt	Kanagawa Agricultural Technology Center (1999)
	-	Gray mould	ten Have *et al* (2007); Finkers *et al* (2008)
S. l. var. *cerasiforme*	*Cf-5*	Leaf mold	Dickinson *et al* (1993); Dixon *et al* (1998)
	ol-2	Powdery mildew	Ciccarese *et al* (1998)

[1] Fusarium wilt caused by fungal pathogen *Fusarium oxysporum* (Schlecht. emend. Snyder & Hansen).
[2] Late blight resistance caused by the oomycete *Phytophthora infestans* (Mont.) de Bary.
[3] Early blight is caused by fungal pathogen *Alternaria* spp.
[4] Bacterial wilt caused by the group of soilborne bacteria in the *Ralstonia solanacearum* species complex.
[5] Bacterial spot caused by several species belonging to the genus *Xanthomonas*. It can be caused by *Xanthomonas euvesicatoria* ex Doidge, *X. vesicatoria* ex Doidge, *X. perforans*, and *X. gardneri* Šutic.
[*] Early blight, bacterial wilt, and bacterial spot (*Rx-1*, *Rx-2*, and *Rx-3*) resistance genes are most likely derived from *S. pimpinellifolium* via cultivated tomato.
[6] Gray leaf spot caused by fungal pathogen *Stemphylium lycopersici* (*S. lycopersici*).
[7] Leaf mold caused by fungal pathogen *Cladosporium fulvum* (syn. *Passalora fulva*).
[8] TSWV, tomato spotted wilt orthotospovirus (order *Bunyavirales*, family *Tospoviridae*, genus *Orthotospovirus*) is transmitted by *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae).
[9] Bacterial speck disease caused by *Pseudomonas syringae* pv. tomato (Pst).
[10] Bacterial canker caused by *Clavibacter michiganensis* subsp. *Michiganesis.*
[11] TYLCV, tomato yellow leaf curl virus disease. TYLCV is caused by whitefly transmitted *Geminiviruses* (begomoviruses). *Ty-1* and *Ty-3* are allelic (Verlaan *et al*, 2013).
[12] ToMV, tomato mosaic virus. ToMV is a member of the family *tobamoviridae* and belongs to the genus *tobamovirus*.
[13] Powdery mildew can be caused by three species of biotrophic fungal pathogens; *Oidium lycopersici*, *Oidium neolycopersici* (syn. *Pseoudoidium neolycopersici*), and *Leveillula taurica*. *Ol-1* and *Ol-3* are allelic (Huang *et al*, 2000).
[14] Gray mould caused by fungal pathogen *Botrytis cinerea* (teleomorph: *Botryotinia fuckeliana*).
[15] Root-knot nematodes can be caused by *Meloidogyne incognita*, *M. javanica,* and *M. arenaria.*
[16] Verticillium wilt caused by the biotrophic fungus *Verticillium dahliae.*
[17] Fusarium crown rot caused by *F. oxysporum* f. sp. *radicis-lycopersici*.
[18] Alternaria stem canker caused by fungal pathogen *Alternaria alternate.*
[19] Whitefly (*Bemisia tabaci*) resistance.

Challenges

The utilization of wild tomatoes in breeding programmes is not without a cost. CWRs generally show poor adaptation beyond their natural distribution range (Bohra *et al*, 2021). Furthermore, the introgressed gene from a wild relative into advanced lines may disrupt long-accumulated horticultural traits due to linkage drag (Tanksley and Nelson, 1996). For example, *S. galapagense* has been identified as a source of insect-pest resistance (Rakha *et al*, 2017; Vendemiatti *et al*, 2021). When it is crossed with cultivated tomatoes, the fruit size and setting reduce significantly, which are undesirable traits. Linkage drag can be removed by conducting backcrosses to the recurrent parents (cultivated tomato). Applications of DNA molecular markers (MAB, marker-assisted backcrossing) allow for the monitoring of the genome around the gene/locus of interest and the genetic background, speeding up the return to the recurrent parent genome (Tourrette *et al*, 2021). Genome editing can also be used to remove the undesirable gene without having extensive backcrossing. For example, CRISPR-Cas9-based gene editing was used to overcome a linkage drag in tomato by editing the *jointless-2* gene introgressed from *S. cheesmaniae* (Roldan *et al*, 2017). The World Vegetable Center is currently testing CRISPR-Cas9 to edit genes implicated with fruit size regulation in interspecific crosses between *S. galapagense* and cultivated tomato (Schafleitner *et al*, 2022).

Genomics-assisted breeding tools

Tomato wild relatives have more to offer. Bai *et al* (2018) stated that about 20 pathogens could be genetically controlled by resistance genes derived from a few wild species. The genome of some tomato wild species, including *S. pennellii* (Bolger *et al*, 2014; Schmidt *et al*, 2017), *S. chilense* (Stam *et al*, 2019), *S. pimpinellifolium* (Razali *et al*, 2018; Wang *et al*, 2020; Gramazio *et al*, 2020) and *S. lycopersicoides* (Powell *et al*, 2022) along with the pan-genome (Gao *et al*, 2019) have been assembled. These efforts have bolstered our knowledge and understanding of tomato wild species along with the genetics of resistance genes. Recent improvements in genomic resources have enabled us to track and genetically map the wild tomato genes in commercially adapted varieties (Anderson *et al*, 2021). The tomato community largely benefits from advanced, rich genomic resources (https://solgenomics.net/) and phenotyping tools; however, rapid generation technology (speed breeding) has not yet been developed. Robust DNA markers for major genes derived from wild relatives have been developed and widely applied in private and public breeding programmes worldwide (Foolad and Panthee, 2012; Hanson *et al*, 2016).

In the past, sources of important disease resistance genes in wild tomato relatives have been intensively investigated. However, the majority of R genes were discovered only in a few species (listed in Table 1). The other wild species that either are not easy to cross with cultivated tomatoes or are self-incompatible or allogamous have not contributed much to this journey (e.g. *S. chmielewskii*, *S. corneliomulleri*, *S. huaylalloasense*, *S. juglandifolium*, *S. ochranthum*, *S. lycopersicoides* and *S. sitiens*). Regarding these species, the literature only represents a few accessions of *S. lycopersicoides* being resistant to grey mould (caused by *Botrytis cinerea*) (Davis *et al*, 2009) or a few accessions of *S. corneliomulleri* being resistant to the TYLCV (Yan *et al*, 2018), but major genes/alleles from these species are yet to be reported. For some of these species, only a few accessions have been collected or are available in genebanks (Table 1). Among these species, some genomic studies were performed on *S. sitiens* (Chetelat *et al*, 2019) and *S. lycopersicoides* (Powell *et al*, 2022), which are potential sources of genes for adaptation to abiotic stresses (i.e. drought and heat stresses). Introgression lines were also developed from *S. chmielewskii* to study the accumulation of secondary metabolites in tomato fruit (Ballester *et al*, 2016).

Conclusions

Now that the scientific community has access to advanced tissue culture techniques, double haploidy protocols, modern phenotyping facilities, and genomic and bioinformatic tools, tomato wild relatives could be explored even more. This may provide new sources of genetic resources and R genes that could be used to pyramid new genes into one variety leading to broad and probably more durable resistance. Furthermore, ongoing advances in sequencing technology can be used to develop reference genome sequences for undiscovered tomato wild relatives, and the development of tomato pan-genomes will be a valuable strategy in harnessing the genetic diversity of these species. Additionally, genome editing enables *de novo* domestication strategies for the targeted use of tomato relatives (Zsögön *et al*, 2018). Thus, exploring the variation in tomato wild species could be an interesting topic for future studies.

Conflict of interest statement

The authors declare that they have no conflict of interest.

Author contributions

Original draft: Hamid Khazaei; review and editing: Hamid Khazaei and Adithya Madduri. All authors read and agreed to the published version of the manuscript.

Funding

Financial support was provided by the Foreign, Commonwealth and Development Office (UK) and by the long-term strategic donors to the World Vegetable Center, Taiwan: UK aid from the UK Government, the United States Agency for International Development (USAID), the Australian Centre for International Agricultural Research (ACIAR), Germany, Thailand, Philippines, Korea, and Japan. The authors thank Roland Schafleitner, Peter Hanson and Ya-ping Lin for their kind suggestions on the manuscript.

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