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Review Article

Viruses and viroids in tomato (*Solanum lycopersicum*) and plant growth promoting rhizobacteria as a management alternative

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ABSTRACT

Abstract. Viruses and viroids cause several diseases in tomato (*Solanum lycopersicum*) worldwide, generating important economic losses. About 312 viruses and seven viroids have been associated, of which more than 28 are present in Mexico. Therefore, the use of Plant Growth-Promoting Rhizobacteria (PGPR) can be an effective alternative for the management of viruses and viroids. The genera *Pseudomonas*, *Bacillus*, *Azospirillum*, *Anabena* and *Stenotrophomonas* have been implemented against main viruses reported in tomato: *Cucumber mosaic virus* (CMV), *Tobacco mosaic virus* (TMV), *Tomato chlorotic spot virus* (TCSV), *Tomato mottle virus* (ToMoV), *Tomato spotted wilt virus* (TSWV), *Tomato yellow leaf curl virus* (TYLCV), *Potato virus Y* (PVY), *Groundnut bud necrosis virus* (GBNV), with benefits in decreased incidence and severity up to 80 % and yield increase over 40 %. In Mexico, only *Bacillus* has been used. The use of PGPR is an strategy that could mitigate the impact of viral and viroid diseases and can be integrated into integrated management.

Keywords: ISR, *Solanum lycopersicum*, PGPR, *Pseudomonas*, *Bacillus*, viruses.

The tomato (*Solanum lycopersicum*), native to South America and currently distributed worldwide, is adapted to tropical and temperate conditions (Hanssen and Lapidot, 2012). It is one of the most cultivated vegetables in both greenhouse and open-field settings (Sánchez-del Castillo *et al.,* 2009). Additionally, it stands as one of the most lucrative and globally consumed crops. In 2021, the global harvest reached 256,770,677 tons (FAO, 2023). In Mexico, the cultivation of tomatoes holds significant social and economic importance due to foreign exchange earnings and job generation (Hernández-Martínez *et al*., 2004). However, pathogens and insect pests can compromise its yield and quality (Savary *et al*., 2019). For instance, diseases caused by viruses and viroids result in economic losses worldwide (Ling and Zhang, 2009; Antignus *et al*., 2002). In Mexico, there are only records of losses of up to 80% of viral infections comparing the use of agribon with the control (without management) (Ramírez-Rojas, 2006), so it is important to have accurate information on the economic impact of these pathogens, since detections are constant (Figure 1) and are a latent risk for national production. A global economic impact exceeding $30 billion annually has been estimated for viral diseases affecting economically significant crops (Sastry, 2013a).

Both viruses and viroids can lead to losses in crop production and quality. Therefore, it is crucial to explore management alternatives that ensure direct, effective, and ecologically safe control (Rojas *et al*., 2018). For decades, chemical pesticides have been employed globally in agriculture to control insect pests and

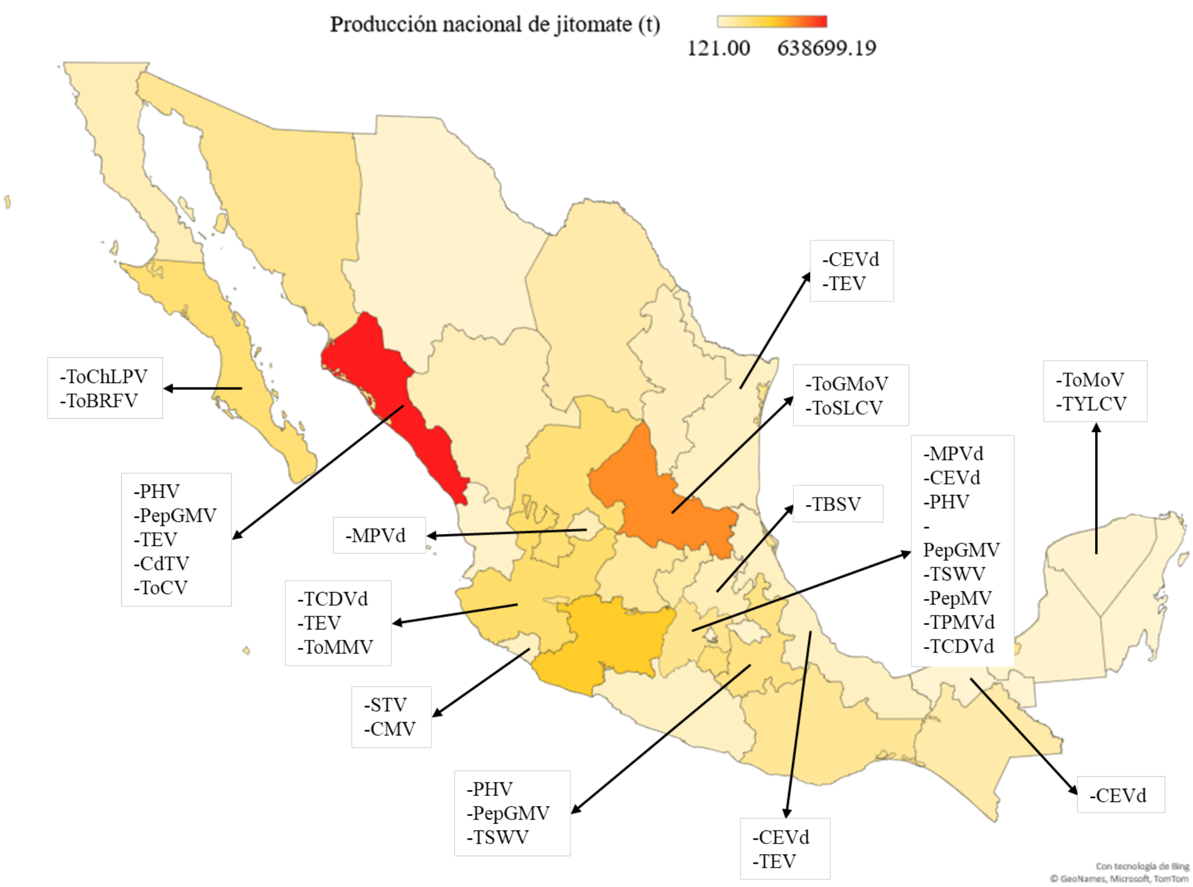

Figure 1. States of the Mexican Republic where viruses and viroids were detected in tomato (See Table 1).

phytopathogens, often applied excessively to both crops and soil, resulting in resistance issues (Karthika *et al*., 2020). Specifically, in the control of diseases caused by viruses and viroids, the use of agrochemicals has been limited to the control of vector insects. However, in recent years, management strategies have shifted towards seeking environmentally friendly alternatives compatible with the surrounding flora and fauna.

Therefore, a comprehensive understanding of these infectious agents and their interaction with hosts is essential to gain knowledge and propose effective management alternatives. While research has been conducted in recent years on the role of Plant Growth-Promoting Rhizobacteria (PGPR) in managing phytopathogenic fungi (Basit *et al*., 2021), little exploration has been done regarding their use in managing viruses and viroids. This exploration aims to reduce the impact of agrochemicals on vector control since, by nature, the best management involves implementing resistant varieties and preventive measures. As a result, the objective of this review is to explore the potential of PGPR for managing viruses and viroids causing diseases in tomatoes, along with examining the current research trends in this field within the country.

Viruses in tomato

Viruses are infectious agents (obligate parasites) composed of nucleic acid (RNA and DNA) enveloped in proteins, capable of replicating within living cells (Hancinský *et al*., 2020). They are exclusively dependent on the host cell's machinery for replication (Sastry, 2013b). Viruses can exhibit various shapes such as rigid and flexible rods, rigid rods, bacilli, polyhedra, geminate, among others (ICTV, 2021).

In 2011, the ten most significant viruses of international importance were identified by the global plant virology community. These included *Tobacco mosaic virus* (TMV), *Tomato spotted wilt virus* (TSWV), *Tomato yellow leaf curl virus* (TYLCV), *Cucumber mosaic virus* (CMV), *Potato virus Y* (PVY), *Cauliflower mosaic virus* (CaMV), *African cassava mosaic virus* (ACMV), *Plum pox virus* (PPV), *Brome mosaic virus* (BMV), and *Potato virus X* (PVX). Notably, six of these viruses infect tomatoes (Scholthof *et al*., 2011). Worldwide, the key viruses causing losses in tomato cultivation comprise *Tomato leaf curl virus* (TYLCV), *Tobacco mosaic virus*, *Beet curly top virus* (BCTV), *Tomato bushy stunt virus* (TBSV), and *Tomato spotted wilt virus* (Sastry, 2013a). Since 2018, the emergence of *Tomato brown rugose fruit virus* (TBRFV) poses a latent threat due to the lack of tolerant varieties and its distribution in major production areas in Mexico (Cambrón-Crisantos *et al*., 2019).

The International Committee on Taxonomy of Viruses (ICTV) has classified viruses into 189 families, 2,224 genera, and 9,110 species (https://talk.ictvonline.

org/taxonomy/) (ICTV, 2021). In tomatoes, approximately 312 viruses have been reported (Rivarez *et al*., 2021), with more than 28 of them documented in Mexico (Table 1). Among the viruses reported in Mexico, ToBRFV, TYLCV, TSWV, *Pepino mosaic virus* (PepMV), and *Tomato wilt virus* (ToMarV) are of greater significance in tomatoes due to their economic impact and prevalence in both field and greenhouse conditions (García-Estrada *et al*., 2022).

Among the primary viruses affecting tomatoes, over 28 viruses belong to the Begomovirus genus (ssDNA) (Hogenhout *et al*., 2008), while the remaining viruses fall into 18 genera. Notably, *Orthotospovirus*, *Potyvirus*, *Tobamovirus*, and

Table 1. Main viruses reported in tomato (*Solanum lycopersicum*) in Mexico and the world.

Family / Genus / Species	Type genome	Reference
Geminiviridae: *Begomovirus* *Pepper golden mosaic virus* (PepGMV), **Tomato chino La Paz virus* (ToChLPV), **Tomato golden mottle virus* (ToGMoV), *Tomato leaf curl Bangladesh virus* (ToLCBV),**Tomato mottle virus* (ToMoV), **Tomato severe leaf curl virus* (ToSLCV), **Tomato yellow leaf curl virus* (TYLCV), *Tobacco leaf curl virus* (TLCV), *Tomato bright yellow mottle virus* (TBYMV), *Tomato enation leaf curl virus* (ToELCV), *Tomato common mosaic virus* (ToCmMV), *Tomato curly stunt virus* (ToCSV), *Tomato chlorotic leaf distortion virus* (ToClLDV), *Tomato chlorotic mottle Guyane virus* (ToCMoGV), *Tomato dwarf leaf virus* (ToDLV), *Tomato golden mosaic virus* (TGMV), *Tomato golden vein virus* (TGVV), *Tomato interveinal chlorosis virus* (ToICV), *Tomato leaf curl New Delhi virus* (ToLCNDV), *Tomato leaf curl Palampur virus* (ToLCPalV), *Tomato leaf curl purple vein virus* (ToLCPVV), *Tomato mosaic Havana virus* (ToMHaV), *Tomato mottle leaf curl virus* (TOMLCV), *Tomato rugose yellow leaf curl virus* (TRYLCV), *Tomato yellow leaf curl Sardinia virus* (TYLCSV), *Tomato yellow mosaic virus* (ToYMV), *Tomato leaf curl virus Arusha virus* (ToLCArV), *Tomato leaf curl Ghana virus* (ToLCGV), **Sinaloa tomato leaf curl virus* (SToLCV), **Tomato leaf curl Sinaloa virus* (ToLCSinV), *Lisianthus enation leaf curl virus* (LELCV), **Chino del tomate virus* (CdTV), **Pepper huasteco yellow vein virus* (PHYVV), **Squash leaf curl virus* (SLCV), **Tomato ápex necrosis virus* (ToANV)	Bipartita, monopartita circular / ssDNA	Green *et al*., 2007; Holguin-Peña *et al*., 2004; Honguin-Peña *et al*., 2007; Mauricio-Castillo *et al.*, 2007; CABI, 2020; Mauricio-Castillo *et al.*, 2007; Cardenas-Conejo *et al*., 2010; Avedi *et al.*, 2021; Idris y Brown, 2007; Rojas *et al.,* 2005: Taniguchi *et al*., 2023; Idris *et al*., 1999; Lugo *et al.,* 2011; Barajas-Ortiz *et al*., 2013; Zuñiga-Romano *et al.*, 2019
Potyviridae: *Potyvirus* **Tobacco etch virus* (TEV), *Potato virus Y* (PVY), *Pepper veinal mottle virus* (PVMV), *Peru tomato mosaic virus* (PTMV); **Tomato necrotic stunt virus* (ToNSV)	Monopartita lineal / ssRNA +	CABI, 2020; Fernandez-Northcote y Fulton, 1980; Li *et al*., 2012
Amalgaviridae: *Amalgavirus* **Southern tomato virus* (SToV)	Lineal / dsRNA	Sabanadzovic *et al.*, 2009
Virgoviridae: *Tobamovirus* **Tobacco mosaic virus* (ToMV), **Tomato brown rugose fruit virus* (ToBRFV), **Tomato mottle mosaic virus* (ToMMV), **Tomato mosaic virus* (ToMV)	Monopartita lineal ssRNA +	CABI, 2020; Cambrón-Crisantos *et al.*, 2019; Zuñiga-Romano *et al.*, 2019

Table 1. Continue...

Family / Genus / Species	**Type genome**	**Reference**
Secoviridae: *Nepovirus* **Tobacco ringspot virus* (TRSV), *Tomato black ring virus* (TBRV)	Bipartita lineal / ssRNA +	CABI, 2020; Perez-Moreno *et al*., 2004
Secoviridae: *Torradovirus* **Tomato torrado virus* (ToTV); *Tomato marchitez virus* (ToMarV), **Tomato chocolate spot virus* (ToChSV), *Tomato chocolate virus* (ToChV)	Bipartita lineal / ssRNA +	CABI, 2020; Verbeek *et al*., 2008
Tombusviridae: *Tombusvirus* **Tomato bushy stunt virus* (TBSV)	Monopartita lineal / ssRNA +	CABI, 2020; De la Torre-Almaráz *et al*., 2004
Closteroviridae: *Crinivirus* **Tomato chlorosis virus* (ToCV), **Tomato infectious chlorosis virus* (TICV)	Bipartita lineal / ssRNA +	CABI, 2020; Méndez-Lozano *et al*., 2012
Tospoviridae: *Orthotospovirus* **Tomato spotted wilt virus* (TSWV), *Chrysanthemum stem necrosis virus* (CSNV), *Pepper necrotic spot virus* (PNSV), *Tomato chlorotic spot virus* (TCSV), *Tomato necrotic ring virus* (TNRV) *Groundnut bud necrosis virus* (GBNV), **Impatiens necrotic spot virus* (INSV)	ssRNA +	CABI, 2020; Nagata y de Ávila, 2000; Suganyadevi *et al*., 2018; Zuñiga-Romano *et al*., 2019; Honguin-Peña *et al*., 2007
Betaflexiviridae: *Carlavirus* *Cowpea mild mottle virus* (CPMMV)	Lineal / ssRNA +	EPPO, 2023
Alphaflexiviridae: *Potexvirus* **Pepino mosaic virus* (PepMV), *Potato virus X* (PVX)	Lineal / ssRNA +	EPPO, 2023; Zuñiga-Romano *et al*., 2019
Tymoviridae: Tymovirus *Eggplant mosaic virus* (EMV)	Lineal / ssRNA +	EPPO, 2023
Secoviridae: *Fabavirus* *Broad bean wilt virus* (BBWV)	Bipartita lineal / ssRNA +	CABI, 2020
Bromoviridae: *Alfamovirus* **Alfalfa mosaic virus* (AMV)	Tripartita lineal / ssRNA	De la Torre-Almaráz *et al*., 2003
Bromoviridae: *Cucumovirus* **Cucumber mosaic virus* (CMV), *Peanut stunt virus* (PSV), *Tomato aspermy virus* (TAV)	Tripartita lineal / ssRNA +	EPPO, 2023; Lecoq y Desbiez, 2012; Zuñiga-Romano *et al*., 2019
Bromoviridae: *Ilarvirus* *Tobacco streak virus* (TSV), *Parietaria mottle virus* (PMoV)	Tripartita lineal / ssRNA +	CABI, 2020
Geminiviridae: Curtovirus *Beet curly top virus* (BCTV)	Monopartita circular / ssDNA	Chen y Gilbertson, 2016

*Viruses reported in Mexico.

Cucumovirus exhibit a higher number of species following the *Begomovirus* genus. In some instances, viruses are transmitted by insect vectors (Figure 2); for instance, Potyviruses are transmitted by aphids, Orthotospoviruses by thrips (Aphidinae) (Gibbs *et al*., 2008; Sastry, 2013b), and Begomoviruses by whiteflies (*Bemisia tabaci*, *Trialeurodes vaporariorum*) (Hogenhout *et al*., 2008). This vector-mediated transmission adds complexity to the management of these phytopathogens.

Typically, symptoms induced by viruses are challenging to identify due to their occurrence in mixed viral infections (Sastry, 2013a). It is evident that these symptoms diminish the vigor, quality, and yield of crops (Figure 3) (Sastry, 2013b).

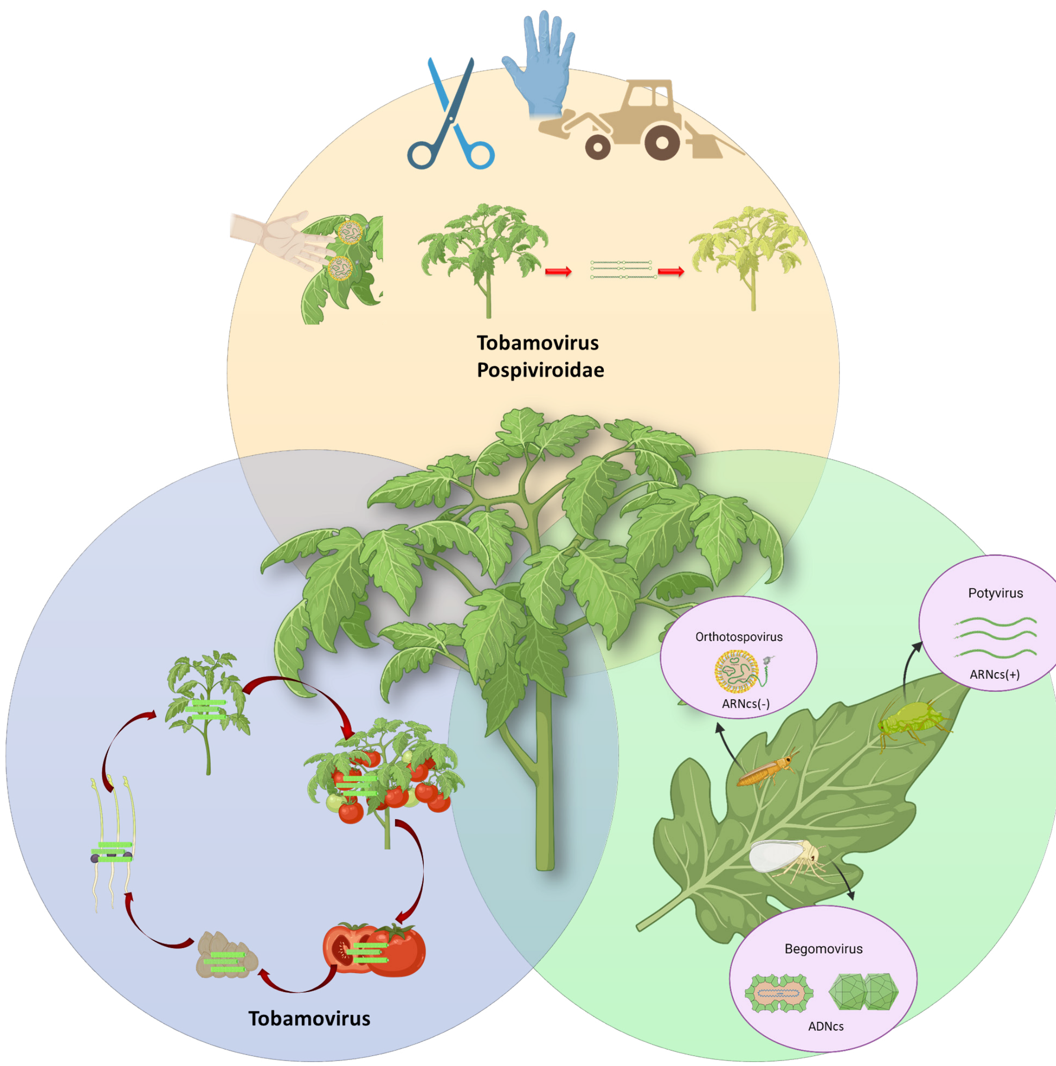

Figure 2. Main forms of transmission of viruses and viroids in tomato. A) Transmission by seed; B) Mechanical transmission, due to the use of work tools, manipulation of plants; C) Transmission by insect vectors.

Figure 3. Symptoms associated with viruses and viroids in tomatoes. A and B) Mosaic, leaf reduction, and mild to severe leaf distortion associated with *Tomato brown rugose fruit virus*; C and D) Stunting, fruit deformation, and purple discoloration in leaves caused by *Mexican papita viroid*; E) Yellow mosaic symptom associated with *Pepino mosaic virus*; F) Symptoms of stunting, deformation, and severe mosaic associated with Begomovirus; G and H) Symptoms of concentric rings and slight fruit deformation associated with Tomato spotted wilt virus; I) Mosaic in leaves caused by *Tobacco mosaic virus*.

Diseases caused by these phytopathogens pose a significant challenge to agriculture. Moreover, imminent climate change and agricultural practices have favored outbreaks of diseases, leading to their spread to unreported or previously unaffected areas (Jones and Naidu, 2019).

Viroids in tomato

Viroids are infectious agents with lower structural and genetic complexity, consisting of a covalently closed circular RNA strand of low molecular weight (246 to 401 nucleotides in length) (Flores *et al*., 1998). Some are pathogenic, while others replicate without inducing symptoms in the host (Flores *et al*., 1998). Most viroids were initially discovered due to the damage they caused in various economically important crops (Flores and Randles, 2003).

The International Committee on Taxonomy of Viruses (ICTV) has classified 33 viroids into two families based on the cellular location of replication: Pospiviroidae (28 species) and Avsunviroidae (five species) (Di Serio and Flores, 2008). Each family consists of genera, and these genera comprise species with numerous sequence variants known as strains (Flores et al., 1998; 2000). Upon entering the host cell, Pospiviroidae move to the nucleus before initiating replication, whereas Avsunsoviroidae replicate in the chloroplasts (Sastry, 2013b).

Since 1988, diseases naturally infected by viroids have been detected in several countries; all of the family Pospiviroidae, such as *Tomato planta macho viroid* (TPMVd) (Galindo *et al.,* 1982), *Mexican papita viroid* (MPVd) which could be considered as a variant of the TPMVd (Verhoeven *et al.,* 2011), *Potato spindle tuber viroid* (PSTVd) (Puchta *et al.,* 1990), *Tomato apical stunt viroid* (TASVd) (Walter *et al.,* 1980; Walter, 1987), *Citrus exocortis viroid* (CEVd) (Mishra *et al.,* 1991; Fagoaga y Duran-Vila, 1996; Verhoeven *et al.,* 2004), *Indian tomato bunchy top viroid* (Mishra *et al.,* 1991) which is considered a CEVd strain (Singh *et al.,* 2003), *Tomato chlorotic dwarf viroid* (TCDVd) (Singh *et al.,* 1999), and *Columnea latent viroid* (CLVd) (Verhoeven *et al.,* 2004). In artificial infections, the tomato was successfully infected with *Chrysanthemum stunt viroid* (CSVd) (Matsushita y Kumar, 2009) and *Pepper chat fruit viroid* (PCFVd) (Table 2) (Verhoeven *et al.,* 2009).

All viroids are transmitted through mechanical inoculation (Sastry, 2013b) and by contact (Figure 2); for instance, through tools used in pruning, via clothing, through crop manipulation, and direct contact between nearby plants (Hammond, 2017). In other cases, transmission occurs through seeds, vegetative propagation, grafting, pollen, and insects (Figure 2) (Verhoeven *et al.,* 2004). The efficiency of viroids in being transmitted through seeds varies among plant and viroid species (Flores *et al*., 2011; Singh *et al*., 2003; Chung and Choi, 2008). Viroid infections

Table 2. Viroids that affect tomato (*Solanum lycopersicum*) in the world.

Species	Found	Symptoms in tomato*	Type of transmission	Losses and incidence	Reference
Tomato planta macho viroid = Mexican papita viroid (TPMVd= MPVd)	México (1982, 2008 and 2020) Canada (2008)	Stunting; chlorosis in the apex, tan or purple leaves, epinasty and severe deformation, reduction in the size and number of fruits and abortion of flowers.	Probable vector *Myzus persicae* Seed by contaminated pollen	Causes significant losses in yield. Incidences of 5% on the crop.	Galindo *et al.,* 1982, 1986; Ling y Zhang, 2009; Mejorada-Cuellar, 2020; Ling y Bledsoe, 2009; Yanagisawa y Matsushita, 2017; Yanagisawa and Matsushita, 2018; Aviña-Padilla *et al*., 2018; Matthews-Berry, 2010; Li y Ling, 2012
Potato spindle tuber viroid (PSTVd)	Discovered in 1922 distributed worldwide but erradicated in most countries. Australia (2011)	Epinasty, chlorosis, violet color with bright yellow central nervation, deformation and reduction in size, brittle, and necrotic central nervation, short internodes, with stunted shoots and necrosis, abortion of flowers, small and hard fruits with dark green spots and irregular maturing	Seed Vector *M. persicae* (Transcap-sidación with *Potato leaf roll virus*)	Reduction of crop biomass and yield by up to 89%. Incidence of 3% in cherry tomato (*S. lycopersicum* cv. Perino).	Owens, 2007; Matthews-Berry, 2010; van Brunschot *et al*., 2014; Yanagisawa y Matsushita, 2017; Matsushita *et al.,* 2011; Diener, 1987; Singh *et al.,* 2003 NSW Government, 2012; Mackie *et al*., 2019
Tomato apical stunt viroid (TASVd)	Israel (1999 y 2000), Some countries in Asia and Africa, several European countries.	Short internodes; deformed, brittle leaves with yellowing; reduction and colorlessness in fruits (pale reddish)		Incidence of almost 100%	Antignus *et al*., 2002, 2007; CABI, 2018; Matsuura *et al*., 2010; Nielsen *et al*., 2012
Citrus exocortis viroid (CEVd)	Distributed worldwide, mainly in citrus fruits	Chlorosis, tanning and distortion, reduction in growth.	Found in commercial seed lots	No reports	Mishra *et al*. 1991; Matthews-Berry, 2010; Verhoeven et al., 2004 Constable *et al.,* 2019
Tomato chlorotic dwarf viroid (TCDVd)	Canada, U.S.A., Mexico, Japan, Hawaii (2017)	Reduction in growth and yellowing (chlorosis) of shoots, deformation of fruits, chlorosis turns bronze-colored, reddish and /or purple, epinasty Death of plants.	By active pollination by bumblebees (*Bombus terrestris and B. ignites*)	100% incidence in greenhouses	Matsushita *et al*., 2008; Singh *et al*., 1999; Ling y Zhang, 2009; Verhoeven *et al.,* 2004 y 2007; Singh y Teixeria, 2006; Olmedo-Velarde *et al*., 2018; Nie, 2012; Matthews-Berry, 2010; Antignus *et al.,* 2007; Matsuura *et al*., 2010; Singh y Dilworth, 2009

Table 2. Continue...

Especie	Found	Symptoms in tomato*	Type of transmission	Losses and incidence	Reference
Columnea latent viroid (CLVd)	Netherlands and Belgium In 2007 in Great Britain and France and in 2011 in Mali.	Severe deformation, tanning and burning of leaves, epinasty, chlorosis and necrosis in nervation, reduction in size or delay in development.	Found in commercial seed lots	Decline in production in Great Britain. Incidence on field of approximately 1.5%.	Nixon et al., 2010; Batuman y Gilbertson, 2013; Matthews-Berry, 2010; Steyer *et al*., 2010; Constable *et al.*, 2019.
Pepper chat fruit viroid (PCFVd)	In 2009 in bell pepper plants and in 2013 in tomato seed shipments	Necrosis in young leaves and necrosis in nervation and petioles, stunting, reduction in fruit size.	Found in commercial seed lots	No reports	Verhoeven *et al*.,2009; Chambers *et al*., 2013; Constable *et al.,*2019

[z]The described symptoms that each viroid can cause can be expressed together or separately in an infected plant.

in commercial tomato crops have been linked to the importation of seeds and ornamental plants (Batuman and Gilbertson, 2013; Van Brunschot *et al*., 2014; Verhoeven *et al*., 2012). Due to the diversity of viroid species, including some endemic ones, and the presence of mixed infections in tomatoes, Mexico represents a center of origin for viroids (Aviña-Padilla *et al*., 2022).

Symptoms induced by viroids in tomatoes depend on the viroid species, cultivar, temperature, and light conditions. Plant responses are additionally influenced by RNA silencing, which plays a significant role in symptom development, combined with structural elements of viroids (Di Serio *et al*., 2013; Flores *et al*., 2015). The variability in symptoms is caused by different forms of gene expression. Moreover, viroid infections may or may not induce symptoms, but they generally lead to chlorosis, bronzing, leaf distortion, stunting, vein clearing, and discoloration, as well as malformation of flowers and fruits, reduced yield, and non-commercial fruit (Figure 1 C and D) (Singh *et al*., 2003; Kovalskaya and Hammond, 2014).

Management of diseases caused by viruses and viroids

There is a global trend towards the consumption of pesticide-free products. Regardless of the agricultural system and phytopathogen, it is ideal to adopt an Integrated Pest Management (IPM) approach that includes measures before, during, and after crop growth. As a first step, the use of virus-resistant cultivars is recommended (Rojas *et al*., 2018), along with cultural sanitation practices as disease management measures (Karthika *et al*., 2020).

The effective control of viruses and viroids involves early detection (diagnosis), eradication, and cultural control methods (Kovalskaya and Hammond, 2014).

Implementing appropriate control measures will help prevent or reduce the severity of viruses and/or viroids in plants. Therefore, diagnosis for virus identification is crucial for implementing management strategies. Diagnostic techniques may include ELISA, immunochromatography or strip tests, nucleic acid hybridization, polymerase chain reaction (PCR), and next-generation sequencers (González-Garza, 2017).

Given the significance of viral and viroidal diseases, alternative approaches have been sought, such as the use of beneficial microorganisms to protect the crop and enhance plant growth and productivity (Sofy *et al.,* 2019).

As mentioned earlier, the use of tolerant varieties has been implemented as part of the management virus and/or viroidal variety; however, in recent years, there has been a growing emphasis on issues related to the induction of natural defenses in plants (Ryals *et al*., 1994; Kloepper *et al*., 2004). The demand for biological products for pest and disease control, along with the use of inducing molecules (elicitors) capable of triggering defense responses in plants, is on the rise (Nasir *et al*., 2014). It should be noted that the magnitude and effectiveness of the induced response will depend on the type of molecule, the signal, or its ability to induce secondary signaling within the tissue (Eder and Cosio, 1994).

By nature, plants possess the ability to defend themselves against phytopathogens through the production of substances that prevent or reduce damage caused by microorganisms. This response is triggered by plant-pathogen recognition after a local infection, where plants activate defense responses systemically to increase the magnitude and speed of the response against the pathogen (Delgado-Oramas, 2020). Induced resistance is a state where plants enhance their defenses against phytopathogen attacks and are triggered by the stimulation of chemical and/or biological inducers (Choudhary *et al*., 2007). In general, induced resistance can function for the control of a broad spectrum of phytopathogens (Kloepper, 1993). Two types of pathogen-induced resistance are known in plants: Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR) (Camarena-Gutiérrez and Torre-Almaráz, 2007).

Induced Systemic Resistance (ISR). The activation of ISR requires the signaling of salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Beneduzi *et al*., 2012; Pieterse *et al.*, 2014). These products coordinately transduce extracellular stimuli recognized by host cell receptors into a large number of target molecules that integrate specific intracellular responses to external stimuli (Walters, 2009; Delgado-Oramas, 2020; Jankiewicz and Koltonowicz, 2012; Choi *et al*., 2014). ISR has been observed in various plant species as part of defense reactions against fungi, bacteria, and viruses (Camarena-Gutiérrez and de la Torre-Almaráz, 2007).

Signaling pathways mediated by ET, AJ, AS and their interaction. The signaling pathways mediated by SA, JA, and ET do not operate independently (Maldonado-Cruz *et al*., 2008; Derksen *et al*., 2013). Through a cascade of signals from mitogen-activated protein kinases (MAPKs), the activation of ethylene-insensitive genes 1, 2, and 3 (EIN1, EIN2, and EIN3) occurs, regulating gene expression in response to pathogens and injuries (Zhu *et al*., 2011). In a study on mustard (Sinapis alba), it was demonstrated that ethylene, in interaction with the mitochondrial alternative oxidase pathway (AOX), induces systemic resistance to Turnip mosaic virus (TuMV). This is attributed to the potential limitation of the virus's systemic infection and its accumulation in the plant (Zhu *et al*., 2011).

Jasmonate signaling plays a crucial role in the induction of defense genes in plants against pests (Garnica *et al*., 2012). The gene for coronatine-insensitive protein (COI1) serves as a central regulator in the JA signaling pathway. Upon binding with Jasmonoyl-Isoleucine (JA-Ile), it facilitates the release of the transcription factor MYC2, leading to the transcription of genes responsive to jasmonates (Garnica *et al*., 2012). Evidence suggests that the expression of the COI1 gene and the N gene in the tobacco-TMV interaction imparts resistance to TMV (Liu *et al*., 2004).

Salicylic acid (SA) is a pivotal signaling molecule in intracellular signal transduction. In addition to contributing to the release of H2O2 and its active oxygen derivatives, it can induce the expression of genes related to defense (Shirasu *et al*., 1997).

Induced Systemic Response in tomato against phytopathogenic viruses mediated by PGPR. The need to ensure crop quality and high yields with low environmental impact has led to the emergence of different inputs formulated with microorganisms, among which the use of Plant Growth-Promoting Rhizobacteria (PGPR) can be highlighted (González *et al.,* 2018; Canchignia *et al*., 2015). These microorganisms enhance Systemic Resistance Induction (SRI) and are saprophytic bacteria that live freely in the rhizosphere. By colonizing the plant root system, they contribute through secretions, vitamins, hormones, and other growth factors that help improve plant growth and productivity (Walters, 2009). What is interesting is their use of the CVRs on foliage and seeds, observing different benefits (Table 3, Figure 4).

Most bacteria reported as Plant Growth-Promoting Rhizobacteria (PGPR) belong to the genera *Pseudomonas* and *Bacillus*. Additionally, bacteria from the following genera have been reported: *Aeromonas*, *Agrobacterium*, *Arthrobacter*, *Alcaligenes*, *Azospirillum*, *Azoarcus*, *Azotobacter*, *Burkholderia*, *Bradyrhizobium*, *Comamonas*, *Cyanobacteria*, *Enterobacter*, *Gluconacetobacter*, *Pizobielonas*, *Serratia*, *Variovorax*, *Streptomyces*, and *Xanthomonas* (Vessey, 2003).

Table 3. Plant growth-promoting rhizobacteria species used for virus management in tomato.

Viruses	PGPR	Result obtained	Reference
Cucumber mosaic virus (CMV)	*Pseudomonas fluorescens, Serratia marcescens*	Reduction in the area under the disease progress curve in diseased plants treated.	Raupach *et al*., 1996
	Bacillus amyloliquefaciens (IN937a), *B. subtilus* (IN937b), *B. pumilus* (SE34)	Symptom reduction from 38% to 58% with PGPR, compared with 88% to 98% without PGPR.	Zehnder *et al*., 2000, 2001
	B. pumilus (SE34), *B. amyloliquefaciens* (IN937a), *B. subtilus* (IN937b), *B. pumilus* (INR7, T4)	Infection rate from 27.5 (SE34) to 85% (T4), compared with control (87.5%). It favored the growth of plants and protected them against the virus.	Murphy *et al*., 2003
	Azospirillum lipoferum (MRB16), *A. brasilienses* (SP7), *A. brasilienses* (N040), *Anabena oryzae*	Infected and treated plants increased their greenhouse yield to 48% and field yield to 40%.	Dashti *et al*., 2007
	P. aeruginosa, *Stenotrophomonas rhizophilia*	Promoted vegetative growth and yield. Prevented infection in 91% of plants.	Dashti *et al*., 2012
Tobacco mosaic virus (TMV)	*Pseudomonas* spp. (B-25)	Promoted plant growth and yield. Reduced the incidence of the virus in plants.	Kirankumar *et al*., 2008
	Bacillus spp.	Favored the development of roots in infected tobacco plants.	Wang *et al*., 2009; Choi *et al*., 2014
	Bacillus amyloliquefaciens (TBorg1)	90 % reduction in virus buildup. Increased total soluble carbohydrates, proteins and ascorbic acid.	Abdelkhalek *et al.*, 2022
	P. fluorescens SM90 y *B. subtilis* DR06	Increased defense-related genes NPR1, COI1 AND PR1-a, promotes growth in plants infected with the virus.	Sharaf *et al*., 2023
Tomato chlorotic spot virus (TCSV)	*B. amyloliquefaciens* (IN937a) *B. pumilus* (SE34) + *B. amyloliquefaciens* (IN937a) *B. pumilus* (SE34) + *B. sphaericus* (SE56) + *B. amyloliquefaciens* (IN937a)	It reduced severity in the field and was the treatment that best controlled the disease.	Abdalla *et al*., 2017
Tomato mottle virus (ToMoV)	*B. amyloliquefaciens* (IN 937a) *B. subtilis* (IN 937b) *B. pumilus* (SE34)	Reduced the incidence of the virus in plants by 30%. Reduced the development of symptoms and incidence.	Murphy *et al*., 2000; Zehnder *et al*., 2001

Table 3. Continue...

Viruses	PGPR	Result obtained	Reference
Tomato spotted wilt virus (TSWV)	*P. fluorescens* (CHA0) *P. fluorescens* (CHA0+CoT-1) *P. fluorescens* (CHA0+CoT-1+CoP-1)	Increased yield and growth of infected and treated plants. Reduced the viral load.	Kandan *et al.* 2005; 2002
	B. amyloliquefaciens (MBI600)	Reduced the incidence of the virus by 80%.	Beris *et al*., 2018
Tomato yellow leaf curl virus (TYLCV)	*Enterobacter asburiae* (BQ9)	Reduced the severity in treated and infected plants by 52%.	Li *et al*., 2016
Potato virus Y	*Bacillus amyloliquefaciens* (strain MBI600)	Reduced the systemic accumulation of viruses.	Beris *et al*., 2018
Groundnut bud necrosis virus (GBNV)	*Bacillus amyloliquefaciens* (VB7)	Reduced symptoms by around 84%.	Vanthana *et al*., 2019

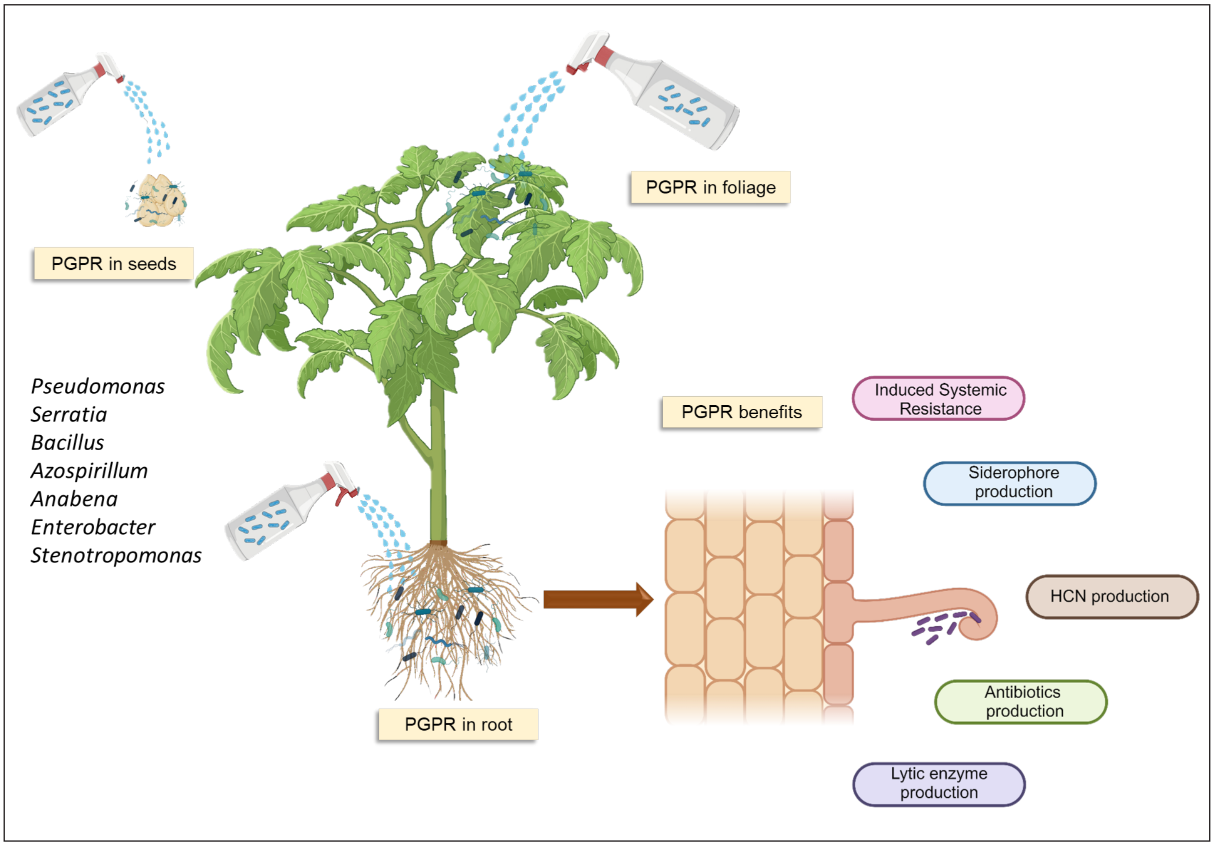

Figura 4. Forms of application and mechanisms of action of Plant Growth-Promoting Rhizobacteria (PGPR) used to protect tomatoes from viral infections.

There are studies on the use of PGPR employed as microbial inoculants to protect tomato plants against viral infections, where, additionally, an increase in crop yield was recorded (Table 3). For instance, in Mexico, Samaniego *et al*. (2017) and Hernández-Santiago *et al*. (2020) reported that the application of *Bacillus* to infected tomato plants not only led to an increase in plant height and weight but also induced systemic resistance. In recent years, research on Systemic Resistance Induction (SRI) using PGPR against economically relevant viruses (20 viruses) in various crops has gained significance (Sofy *et al*., 2019). However, despite efforts to counteract viruses, research remains scarce, particularly in the case of viroids. The work has mainly focused on crops such as *Musa* spp., *Vigna unguiculata*, *V. mungo*, *Vicia faba*, *Momordica charantia*, *Cucumis sativus*, *Citrullus lanatus*, *Solanum lycopersicum*, *S. tuberosum*, *Capsicum annuum*, *Nicotiana tabacum*, *N. tabacum* cv. *Xanthi*-nc, *Arabidopsis thaliana*, *Chenopodium quinoa*, *Helianthus annuus*, *Phaseolus vulgaris*, *Datura metel*, and *Cucurbita maxima* (Sofy *et al*., 2019).

There are other microorganisms, such as endophytic fungi (*Trichoderma* spp.), which are also resistance inducers in plants, and they are even sold as biocontrollers of phytopathogenic fungi by companies in Mexico, to be applied to various crops. However, the use of these microorganisms and their effect on infected plants by viruses and viroids has been shallowly studied. Nevertheless, some species of rhizosphere and endophytic fungi seem to have a favorable effect as plant growth promoters in virus-infected tomato plants (Ramos-Villanueva *et al*., 2023).

Conclusions

Diseases caused by viruses and viroids impact the yield and quality of tomatoes, as well as other economically significant crops worldwide. In Mexico, there are records of over 28 viruses, mostly belonging to the Begomovirus genus. However, research on Plant Growth-Promoting Rhizobacteria (PGPR) in tomatoes as inducers of resistance against these pathogens or to enhance crop health is limited. The use of *B. subtilis* has been reported for controlling *Tobacco mosaic virus* in tomatoes (Samaniego *et al*., 2017; Hernández-Santiago *et al*., 2020). Globally, PGPR such as *Pseudomonas*, *Serratia*, *Bacillus*, *Azospirillum*, *Anabena*, *Enterobacter*, and *Stenotropomona* have been evaluated against nine virus species in tomatoes, with a focus on *Cucumber mosaic virus*. Nevertheless, it is essential to strengthen such research due to the significance of tomato cultivation in Mexico. Promisingly, PGPR has demonstrated effects in reducing incidence and severity by up to 80%. Additionally, a yield increase of up to 48% has been recorded compared to plants without PGPR application. Therefore, the use of growth promoting microorganisms are a promising alternative for integration into an integrated management of viral infections, given its compatibility with the environment and experimentally effective for the control of a variety of viruses.

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