

Review Article

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Solanum americanum: An alternative model crop in plant pathology

Abdul Razak AHMED[®], Abdellahi GALLEDOU[®], Utku DEMIRTAS[®], Hakan FIDAN[®], Ozer CALIS[®]

Akdeniz University, Faculty of Agriculture, Plant Protection Department, 07059, Kampüs, Konyaaltı, Antalya, Türkiye

Corresponding author: O. Calis, e-mail: ozercalis@akdeniz.edu.tr Author(s) e-mail: abdulairazakahmed89@gmail.com, galledou4@gmail.com, utkudemirtas0748@gmail.com, hakanfidan@akdeniz.edu.tr

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ABSTRACT

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Nightshade plant Model plant Resistance Solanum americanum The *Solanum americanum*, possesses valuable features that earn it a deserved addition to the expanding list of model plants that are utilized in the fields of plant genetics, plant breeding and biotechnology. This review attempts to comprehensively highlight the crucial role of this model plant and its genetic diversity in terms of resistance against biotic pathogens. In summary, we recommend the use of this plant in future studies focused on plant-pathogen interactions.

1. Introduction

Plant pathogens have become a major global concern, especially among crop farming communities. This concern is aggravated by significant changes in climate patterns, which have informed the importance of identifying, researching, and effectively addressing these pathogens and their economic impact. This poses a significant struggle for plant pathologists, who strive to bring to light the complete array of effects caused by these pathogens and find lasting solutions to them. In the pursuit of complete understanding and the scrutiny of viable alternatives, researchers and plant pathologists have turned to the utilization of model crops as indispensable tools in their research endeavors.

Model plants are pivotal in phytopathology as they are used in research on plant-pathogen interactions, disease resistance mechanisms, and genetic variability of plants. Plants such as Arabidopsis thaliana (Padole and Ingle 2017), maize (Gaut et al. 2000; Strable and Scanlon 2009), tomato (Meissner et al. 1997), wheat (Feldman et al. 2012), rice (Izawa and Shimamoto 1996) and others have been reported to be used as model crops. These crops, by virtue of valuable characteristics such as genetic tractability, and rapid growth, provide a controlled environment to investigate the complexity of plant diseases and other agronomic features. They offer insights into host responses, pathogen virulence, and underlying molecular pathways involved in resistance or susceptibility. The understanding of these interactions helps researchers gain fundamental knowledge applicable to diverse crops, aiding in the development of diseaseresistant varieties.

Aside from their role in plant pathology, they also serve as valuable tools for assessing the evolutionary trajectories of plant genomes. For example, maize, as a model plant, has been used to decipher complex subjects of heterosis, epigenetics, and quantitative inheritance, thereby enhancing our comprehension of these complex phenomena (Strable and Scanlon 2009). Amongst other reported model plants, A. thaliana has been investigated the most and has been widely used in research studies. The preference of this plant for research studies can be attributed to its short life cycle, ability to produce a multitude of seeds, small genome size (about 143 Mbp) and the ability to generate mutants using simple agrobacterium transformation systems such as the flower dip method (Meyerowitz 2001). Despite the popularity of A. thaliana, another interesting crop group that are used in the understanding of plant pathogen interactions are the Solanaceae group. In a review paper by Arie et al. (2007), the importance of tomato (Solanum lycopersicum L.) in understanding the interaction between tomato and its viral, bacterial, fungal and nematode pathogens were highlighted. Also, they listed resistance and susceptibility genes discovered in tomato plants. Nevertheless, recent attention has shifted towards another member of this botanical family, Solanum americanum Mill., Black nightshade (Fig. 1), which is emerging as a promising candidate for plant-pathogen studies. Consequently, this paper aims to comprehensively review current research on S. americanum, particularly focusing on its morphology and role in plant-pathogen interaction studies.

2. S. americanum morphology

Solanum americanum is commonly known as Black nightshade. Despite its importance and diversity within the Solanum group, it has been classified as a weed and of less usage in most countries (Vandeventer et al. 1982). Often mistaken for S. nigrum, S. americanum is a diploid whilst S. nigrum is a polyploid. Moreover, the seeds of S. americanum are smaller and range from 1.2 - 1.6 mm in length, contrasting with the larger seeds of S. nigrum (1.8 - 2.2 mm). Phenotypically, S. americanum can be distinguished by its umbellate inflorescence, purplishblackish shiny fruits (Fig. 2), 1 - 2 mm long anthers and pollens with diameter between 19 - 27 μ m (Schilling et al. 1992).

3. S. americanum as a model plant

When comparing *S. americanum* with established model plants such as *A. thaliana*, distinct differences and potential advantages emerge. *A. thaliana* has been a cornerstone in plant research due to its well-characterized genome and extensive genetic tools, but *S. americanum* offers a unique perspective. Numerous studies have reported and documented various genes conferring resistance to plant pathogens in this emerging model plant. For instance, Moon et al. (2021) identified *RipAZ1* in *S. americanum*, which serves as an avirulent factor against *Ralstonia solanacearum*, the causal agent of bacterial wilt in most crops. In addition, two resistance genes (*Rpi-amr1* and *Rpi-amr3*) to late blight (*Phytophthora infestans*) resistant - potato plants were reported by Lin et al. (2023). The integration of these genes into vegetable and other crop species could confer

resistance against these pathogens. Other analogous investigations focusing on pathogen-microbe interactions in *S. americanum* have also been conducted, as outlined in Table 1. However, there is insufficient knowledge on other important plant pathogens. Notably, the impact of *Rhizoctonia solani* infection on *S. americanum* remains unknown. However, research on *S. nigrum* extract had proven to have high fungicidal (88%) properties against this pathogen (Pathak et al. 2020). Similar instances were observed for *Fusarium solani* and *Pseudomonas syringae* where a 10% concentration of *S. nigrum* extract were effective in inhibiting these pathogens' growth (Opande et al. 2017). These findings underscore the potential for uncovering possible resistance gene resource in *S. americanum* since these pathogens are of serious economic importance.

Beyond studies on plant pathogens, liquid and aqueous extracts from *S. americanum* have exhibited efficacy against diverse pathogens, offering potential applications in clinical studies (Afolabi et al. 2008; Cáceres et al. 1998).



Figure 1. Solanum americanum plant.



Figure 2. Morphology of *S. americanum* plant. A) *S. americanum* flowers (white, small, star-shaped), B) *S. americanum* flowers and leaves (leaves are ovate, arranged alternately along the stems), C) colour (initially green and may darken as it ripens), shape, and size (pea-sized) of *S. americanum* fruits.

Pathogen	Research findings	Recommendations	References
	1. <i>RipAZ1</i> was discovered to be an <i>avirulent</i> gene against <i>Rastolnia solanacearum</i>	The S. americanum R gene	
Ralstonia solanacearum	2. The 213-amino acid central region of RipAZ1 was reported to induce programmed cell death in <i>R. solanacearum</i> -infected <i>S. americanum</i>	recognizing RipAZ1 offers potential for creating potato varieties resistant to both <i>P.</i> <i>infestans</i> and <i>R. solanacearum</i> in breeding programs	(Moon et al. 2021)
	3. The gene can initiate early defense mechanism in the cytoplasm of the host cell.		
Phytophthora infestans	Nine (9) <i>Rpi-amr1</i> genes which offers broad spectrum resistance against different isolates of <i>P. infestans</i> were successfully identified and isolated from <i>S. americanum</i>	Combination of these genes and other R <i>pi</i> genes may help in the development of other crop varieties that are resistant to late blight disease	Witek et al. (2021)
	Rpi-amr recognized the effectors of Phytophthora parasitica and Phytophthora cactorum		
Xanthomonas perforans	<i>X. perforans</i> was isolated from wild <i>S. americanum</i> on tomato fields.	<i>S. americanum</i> weed plants on tomato fields should be eliminated since they are favourable hosts for <i>X. perforans</i> .	Araújo et al. (2015)
Cariogenic Streptoccoccus mutants	Extracts from <i>S. americanum</i> together with <i>Hibiscus</i> subdariffa, and Garcinia kola in addition to methanol were analyzed for their role as growth inhibitors of Cariogenic bacteria.	<i>S. americanum</i> liquid extracts should not be used in the treatment of cariogenic <i>Streptococcus</i> mutants	Afolabi et al. (2008
	2.5 g ml ⁻¹ of <i>S. americanum</i> extracts were ineffective in inhibiting growth of <i>Streptococcus</i> mutants		
Artemia salina	50 mg kg ⁻¹ of <i>S. americanum</i> extracts inhibited the growth of <i>A. salina</i>	<i>S. americanum</i> extracts can be used in the treatment of A. <i>salina</i> .	Cáceres et al. (1998

 Table 1. List of research conducted on S. americanum

4. S. americanum and plant viruses

Plant viruses are responsible for severe losses in the yield of economic crops. Plant viruses pose significant threats to crop production worldwide, impacting both quantity and quality of agricultural yields. Cao et al. (2020) estimated that more than 1500 viruses belonging to 26 families negatively affect plants. With the advent of new detection and sequencing methods, these numbers are expected to increase. Viruses infect crops, causing a range of detrimental effects with symptoms manifesting as leaf discoloration, distorted growth patterns, stunted growth, reduced yields, and in severe cases, plant death. Viruses are regularly transmitted through insect vectors, contaminated seeds, and agricultural tools.

Weeds and natural hosts within plant ecosystems serve as active reservoirs for these viruses. For instance, studies conducted in Poland revealed significant coinfections in weeds belonging to the *Asteraceae* family, including *Achillea millefolium*, *Sonchus oleraceus*, and *Crepis tectorum*, with pathogens such as Tomato spotted wilt virus (TSWV), Tobacco mosaic virus (TMV), Potato virus Y (PVY), Cucumber mosaic virus (CMV), and Tobacco ringspot virus (*TRSV*) (Korbecka-Glinka et al., 2021). Additionally, in a survey conducted in Saudi Arabia by Al-Shahwan et al. (2017), *Sonchus oleraceus* was found to be infected with Alfalfa mosaic virus (AMV), Bean common mosaic virus (BCMV), Bean leaf roll virus (BLRV), Bean yellow mosaic virus (BYMV), Cucumber mosaic virus (CMV), Lucerne transient streak virus (LTSV), Pea streak virus (PeSV), Red clover vein mosaic virus (RCVMV), Tobacco streak virus (TSV), and White clover mosaic virus (WCMV).

Weeds of the Solanaceae family have been identified as significant reservoirs for numerous plant viruses in a review by Haňcinský et al. (2020). The review highlighted Carolina horse nettle as a natural host for Peach rosette mosaic virus (PRMV), and petunia as a host of Potato virus B (PVB) and Tomato ringspot virus (ToRSV). Various viruses have been observed and documented on S. americanum across different global locations. For instance, in 2016, Potato yellow mosaic virus was recorded on both S. americanum and S. pimpinellifolium in Venezuela (Romay et al., 2016). Similarly, in the United States, Tomato chlorotic spot virus was reported on S. americanum (Badillo-Vargas et al. 2015), while in South America, Tomato chlorosis virus was also reported on S. americanum and S. sisymbriifolium (Arruabarrena et al. 2015). Although Tomato spotted wilt virus has not been officially reported on S. americanum, it has been found on other weed species such as Amaranthus hybridus, S. nigrum, Tagetes minuta, and Datura stramonium (Macharia et al. 2016). The confirmation of TWSV infection on S. nigrum, a close relative of S. americanum, prompts research questions regarding the potential for this virus to infect S. americanum as well.

Presently, within our research facility, there are ongoing research to investigate the susceptibility of *S. americanum* to TSWV and Tomato brown rugose fruit virus (ToBRFV). The prospect of identifying inherent resistance genes within this plant against these pathogens will serve as a roadmap in engineering resistant crop varieties. Since there are limited research studies

on the susceptibility or resistance of the plant against important plant viruses (for example Tomato leaf curl new Delhi virus-ToLCNDV, and Tomato yellow leaf curl virus- TYLCV), future research directions can be tailored to that.

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