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GENETIC POTENTIAL OF WILD TOMATO RELATIVES FOR RESISTANCE BREEDING IN *SOLANUM LYCOPERSICUM*

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The tomato *Solanum lycopersicum* ranks among the top three most produced vegetables worldwide, yet it remains vulnerable to various diseases, pests and abiotic stresses. Climate change exacerbates disease severity and abiotic impacts, increasing the demand for adaptive varieties and hybrids. Interspecific hybridization expands genetic diversity via introgression of target trait genes, potentially reducing reliance on chemical protectants, enhancing plant adaptive potential and improving abiotic stress tolerance. Recent studies focus on wild *Solanum* species as a source of valuable traits for tomato breeding. This review addresses the reproductive barriers between cultivated and wild species, which are of critical significance for plant breeding and examines the methodologies developed to overcome these barriers. Currently, wild species are most actively involved in breeding programs and in the introgression of traits into the cultivated tomato include *S. cheesmaniae*, *S. habrochaites*, *S. pennellii*, *S. pimpinellifolium*. Species *S. peruvianum*, *S. chmielewskii*, *S. corneliomulleri*, *S. sitiens*, *S. ochranthum*, *S. lycopersicoides*, *S. sisyrifolium* are difficult to hybridize with cultivated tomato, and have not yet contributed substantially to the introgression of valuable traits. The success of interspecific hybridization with wild relatives largely depends on the choice of compatible tomato genotypes, the utilization of cultivated tomato as the maternal parent, and the application of embryo culture techniques to rescue hybrids in cases of embryo abortion. Somatic hybridization offers an alternative approach for overcoming interspecific crossing barriers. However, its effectiveness in facilitating the introgression of desirable traits into tomato remains insufficiently evaluated.

Keywords: interspecific hybridization, wild *Solanum* species, sources of resistance, abiotic stress, disease resistance, incompatibility

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Introduction

The tomato *Solanum lycopersicum* L. is among the most economically valuable vegetable crops worldwide. The global tomato market was valued at approximately USD 207.17 billion in 2024 and is projected to reach USD 261.41 billion by 2029 (Lopes Sobrinho et al., 2024). Russia ranks 12th globally in tomato production. Tomato crop is highly susceptible to a wide range of pathogens and stresses, including late blight, viral mosaics, root and stem rot, fusarium and verticillium wilts, various insect pests, as well as several abiotic stress factors (Sarwar et al., 2022). To mitigate crop losses, a combination of agronomic practices, chemical control measures, and integrated pest management strategies is employed, particularly the use of resistant varieties and hybrids, along with biological control methods, which collectively help to reduce dependence on chemical pesticides (Abbas et al., 2024).

The principal approach to developing genetically resistant tomato genotypes involves the creation of interspecific hybrids and the introgression of resistance genes from wild relatives into cultivated varieties (Ajaharuddin et al., 2024). The genus *Solanum*, comprising approximately 1,500 species, is the largest in the Solanaceae family; however, the domestication of *S. lycopersicum* resulted in the retention of less than 5% of the genetic diversity present within the *Lycopersicon* section (Bai, Lindhout, 2007). This genetic erosion has led to the loss of several important characteristics such as fruit flavor and aroma, color variability, shelf life, and resistance to biotic and abiotic stresses (Almeida et al., 2023). Interspecific hybridization has

a long and successful history in tomato breeding and continues to serve as an effective strategy for crop improvement (Menda et al., 2014; Pyshnaya, Dzhos, 2021).

To date, numerous disease-resistance genes from wild *Solanum* species have been successfully introgressed into cultivated tomato (Zamir et al., 1994; Merk et al., 2012; Rubio et al., 2016; Chunwongse et al., 2002; Hanson et al., 2006; Seah et al., 2004; Barham, Winstead, 1957; Yerasu et al., 2023). However, due to the high variability and adaptability of pathogens, many of these resistance genes gradually lose their effectiveness as new virulent strains emerge (Jewehan, 2022a). Moreover, diseases that were previously of minor importance have become economically significant, such as tomato brown rugose fruit virus, which has recently caused severe damage in greenhouse production systems (Karimova et al., 2023). Both wild species within the *Lycopersicon* section and those belonging to other sections of the *Solanum* genus serve as valuable sources of resistance genes. Nevertheless, their utilization in breeding programs remains limited (Foolad, 2007), primarily due to pre- and post-zygotic incompatibility barriers that restrict gene transfer and practical exploitation of the available genetic diversity (Abbas et al., 2024). In this article, we review the genetic resources of the *Solanum* genus as sources of resistance to biotic and abiotic stresses, the reproductive barriers between the tomato and its wild relatives, and the outcomes of interspecific hybridization research.

Adaptive Strategies and Reproductive Mechanisms

Wild tomatoes (section *Lycopersicon*) and their related *Solanum* species from the sections *Lycopersioides* and *Juglandifolia* share a common center of origin in the Andean region of South America and the Galápagos Islands. These species occupy diverse ecological niches, which underlie their remarkable adaptive potential to a wide range of environmental conditions. Currently, twelve species of wild tomatoes are recognized: *Solanum arcanum* Peralta, *Solanum cheesmaniae* (L. Riley) Fosberg, *S. chilense* Dunal, *S. chmielewskii* (C. M. Rick, Kesicki, Fobes, and M. Holle) D. M. Spooner, G. J. Anderson and R. K. Jansen, *S. corneliomulleri* J. F. Macbride, *S. galapagense* S. C. Darwin and Peralta, *S. habrochaites* S. Knapp and D. M. Spooner, *S. huaylasense* Peralta, *S. neorickii* D. M. Spooner, G. J. Anderson and R. K. Jansen, *S. pennellii* Correll, *S. peruvianum* L., and *S. pimpinellifolium* L. Additionally, four closely related species from two phylogenetically allied sections – *Juglandifolia* and *Lycopersioides* – include *S. juglandifolium* Dunal, *S. ochranthum* Dunal, *S. lycopersioides* Dunal, and *S. sitiens* I. M. Johnston (Peralta et al., 2008). *Solanum sisymbriifolium* Lam., which originates from the Southern Cone of South America (Biswas et al., 2023), is also regarded as a promising sources of valuable traits for introgression

into cultivated tomato. This has been confirmed through the successful production of viable hybrid progeny (Piosik et al., 2019).

For the effective utilization of wild species in breeding programs, it is essential to have comprehensive information on their ecological requirements, pollination systems, self-compatibility, and cross-compatibility with the cultivated tomato (Table 1).

A study by Ramírez-Ojeda et al. (2021) reported that *Solanum* species such as *S. habrochaites*, *S. arcanum*, *S. ochranthum*, and *S. juglandifolium* exhibit a high degree of adaptability to diverse climatic conditions. In contrast, species such as *S. sitiens*, *S. lycopersioides*, *S. corneliomulleri*, and *S. chmielewskii* display more restricted ecological preferences. Based on median elevation data, *S. cheesmaniae*, *S. galapagense*, and *S. pimpinellifolium* occur within a relatively narrow altitudinal range, whereas *S. lycopersioides*, *S. sitiens*, and *S. ochranthum* are distributed across a much broader range of elevations.

Thermophilic species such as *S. cheesmaniae*, *S. galapagense*, and *S. pimpinellifolium* are typically distributed in regions with mean annual temperatures above 20 °C; whereas *S. lycopersioides* and *S. sitiens* are adapted to cooler

Table 1. Biological characteristics of wild *Solanum* species

Species	Compatibility	Pollination system	Crossability with tomato	Ecological distribution (Peralta et al., 2008)
<i>S. cheesmaniae</i>	SC	S	♀♂	Endemic to the Galapagos Islands. It inhabits dry, open, and rocky slopes
<i>S. galapagense</i>	SC	S	♀♂	Endemic to the Galápagos Islands; coastal lava flows and volcanic slopes
<i>S. pimpinellifolium</i>	SC	FS	♀♂	From southern Ecuador to northern Chile; coastal areas, plains
<i>S. lycopersicum</i> var. <i>cerasiforme</i>	SC	S	♀♂	Found worldwide in tropical and subtropical regions
<i>S. arcanum</i>	SI, rarely SC	S, C, FC	-	Northern Peru in inter-Andean dry valleys and coastal ecosystems with seasonal fog. Generally dry sites, rocky slopes
<i>S. chmielewskii</i>	SC	FC	♂	Southern zone of Peru and the northern zone of Bolivia. Wet and well-drained rocky slopes
<i>S. neorickii</i>	SC	S	♂	Southern Ecuador to southern Peru, in inter-Andean dry valleys
<i>S. corneliomulleri</i>	SI	C	♂	Southern Peru, western slopes of the Andes, dry and rocky slopes
<i>S. peruvianum</i>	SI, rarely SC	C	♂	Central region of Peru to northern Chile. Dry coastal deserts and slopes
<i>S. chilense</i>	SI	C	-	Coastal zone of Chile and northern Peru, on dry rocky slopes, and occasionally saline
<i>S. habrochaites</i>	SI, rarely SC	FC	♂	Andean region of Ecuador and Peru in montane forests and dry slopes, occasionally found in seasonal fog ecosystems
<i>S. pennellii</i>	SI	FC	♂	North of Peru to the north of Chile, in areas of dry slopes, generally in flat areas
<i>S. ochranthum</i>	SI	C	-	Andean region of Colombia, Ecuador, and Peru, areas of mountain mesophilic forest
<i>S. lycopersioides</i>	SI	C	♂	Southern area of Peru and northern Chile. In ravines and rocky slopes
<i>S. sitiens</i>	SI	C	♂	Endemic to the Atacama Desert, hyper-arid areas
<i>S. juglandifolium</i>	SI	C	-	Andean region of Colombia, Ecuador, and Peru in areas of mountain mesophilic forest
<i>S. sisymbriifolium</i>	SI	C	♂*	Areas with tropical, subtropical, and temperate climates

Note: SC – self-compatible, SI – self-incompatible; S – self-pollinator, C – cross-pollinator, FS – facultative self-pollinator, FC – facultative cross-pollinator; ♀♂ – hybrid seeds may be produced when acting as both the paternal and maternal components of the cross; ♂ – hybrid seeds may be produced when acting as the paternal component of the cross, ♂* – hybrid seeds may be produced when acting as the paternal component of the cross, but the hybrid origin of the seeds without the use of embryo culture has not been proven; «-» – does not produce hybrid seeds without the use of additional techniques.

Таблица 1. Биологические особенности дикорастущих видов *Solanum*

Вид	Совместимость	Тип опыления	Скрещиваемость с томатом	Происхождение и условия произрастания (по Peralta et al., 2008)
<i>S. cheesmaniae</i>	СС	С	♀♂	Эндемик Галапагосских островов, сухие, открытые, каменистые склоны
<i>S. galapagense</i>	СС	С	♀♂	Эндемик Галапагосских островов, прибрежные лавовые потоки и вулканические склоны
<i>S. pimpinellifolium</i>	СС	ФС	♀♂	От Южного Эквадора до севера Чили. Прибрежные районы, равнины
<i>S. lycopersicum var. cerasiforme</i>	СС	С	♀♂	Распространен по всему миру в тропиках и субтропиках
<i>S. arcanum</i>	СН, редко СС	С, П, ФП	-	Север Перу. Прибрежные зоны с сезонными туманами и внутренние долины Анд, на сухих каменистых склонах
<i>S. chmielewskii</i>	СС	ФП	♂	Юг Перу и север Боливии. Влажные и хорошо дренированные каменистые склоны
<i>S. neorickii</i>	СС	С	♂	Юг Эквадора - юг Перу. В сухих долинах между Андами
<i>S. corneliomulleri</i>	СН	П	♂	Южное Перу, Западные склоны Анд, сухие каменистые склоны
<i>S. peruvianum</i>	СН, редко СС	П	♂	Центральный регион Перу, север Чили. Сухие прибрежные пустыни и склоны
<i>S. chilense</i>	СН	П	-	Прибрежная зона Чили и северного Перу, на сухих каменистых склонах, иногда на солончаках
<i>S. habrochaites</i>	СН, редко СС	ФП	♂	Регион Анд Эквадора и Перу. Горные леса, сухие склоны и иногда экосистемы с сезонными туманами
<i>S. pennellii</i>	СН	ФП	♂	От севера Перу до севера Чили, на равнинных сухих каменистых склонах и песчаных участках
<i>S. ochranthum</i>	СН	П	-	Регион Анд Колумбии, Эквадора и Перу. Горные леса
<i>S. lycopersicoides</i>	СН	П	♂	Юг Перу и север Чили. Ущелья и каменистые склоны.
<i>S. sitiens</i>	СН	П	♂	Эндемик пустыни Атакама, гипераридные районы
<i>S. juglandifolium</i>	СН	П	-	Умеренные дождевые леса Колумбии, Эквадора и Перу
<i>S. sisymbriifolium</i>	СН	П	♂*	Регионы с тропическим, субтропическим и умеренным климатом

Примечание: СС – самосовместимость, СН – самонесовместимость; С – самоопылитель, П – перекрестник, ФС – факультативный самоопылитель, ФП – факультативный перекрестник; ♀♂ – возможно получение гибридных семян, когда выступает как в качестве отцовского, так и материнского компонента скрещивания, ♂ – возможно получение гибридных семян, когда выступает отцовским компонентом скрещивания; ♂* – возможно получение семян, когда выступает отцовским компонентом скрещивания, однако гибридное происхождение семян без применения эмбриокультуры не доказано; «-» – не завязывает гибридных семян без применения дополнительных методик.

environments. *S. peruvianum* occurs in habitats characterized by relatively stable daily temperatures, in contrast to *S. chilense*, which thrives under conditions of high diurnal temperature variation. *S. juglandifolium* and *S. ochranthum* are associated with humid regions, while *S. lycopersicoides* and *S. sitiens* are characteristic of arid zones. *S. pennellii*

exhibits exceptional drought tolerance, attributed to efficient regulation of transpiration, high water-use efficiency, and salinity tolerance (Ramírez-Ojeda et al., 2021). Additionally, *S. sisymbriifolium* demonstrates broad adaptive capacity and has become widely established across multiple regions globally (Biswas et al., 2023).

Genomic research and chromosomal characteristics

All species listed in Table 1 possess a diploid chromosome complement of 24 ($2n = 24$), whereas natural tetraploid populations have been reported only in *S. chilense*. In wild tomatoes and related species, gene order is highly conserved despite the presence of some chromosomal rearrangements, which facilitates trait introgression (Kole, 2011). Although successful hybridization between *S. sisymbriifolium* and tomato has been reported (Piosik et al., 2019), this species remains poorly studied. No genetic map has yet been constructed, although high-quality karyotyping has been performed and chromosome morphology has been described (Biswas et al., 2024).

A set of genomes from wild tomato species, including *S. pimpinellifolium*, *S. habrochaites*, *S. pennellii*, *S. galapagense*, *S. chilense*, *S. arcanum*, *S. peruvianum*, *S. corneliomulleri*, *S. neorickii*, *S. chmielewskii*, and *S. lycopersicoides*, has been successfully sequenced, thereby providing a foundation for the identification and mapping of valuable traits (Du et al., 2025). To date, tomato researchers have identified thousands of QTLs and hundreds of genes associated with key agronomic traits, including disease resistance. In this review, we focus specifically on the major biotic stress-resistance genes identified in wild tomato relatives.

Resistance to biotic and abiotic stresses

Over the past decade, research interest in wild tomato species and several related *Solanum* species as sources of resistance to tomato diseases has increased markedly. When considering wild species as donors of valuable traits, it is important to note that different accessions within the same species may exhibit substantially different levels of resistance, as shown by Grushetskaya et al. (2010), Jewehan et al. (2022b), Solankey et al. (2017), and Arafa et al. (2017). Therefore, prior to their inclusion in hybridization programs, the target trait should be carefully evaluated in the selected material. Table 2 summarizes wild species and the valuable resistance traits to biotic and abiotic stresses identified in them.

When considering sources for improved tomato tolerance to abiotic stresses, particular attention should be given to species such as *S. sitiens*, which exhibits resistance to soil salinity, drought, and sub-zero temperatures (Rick, 1988; Chetelat et al., 2009). Foolad (2004) identified *S. pimpinellifolium*, *S. peruvianum*, and *S. pennellii* as important genetic sources of salinity tolerance. *S. habrochaites* carries genes conferring resistance to chilling injury, and successful introgression of these genes into cultivated tomato has been reported (Dolstra et al., 2002).

An important research priority is the transfer of insect resistance genes, given that insects serve as primary vectors of tomato viral diseases. This resistance is primarily conferred by a high density of glandular trichomes (Almeida et al., 2023). Among wild species, *S. pennellii*, *S. habrochaites* var. *hirsutum*, and *S. galapagense* exhibit resistance to whiteflies attributable to these traits. Low susceptibility to the tomato leafminer *Tuta absoluta* (Meyrick, 1917) has been observed in *S. pennellii*, *S. chmielewskii*, *S. habrochaites*, and *S. galapagense*, associated with the production of allelochemicals, glandular trichome density, and specific leaf morphology; notably, high heritability of both trichome density and allelochemical content has been demonstrated, including in interspecific crosses (Almeida et al., 2023). *S. sisymbriifolium* is distinguished by its resistance to the carmine spider mite *Tetranychus cinnabarinus* Boisduval; although the heritability of this trait remains unstudied (Piosik et al., 2019).

In uncontrolled field conditions, particularly in protected and open-ground cultivation in southern Russia, root-knot nematodes *Meloidogyne* spp. cause substantial damage to tomato crops. Resistance to these nematodes is primarily conferred by *Mi* genes, several of which have been successfully introduced into cultivated tomatoes. These genes were originally identified in *S. peruvianum* (*Mi1–Mi8*) and *S. arcanum* (*Mi-9*), with the latter mapped to chromosome 6 and notable for retaining activity at elevated temperatures (Jiang et al., 2023). Additionally, *S. sisymbriifolium* represents a promising alternative source of nematode resistance that is employed as a trap crop (Hajhassani et al., 2020; Perpétuo et al., 2021).

Bacterial diseases of tomato cause significant yield losses and have a worldwide distribution. Genetic resistance to the bacterial canker, caused by *Clavibacter michiganensis* subsp. *michiganensis* (Smith) Davis et al., has been identified in *S. chilense*, *S. habrochaites*, and *S. pimpinellifolium* (Khazaei, Madduri, 2022). Resistance to the bacterial spot, induced by *Xanthomonas* spp., occurs in *S. habrochaites* (Almeida et al., 2023), *S. pennellii*, and *S. pimpinellifolium* (Khazaei,

Madduri, 2022). Finally, resistance to the bacterial wilt, provoked by *Ralstonia solanacearum* (Smith) Yabuuchi et al., has been reported in *S. pimpinellifolium* (Khazaei, Madduri, 2022) and *S. sisymbriifolium* (Collonnier et al., 2003). In wild and related tomato species, resistance to bacterial diseases is predominantly polygenic, with QTLs mapped in only a limited number of species. For example, resistance to bacterial spot is controlled by the *Pto/Prf* gene cluster from *S. pimpinellifolium*, which has been successfully introgressed into several modern tomato varieties (Hassan et al., 2024).

Among the most dangerous viral diseases of tomato classified as quarantine pathogens in Russia are Pepino mosaic virus (PepMV), Tomato spotted wilt virus (TSWV), and tomato brown rugose fruit virus (ToBRFV) (“Dangerous Quarantine Diseases of Tomatoes,” 2024), for which no effective control measures currently exist. Resistance to PepMV has been identified in *S. habrochaites* (Ling, Scott, 2007) and in *S. lycopersicoides* (Soler et al., 2011). However, successful introgression of this trait into cultivated tomato has not been reported. Tolerance to ToBRFV has been reported in *S. pimpinellifolium*, *S. pennellii*, and *S. chilense* (Kabas et al., 2022), with highly resistant accessions specifically identified among *S. pimpinellifolium* (Jaiswal et al., 2024).

Qi et al. (2021) identified eight resistance genes against tomato spotted wilt virus (genus *Tospovirus*) in wild tomato species, including *S. pimpinellifolium*, *S. peruvianum* and *S. chilense*, of which only the dominant *Sw-5* gene, originally derived from *S. peruvianum*, confers high-level resistance. This gene also provides resistance to tomato chlorotic spot virus (Shahriari, 2023). Additional sources of Tomato spotted wilt virus (TSWV) resistance have been identified by Kabaş et al. (2021) in accessions of *S. pennellii*, *S. chmielewskii*, *S. habrochaites*, *S. peruvianum*, and *S. sitiens*.

Tobacco mosaic virus, tomato mosaic virus, and tomato brown rugose fruit virus belong to the genus *Tobamovirus*. The principal defense against tobamoviruses in tomato is provided by three mapped resistance genes: *Tm-1* on chromosome 2 of *S. habrochaites*, which is inherited in an incompletely dominant manner and confers partial resistance, and the dominant genes *Tm-2* and *Tm-2²* on chromosome 9 of *S. peruvianum*, of which *Tm-2²* is the most effective (Shahriari et al., 2023). In addition, Jewehan et al. (2022b) detected high resistance to tobacco mosaic virus and tomato mosaic virus in two *S. ochranthum* accessions.

Tomato yellow leaf curl disease, caused by begomoviruses of the family Geminiviridae, severely impacts tomato yield and fruit quality. To date, six major independently inherited resistance genes *Ty-1*, *Ty-3*, *Ty-4*, and *Ty-6* from *S. chilense*; *Ty-2* from *S. habrochaites*; and *Ty-5* from *S. peruvianum*, along with several QTLs, have been identified and mapped in wild tomato species (Dhaliwal et al., 2020). The *Ty-1*, *Ty-2*, *Ty-3*, *Ty-4*, and *Ty-6* genes are dominantly inherited, whereas *Ty-5* is recessive; notably, *Ty-1* and *Ty-5* exhibit broad-spectrum activity, while *Ty-4* and *Ty-6* genes merely enhance the resistance conferred by *Ty-3* and *Ty-5* (Shahriari et al., 2023).

Resistance to Tomato chlorosis virus (ToCV) has been identified in accessions of *S. peruvianum* and *S. chmielewskii* (García-Cano et al., 2010, Mansilla-Córdova et al., 2018); subsequent studies confirmed the quantitative nature of this resistance inheritance (Gao et al., 2025).

Among the fungal diseases affecting tomato cultivation in Russia, late blight (causal agent *Phytophthora infestans* de Bary), *Alternaria* blight (*Alternaria* spp.), and leaf mold (*Fulvia fulva* (Cooke) Cif.) are particularly destructive. Sources of late blight resistance have been identified in *S. chilense* (Solankey et al., 2017; Arafa et al., 2017), *S. peruvianum* (Solankey et al., 2017), and *S. habrochaites* (Ph-4 gene; Khazaei, Madduri, 2022). *S. sisymbriifolium* exhibits hypersensitivity response to several European isolates of *P. infestans* pathogenic to potato (Flier et al., 2003). Several late blight resistance genes have been mapped, including the *Ph-2* gene from *S. pimpinellifolium*, located on the long arm of chromosome 10 and conferring

partial resistance that effectively slows disease progression. The *Ph-3* gene from the same species, mapped to the long arm of chromosome 9, provides more reliable resistance (Zhi et al., 2021). The *Ph-5*, also derived from *S. pimpinellifolium*, is mapped to the long arm of chromosome 1 (Foolad et al., 2014).

Resistance to the *F. fulva* has been identified in *S. neorickii* (Grushetskaya et al., 2010), *S. lycopersicum* var. *cerasiforme* (Khazaei, Madduri, 2022; Grushetskaya et al., 2010), and *S. cheesmaniae* (Grushetskaya et al., 2010). Among the leaf mold resistance genes, *Cf-9* first identified in *S. pimpinellifolium*, and *Cf-4* from *S. habrochaites* have been most extensively characterized (Kahlon et al., 2020).

Table 2. Genetic sources of resistance to biotic and abiotic stresses in the genus *Solanum*

	<i>S. cheesmaniae</i>	<i>S. galapagense</i>	<i>S. pimpinellifolium</i>	<i>S. lycopersicum</i> var. <i>cerasiforme</i>	<i>S. arcanum</i>	<i>S. chmielewskii</i>	<i>S. neorickii</i>	<i>S. cornelomulleri</i>	<i>S. peruvianum</i>	<i>S. chilense</i>	<i>S. habrochaites</i>	<i>S. pennellii</i>	<i>S. ochranthum</i>	<i>S. lycopersicoides</i>	<i>S. sitchensis</i>	<i>S. sisymbriifolium</i>
Abiotic stress																
Heat tolerance	+		+			+					+	+				
Drought tolerance	+		+							+	+	+				+
Salinity tolerance			+				+				+	+				
Pests																
Whitefly <i>Bemisia tabaci</i>			+			+					+	+				
Two-spotted spider mite <i>Tetranychus urticae</i>																+
Root-knot nematode <i>Meloidogyne</i> spp					+				+							+
Tomato leafminer <i>Tuta absoluta</i>											+	+				
Bacterial diseases																
Bacterial spot <i>Xanthomonas euvesicatoria</i> ex Doidge, <i>X. vesicatoria</i> ex Doidge, <i>X. perforans</i> , <i>X. gardneri</i> Šutic			+								+	+				
Bacterial wilt <i>Ralstonia solanacearum</i> (Smith) Yabuuchi et al.			+													+
Bacterial stem canker of tomato <i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i> (Smith) Davis et al.			+		+					+	+					
Bacterial speck <i>Pseudomonas syringae</i> pv. <i>tomato</i> van Hall			+													
Viral diseases																
Tomato brown rugose fruit disease <i>Tomato brown rugose fruit virus</i> , ToBRFV			+	+				+	+	+	+		+			
Tomato yellow leaf curl disease <i>Tomato yellow leaf curl virus</i> , TYLCV			+						+	+	+					
Pepino mosaic <i>Pepino mosaic potexvirus</i> , PepMV											+				+	
Tomato mosaic <i>Tomato mosaic tobamovirus</i> , ToMV									+		+		+			
Tobacco mosaic <i>Tobacco mosaic tobamovirus</i> , TMV													+			
Tomato spotted wilt <i>Tomato spotted wilt orthotospovirus</i> , TSWV			+			+			+	+	+	+				+
Tomato chlorotic spot virus <i>Tomato chlorotic spot virus</i> , TCSV									+							
Tomato chlorosis virus <i>Tomato chlorosis virus</i> (ToCV)						+			+							
Fungal diseases																
<i>Alternaria</i> blight <i>Alternaria linariae</i> (Neerg.) E.G. Simmons, <i>A. solani</i> Sorauer, <i>A. alternata</i> (Fr.) Keissl			+										+			
Verticillium wilt <i>Verticillium albo-atrum</i> Reinke & Berthold and <i>V. dahliae</i> Kleb.			+	+												+
Leaf mold <i>Fulvia fulva</i> (Cooke) Cif.	+		+	+			+				+					
Powdery mildew <i>Erysiphe neolyopersici</i> (L. Kiss) H. Y. Hsiao & Y. M. Shen, <i>Leveillula taurica</i> (Lév.) G. Arnaud			+	+	+				+	+	+					
Gray mold <i>Botrytis cinerea</i> Pers.			+				+				+					
Fusarium wilt <i>Fusarium oxysporum</i> Schltdl., rarely <i>F. solani</i>			+						+		+					
Late blight <i>Phytophthora infestans</i> (Mont.) de Bary	+		+						+	+	+	+				+
Septoria leaf spot <i>Septoria lycopersici</i> Speg.			+	+					+	+	+					
Gray leaf spot <i>Stemphylium solani</i> G. F. Weber, <i>S. lycopersici</i> (Enjoi) W. Yamam., <i>S. botryosum</i> Wallr.			+						+		+					

Таблица 2. Генетические источники устойчивости к биотическим и абиотическим стрессам в роде *Solanum*

	<i>S. cheesmaniae</i>	<i>S. galapagense</i>	<i>S. pimpinellifolium</i>	<i>S. lycopersicum</i> var. <i>cerasiforme</i>	<i>S. arcanum</i>	<i>S. chmielewskii</i>	<i>S. neorickii</i>	<i>S. corneliumulleri</i>	<i>S. peruvianum</i>	<i>S. chilense</i>	<i>S. habrochaites</i>	<i>S. pennellii</i>	<i>S. ochranthum</i>	<i>S. lycopersicoides</i>	<i>S. sitchensis</i>	<i>S. sisymbriifolium</i>
Абиотический стресс																
Жаростойкость	+		+			+					+	+				
Засухоустойчивость	+		+							+	+	+				+
Устойчивость к засолению почвы			+				+				+	+				
Вредители																
Табачная белокрылка <i>Bemisia tabaci</i>		+				+					+	+				
Красный паутинный клещ <i>Tetranychus urticae</i>																+
Нематода <i>Meloidogyne spp</i>					+				+							+
Томатная минирующая моль <i>Tuta absoluta</i>											+	+				
Бактериальные заболевания																
Бактериальная пятнистость <i>Xanthomonas euvesicatoria</i> ex Doidge, <i>X. vesicatoria</i> ex Doidge, <i>X. perforans</i> , <i>X. gardneri</i> Šutic			+								+	+				
Бактериальное увядание <i>Ralstonia solanacearum</i> (Smith) Yabuuchi et al.			+													+
Бактериальный рак стеблей томата <i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i> (Smith) Davis et al.			+		+					+	+					
Бактериальная крапчатость томата <i>Pseudomonas syringae</i> pv. <i>tomato</i> van Hall			+													
Вирусные заболевания																
Бурая (коричневая) морщинистость томата <i>Tomato brown rugose fruit virus</i> , ToBRFV			+	+				+	+	+	+		+			
Желтая курчавость листьев томата <i>Tomato yellow leaf curl virus</i> , TYLCV			+						+	+	+					
Мозаика пегино <i>Pepino mosaic potexvirus</i> , PepM											+				+	
Мозаика томата <i>Tomato mosaic tobamovirus</i> , ToMV									+		+		+			
Табачная мозаика <i>Tobacco mosaic tobamovirus</i> , TMV													+			
Бронзовость, или пятнистое увядание томата <i>Tomato spotted wilt orthotospovirus</i> , TSWV			+			+			+	+	+	+			+	
Вирус хлоротической пятнистости томатов <i>Tomato chlorotic spot virus</i> , TCSV									+							
Вирус хлороза томатов <i>Tomato chlorosis virus</i> , (ToCV)						+			+							
Грибные заболевания																
Альтернариоз томата <i>Alternaria linariae</i> (Neerg.) E.G. Simmons, <i>A. solani</i> Sorauer, <i>A. alternata</i> (Fr.) Keissl			+									+				
Вертициллез <i>Verticillium albo-atrum</i> Reinke & Berthold u <i>V. dahliae</i> Kleb.			+	+												+
Кладоспориоз <i>Fulvia fulva</i> (Cooke) Cif.	+		+	+			+				+					
Мучнистые росы томата <i>Erysiphe neolycopersici</i> (L. Kiss) H. Y. Hsiao & Y. M. Shen, <i>Leveillula taurica</i> (Lév.) G. Arnaud			+	+	+				+	+	+					
Серая гниль <i>Botrytis cinerea</i> Pers.			+				+				+					
Фузариоз <i>Fusarium oxysporum</i> Schldl., реж <i>F. solani</i>			+						+			+				
Фитофтороз паслёновых <i>Phytophthora infestans</i> (Mont.) de Bary	+		+						+	+	+	+				+
Септориоз, или белая пятнистость <i>Septoria lycopersici</i> Speg.			+	+					+	+	+					
Серая пятнистость листьев <i>Stemphylium solani</i> G. F. Weber, <i>S. lycopersici</i> (Enjoji) W. Yamam., <i>S. botryosum</i> Wallr.			+						+		+					

Genetic resistance to *Alternaria* pathogens has been identified in *S. pennellii*, which carries the *Asc* gene conferring resistance to *Alternaria* stem canker, and in *S. pimpinellifolium*, which harbors the *EB-5* and *EB-9* genes for resistance to *Alternaria* blight (Khazaei, Madduri, 2022). Additionally, resistance to *Alternaria* spp. has been documented in *S. peruvianum*, *S. habrochaites*, and *S. arcanum*, where

multiple QTLs contributing to this resistance have been mapped (Adhikari et al., 2017).

Resistance to powdery mildew has been detected in multiple wild tomato species, including *S. pimpinellifolium* and *S. peruvianum* (Emelina et al., 2010), *S. habrochaites* (Emelina et al., 2010; Khazaei, Madduri, 2022), *S. lycopersicum* var. *cerasiforme*, *S. chilense*, and *S. arcanum* (Khazaei, Madduri,

2022). Among the characterized resistance genes, *Ol-1* and *Ol-3* were mapped from *S. habrochaites*, *Ol-4* from *S. peruvianum*, three QTLs were identified in *S. neorickii*, and a recessive *ol-2* gene was detected in *S. lycopersicum* var. *cerasiforme* (Bai et al., 2005).

Three major genes conferring resistance to Fusarium wilt (causal agent *Fusarium oxysporum* Schltdl.) – *I*, *I-2*, and *I-3* – have been successfully introgressed into cultivated tomato varieties. The dominant genes *I* and *I-2*, originating from *S. pimpinellifolium*, confer resistance to races 1 and 2 of the pathogen, respectively, while *I-3*, introgressed from *S. pennellii*, provides resistance to races 1 through 3 (Shamshin et al., 2022).

Two dominant genes *Ve-1* and *Ve-2*, conferring resistance to Verticillium wilt induced by *Verticillium dahliae* Kleb. and *V. albo-atrum* Reinke & Berthold, have been introgressed into cultivated tomato from *S. pimpinellifolium*. These genes, mapped to the short arm of chromosome 9, have been extensively characterized using molecular genetic approaches (Robb and Nazar, 2021). *Ve-1* provides resistance to race 1 strains of both pathogens but offers no protection against race 2 (Fradin et al., 2009). Additionally, *S. sisymbriifolium* represents a promising novel source of Verticillium wilt resistance (Piosik et al., 2019).

Reproductive barriers and optimal strategies for interspecific hybridization between *S. lycopersicum* and wild relatives

Information on reproductive relationships between *Solanum* species is critical for effective breeding strategies (Bukharova, Bukharov, 2009). Most *Solanum* species exhibit S-RNase-based gametophytic self-incompatibility (GSI), controlled by the S-locus. This system is based on the interaction of S-RNases in the pistil and S-locus F-box proteins in pollen, which form an SCF-type ubiquitin ligase complex that mediates the recognition and degradation of incompatible S-RNases via the ubiquitin-proteasome pathway. Self-compatibility (SC) in *S. lycopersicum*, *S. cheesmaniae*, *S. galapagense* and *S. pimpinellifolium* results from disruption of this system that occurred due to the loss of functional S-RNase alleles and key pollen factors, including the SpSLF-23 protein (encoded by the *ui1.1* gene) and Cullin1 (*ui6.1*) (Li and Chetelat, 2015). In addition to the aforementioned species, *S. chmielewskii* and *S. neorickii* are self-compatible; however, they exhibit unilateral incompatibility (UI) when crossed with cultivated tomato. UI represents a post-mating reproductive barrier that restricts hybridization between related species, in which pollen from a self-compatible species is rejected by the pistil of a self-incompatible species, whereas the reciprocal cross typically succeeds. The molecular basis of UI is closely associated with self-incompatibility (SI). Core components of the SI pathway, including S-RNase, the CUL1 protein (encoded by the *ui6.1* locus), and the HT protein, have been shown to play critical roles in mediating UI responses (Li and Chetelat, 2015). Within the tomato clade, several wild species such as *S. corneliomulleri*, *S. chilense*, *S. pennellii*, *S. ochranthum*, *S. lycopersicoides*, *S. sitiens*, *S. juglandifolium*, and *S. sisymbriifolium* are characterized by self-incompatibility. Conversely, self-compatible forms have been identified in *S. arcanum*, *S. peruvianum*, and *S. habrochaites* (Table 1).

Interspecific hybridization within the genus *Solanum* is governed by prezygotic and postzygotic incompatibility barriers

Cultivated tomato exhibits high susceptibility to gray mold, caused by *Botrytis cinerea* Pers. Resistance identified in wild species such as *S. neorickii* and *S. pimpinellifolium* is predominantly quantitative in nature (Khazaei, Madduri, 2022). Partial resistance has also been documented in *S. habrochaites*, associated with a QTL locus (Finkers et al., 2007).

Tomato septoria leaf spot (causal agent *Septoria lycopersici* Spreng.) is widespread throughout Russia, particularly in the southern regions, Siberia, and the Far East. Wild tomato species serve as important sources of resistance, with *S. chilense*, *S. habrochaites*, *S. peruvianum*, and *S. cerasiforme* demonstrating high levels of disease resistance (Pandey et al., 2024). Although resistance loci have been successfully transferred from *S. habrochaites* and *S. peruvianum* (Pandey et al., 2024), no commercial tomato varieties currently offer resistance levels satisfactory to vegetable growers.

Gray leaf spot poses low risk in Russia, primarily affecting open fields and plastic greenhouse cultivation. A single dominant resistance gene *Sm* from *S. pimpinellifolium* has been introgressed into tomato. Reis and Boiteux (2020) additionally identified resistant accessions in *S. lycopersicum*, *S. peruvianum*, and *S. habrochaites*; however, it remains unclear whether this resistance represents *Sm* alleles or novel genes.

(Bedinger et al., 2011). Several wild and semi-domesticated species, including *S. cheesmaniae*, *S. galapagense*, *S. pimpinellifolium*, and the ancestral form *S. lycopersicum* var. *cerasiforme*, exhibit minimal reproductive barriers and readily hybridize with cultivated tomato in both direct and reciprocal crosses (Kole, 2011). Crosses between *S. lycopersicum* and certain wild relatives, such as *S. habrochaites* and *S. pennellii*, tend to produce hybrid seeds; however, a substantial proportion of these seeds remain underdeveloped, reflecting partial postzygotic incompatibility (Bukharova, Bukharov, 2009). Moreover, interspecific hybridization involving *S. habrochaites* displays unilateral incompatibility when this species serves as the maternal parent (Hogenboom, 1972).

Crosses between *S. lycopersicum* and *S. peruvianum* are typically characterized by unilateral incompatibility and frequent embryo abortion (Kole, 2011). Nonetheless, recent studies by Zeist et al. (2023) have reported successful seed set in reciprocal crosses between these species. In earlier work, Bukharova and Bukharov (2009) observed a fruit set of approximately 40% in *S. lycopersicum* × *S. peruvianum* hybrids, although seed germination remained relatively low (27%). Among the resulting progeny, only 3% were confirmed hybrids, while the majority were determined to be of apomictic origin. These findings indicate that judicious selection of *S. lycopersicum* cultivars can facilitate hybridization with wild *Solanum* species and enhance the efficiency of interspecific hybrid production.

All wild species hybridized with *S. lycopersicum* possess a diploid chromosome number of $2n = 24$; thus, manipulations involving polyploidization or chromosome doubling—techniques commonly employed in interspecific potato hybridization (Jansky, 2006)—are not required.

To address incompatibility barriers related to impaired pollen tube growth and fertilization in various dicotyledonous

plants, including members of the Solanaceae family, *in vitro* pollination has been successfully combined with ovule, ovary, or isolated embryo culture techniques (Tomiczak et al., 2022). However, to date, no reports describe the application of such approaches to overcome reproductive barriers within the genus *Solanum*.

To promote pollen tube germination, fertilization, and hybrid embryo development, various pre- and post-pollination treatments with phytohormones have been employed (Jansky, 2006; Pershina, Trubacheeva, 2016, Vishnyakova et al., 2024). Another effective technique involves pollination using a mixture of pollen from cultivated and wild relatives (Picó et al., 2002). Within the genus *Solanum*, Picó et al. (2002) applied these methods to facilitate hybridization between *S. lycopersicum* and the wild species *S. peruvianum* and *S. chilense*. Pretreatment of tomato stigmas with boric acid followed by pollination with *S. peruvianum* pollen, combined with gibberellic acid application to prevent fruit abscission, yielded globular embryos with low seed set, some of which were successfully regenerated into plants via embryo culture. Additionally, the use of mixed pollen proved beneficial in overcoming the limited growth of *S. chilense* pollen tubes within tomato stigmas, resulting in a small number of hybrid plants, with *S. chilense* crosses producing approximately 0.1–0.6 hybrid seeds per fruit.

The classical bridge method developed by I.V. Michurin has been employed to overcome incompatibility between *S. lycopersicum* and wild species such as *S. sitiens* and *S. pennellii* (DeVerna et al., 1990, 1991). In many cases, incompatibility could only be bypassed through somatic hybridization, which enables the fusion of protoplasts from

distinct species to produce viable heterokaryons and hybrid plants (Handley et al., 1986; Kochevenko et al., 1996; Kobayashi et al., 1996; Gavrilenko et al., 2001).

A promising direction for overcoming interspecific incompatibility in *Solanum* hybridization involves genetic engineering approaches that target the modification or suppression of genes responsible for reproductive barriers. Such genes include S-locus genes encoding S-RNases and HT-B proteins (Bedinger et al., 2011). Alternatively, once these barrier-associated genes are identified and characterized, marker-assisted selection could be used to identify genotypes from natural populations that lack undesirable genes and to incorporate them into hybridization programs (Bedinger et al., 2011).

Postzygotic incompatibility barriers associated with defects in embryonic development in the genus *Solanum* can generally be overcome successfully through the *in vitro* culture of immature embryos. This approach has been successfully applied to facilitate the introgression of resistance genes from *S. peruvianum* (De Nettancourt et al., 1974; Sohrab et al., 2015) and has proven effective even in relatively distant crosses, such as *S. lycopersicum* × *S. sisymbriifolium* (Piosik et al., 2019) and *S. lycopersicum* × *S. sitiens* (Chetelat, 2016).

In some instances, postzygotic incompatibility is expressed as sterility in the hybrid progeny, as observed in crosses between *S. lycopersicum* and *S. peruvianum* (De Nettancourt et al., 1974), and between *S. lycopersicum* and *S. sisymbriifolium* (Piosik et al., 2019). Fertility restoration in sterile interspecific hybrids has been achieved through chromosome doubling with colchicine treatment during hybridization involving *S. sitiens* (DeVerna et al., 1990).

Conclusion

Tomato breeding relies heavily on the introgression of beneficial traits from wild *Solanum* species. The incorporation of these species into breeding programs is often prompted by the emergence of new diseases, virulent pathogen strains, or environmental stresses associated with climate change. Wild tomato relatives have served as important genetic donors, contributing resistance and adaptive traits to cultivated *S. lycopersicum*. The most frequently utilized species include *S. cheesmaniae*, *S. pimpinellifolium*, *S. habrochaites*, *S. pennellii*, and *S. peruvianum*. Using genes from these taxa, both Russian and international breeding programs have developed cultivars such as Gardemarin and Linkor, which carry powdery mildew resistance derived from *S. cheesmaniae* (Emelina et al., 2010), as well as Plum Regal containing the Ph-3 gene and Mountain Merit with Ph-2 and Ph-3 genes from *S. pimpinellifolium* (Coomber et al., 2025). Species such as *S. chmielewskii*, *S. corneliomulleri*, *S. ochranthum*, *S. lycopersicoides*, *S. sitiens*, and *S. sisymbriifolium* are difficult to cross with cultivated tomato, which has limited

their use in breeding to date. In interspecific hybridization, unilateral incompatibility is frequently observed, with higher success rates achieved when *S. lycopersicum* serves as the female parent. Numerous studies have demonstrated that hybridization efficiency and trait introgression are highly dependent on the selection of the *S. lycopersicum* genotype employed.

A recurrent phenomenon in distant hybridization of tomatoes is apomixis; therefore, the use of cultivated forms carrying marker traits – such as the potatoleaf type – can facilitate the identification and selection of true hybrid plants. To overcome prezygotic barriers, approaches including pollination with pollen mixtures, phytohormone treatments, the bridge-cross method, and somatic hybridization have proven effective. In cases of postzygotic barriers, *in vitro* embryo culture and chromosome doubling using colchicine are the primary methods for rescuing hybrid embryos and restoring fertility in sterile progeny.

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ГЕНЕТИЧЕСКИЙ ПОТЕНЦИАЛ ДИКИХ РОДСТВЕННИКОВ ТОМАТА
В СЕЛЕКЦИИ НА УСТОЙЧИВОСТЬ *SOLANUM LYCOPERSICUM*

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Томат *Solanum lycopersicum* входит в тройку самых производимых овощей в мире, при этом является культурой, уязвимой к различным заболеваниям, вредителям и абиотическим стрессам. В настоящее время вследствие изменения климата повышается вредоносность заболеваний, усиливается влияние абиотических факторов, поэтому возрастает потребность в создании адаптивных сортов и гибридов. Межвидовая гибридизация позволяет расширить генетическое разнообразие за счет интрогрессии генов целевых признаков и в перспективе позволяет снизить зависимость производства товарной продукции от химических средств защиты, повысить адаптивный потенциал растений и устойчивость к абиотическим стрессам. В последние годы проводится много исследований диких видов *Solanum* как источников ценных признаков для селекции томата. Данный обзор аккумулирует исследования по изучению диких видов рода *Solanum* в контексте источников устойчивости к биотическим и абиотическим факторам для томата, с обсуждением видов, гибридизация с которыми позволила получить жизнеспособное потомство. Обсуждается наличие барьеров нескрещиваемости и подходы к их преодолению, что важно для практической селекции. На современном этапе виды *S. cheesmaniae*, *S. habrochaites*, *S. pennellii*, *S. pimpinellifolium*, *S. peruvianum* наиболее активно вовлечены в селекцию и интрогрессия признаков в томат была осуществлена в основном из этих видов. *S. chmielewskii*, *S. corneliomulleri*, *S. sitiens*, *S. ochranthum*, *S. lycopersicoides*, *S. sisymbriifolium* сложно скрещиваются с культурным томатом, поэтому пока не внесли значительного вклада в интрогрессию ценных признаков. Успех гибридизации с дикими видами связан с подбором генотипов томата для гибридизации, использовании культурного томата в качестве материнского компонента скрещивания, а также использовании эмбриокультуры при абортации зародышей. Отдельным направлением преодоления нескрещиваемости видов является соматическая гибридизация, однако ее эффективность в интрогрессии ценных признаков в томат практически не оценивается.

Ключевые слова: дикие виды томата, источники устойчивости, абиотический стресс, устойчивость к заболеваниям, межвидовая гибридизация, нескрещиваемость

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