



## Natural co-infection of *Pospiviroid machoplantae* and *Begomovirus solanumseveri* in tomato

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**Section:**

Periodical edition

**Received:**

March 08, 2026

**Accepted:**

July 19, 2026

**Published:**

July 27, 2026

**Citation:**

Zuñiga-Romano MC, Ochoa-Martínez DL, Rojas-Martínez RI, Aranda-Ocampo S, Ortega-Acosta C, et al. 2026. Natural co-infection of *Pospiviroid machoplantae* and *Begomovirus solanumseveri* in tomato. Mexican Journal of Phytopathology 44(3): 128. <https://doi.org/10.18781/R.ME.X.FIT.2603-1>

### ABSTRACT

**Background/Objective.** High whitefly populations and incidence of up to 90% of tomato plants showing mosaic, intervenial chlorosis, deformation, rugosity and leaf necrosis, associated with virus and viroids, were observed at a high-tech greenhouse in Atlacomulco, State of Mexico. To identify the viruses or viroids associated with these symptoms, the whitefly species, as well as to determine if the insects were carrying any of these pathogens, monthly sampling was conducted over a two-year period, collecting plant leaf tissue and adult whiteflies.

**Materials y Methods.** A total of 347 plants (211 symptomatic and 136 asymptomatic) were analyzed using immunostrips for impatiens necrotic spot virus (*Orthotospovirus impatiensnecromaculae*), tomato spotted wilt virus (*O. tomatomaculae*), tobacco mosaic virus (*Tobamovirus tabaci*), tomato mosaic virus (*T. tomatotessellati*), pepino mosaic virus (*Potexvirus pepini*) and cucumber mosaic virus (*Cucumovirus CMV*), as well as by RT-PCR and PCR using universal primers for viroids and viruses of the genera *Pospiviroid* and *Begomovirus*, respectively. DNA was extracted from the insects and analyzed by PCR with specific primers that amplify a fragment of the mitochondrial gene (mtCOI) to identify the whitefly species, as well as universal primers for begomoviruses to determine if the insects were carriers of these viruses.

**Results.** The results obtained using immunostrips were negative. The fragments amplified by RT-PCR and PCR were sequenced and corresponded to tomato planta macho viroid (*Pospiviroid machoplantae*) and tomato severe leaf curl virus (*Begomovirus solanumseveri*). Of the plants analyzed, 49.56% tested positive for the pospiviroid, 23.9% for the begomovirus, and 8.93% for both. Infection caused solely by the viroid was the only one that resulted in an asymptomatic condition. *Bemisia tabaci* was identified as the whitefly species and was determined to be a carrier of *B. solanumseveri*.

**Conclusions.** Symptoms of mosaic, intervenial chlorosis, leaf deformation and necrosis, blistering, and rugosity observed in tomato plants were associated with individual infection by tomato planta macho viroid (*Pospiviroid machoplantae*), and tomato severe leaf curl virus (*Begomovirus solanumseveri*), as well as co-infection by both. This is the first report of natural co-infection of tomato planta macho viroid and tomato leaf curl virus. The presence of asymptomatic plants is a key factor to consider when carrying out cultural practices to minimize mechanical transmission of the viroid.

**Keywords:** Mixed infection, Viral-viroidal, Pospiviroids, Whitefly, *Solanum lycopersicum*



## INTRODUCTION

In Mexico, the tomato (*Solanum lycopersicum*) is one of the most important horticultural crops, with a production of 3.7 million tons in 2024. Currently, 66% of the country's tomato production takes place under covered cultivation, the rest is produced in open fields and approximately 5% is exported to the United States of America (SIAP, 2025). Viruses are an important limitation for this crop, since it directly affects fruit production and quality (Rojas *et al.*, 2005a). The main viruses that affect tomato belong to the *Bromoviridae*, *Potyviridae*, *Virgaviridae*, *Alphaflexiviridae*, *Secoviridae*, *Closteroviridae*, *Bunyaviridae* and *Geminiviridae* families (Afouda *et al.*, 2013; Hanssen *et al.*, 2010; Massumi *et al.*, 2009). Within the latter one, viruses from the *Begomovirus* genus are widely distributed in tropical and subtropical areas (Rojas *et al.*, 2005b) and they are persistently transmitted by the whitefly (*Bemisia tabaci*) (Polston *et al.*, 2014). The begomoviruses are composed of one or two circular single-strand DNA molecules of approximately 2.6 kb each, surrounded by a twinned icosahedral capsid, approximately 18 nanometers in diameter (Brown *et al.*, 2015). The begomoviruses detected thus far in tomato crops in Mexico are the *Begomovirus coheni* (tomato yellow leaf curl virus), *B. solanumflavi* (the tomato yellow leaf curl China virus), *B. capsicumhuastecoense* (pepper huasteco yellow vein virus), *B. solanumaureivariati* (tomato golden mottle virus) and the *B. solanumseveri* (tomato severe leaf curl virus) (Brown and Idris, 2006; González-Pérez *et al.*, 2024; Idris *et al.*, 2007; Zuñiga-Romano *et al.*, 2019).

On the other hand, to date there are at least seven reported viroids of the *Pospiviroidae* family that infect tomato naturally: *Pospiviroid exocortiscitri* (citrus exocortis viroid), *P. latenscolumnneae* (columnnea latent viroid), *P. parvicapsici* (pepper chat fruit viroid), *P. fusituberis* (potato spindle tuber viroid), *P. apicimpeditum* (tomato apical stunt viroid), *P. chloronani* (tomato chlorotic dwarf viroid) and *P. machoplantae* (tomato planta macho viroid) (Zhang and Groth, 2024).

It has been proven that the coinfection of different pathogens in the same host does exist, such as of phytoplasmas and begomoviruses in eggplant (*Solanum melongena*) (Venkataravanappa *et al.*, 2018) and the simultaneous infection of viruses such as *Potyvirus yituberosi* (potato virus Y), *Crinivirus flavisolani* (potato yellow vein virus) y *Potexvirus ecspotati* (potato virus X) in potato (García *et al.*, 2019). Mixed infections between viruses and viroids have also been reported in grapevine (*Vitis vinifera*), such as *Foveavirus rupestris* (grapevine stem pitting-associated virus), *Marafivirus syrahense* (grapevine Syrah 1 virus) and the viroids *Hostuviroid impedi humuli* (hop-stunt viroid) and *Apscaviroid alphaflavivitis* (grapevine yellow speckle viroid 1) (Al Rwahnih *et al.*, 2009; Giampetruzzi *et al.*, 2012; Jo *et al.*, 2015; Seguin *et al.*, 2014). Up to 12 different viruses and viroids have been identified in tomato (*Pospiviroid parvicapsici* and *P. latenscolumnneae*) (Choi *et al.*, 2020). Co-infections can cause greater severity, which can lead to a strong reduction in production, with a significant effect on the crop yields (Hameed *et al.*, 2014).

In Mexico, mixed infections have been found, caused by two or more species of begomoviruses or with viruses of another genus in the chili pepper crop (Anaya *et al.*, 2003; Reveles *et al.*, 2012). In the tomato crop under greenhouse conditions, the co-infection of two viroids has been reported: tomato planta macho viroid (*Pospiviroid machoplantae*), for some time erroneously known as the Mexican papita viroid, and the tomato chlorotic dwarf virus (*P. chloronani*) (Ling and Zhang, 2009). Lugo *et al.* (2011) found the co-infection of tomato yellow leaf curl virus (*Begomovirus coheni*) and squash leaf curl virus (*B. cucurbitapeponis*), whereas González-Pérez *et al.* (2024) reported the co-infection of

tomato mosaic virus (*Tobamovirus tomatotessellati*), tomato golden mosaic virus (*Begomovirus solanumaureimusi*) and Pepper huasteco yellow vein virus (*B. capsicumhuastecoense*).

In a high-technology tomato production greenhouse located in Atlacomulco, State of Mexico, an incidence was observed of up to 90% of plants with mosaic, inter-venial chlorosis, deformation, necrosis, blistering and leaf roughness in different stages of crop development, which affect fruit yield and quality. This situation has appeared in different crop cycles, therefore the aim of this investigation was to identify viruses or viroids associated with these symptoms, as well as the species of whitefly in question.

## MATERIALS AND METHODS

**Collect of plant material and whiteflies.** Every month for two years, leaf tissue was collected from symptomatic and asymptomatic tomato plants showing the alterations mentioned earlier in a high-technology greenhouse located in Atlacomulco, State of Mexico. The sampled plants were of different ages, and the number of collected plants every month varied, depending on the frequency with which the symptoms appeared. Likewise, in each sampling, leaves were taken from plants that showed no symptoms as a reference. The samples were wrapped in absorbent paper and placed in plastic bags to be transported to the laboratory, where they were stored at 4 °C until processing. In the base of the plants with symptoms, Moëricke traps were placed, containing water + liquid soap (1000:1 v/v), to collect insects in 15 mL Falcon tubes with 96% ethanol every week, from which whitefly adults were taken for their molecular identification by PCR and sequencing.

**Detection of viruses and viroids.** The samples were analyzed using ImmunoStrips® (Agdia Inc.) for impatiens necrotic spot virus (*Orthotospovirus impatiensnecromaculae*), tomato spotted wilt virus (*O. tomatomaculae*), tobacco mosaic virus (*Tobamovirus tabaci*), tomato mosaic virus (*T. tomatotessellati*), pepino mosaic virus (*Potexvirus pepini*) and cucumber mosaic virus (*Cucumovirus CMV*), following the manufacturer's instructions. Additionally, total nucleic acids were extracted from 0.1 g of leaf tissue from plants with and without symptoms, following the protocol by Dellaporta *et al.*, (1983) from all the samples analyzed in the study period. In the case of whitefly, the method used was CTAB 2%, from four samples, each composed of five adult individuals, following the methodology described by Zuñiga-Romano *et al.*, (2019). RT-PCR and PCR (GoTaq® Flexi DNA Polymerase, Promega®) were carried out with universal oligonucleotides Pospiviroid For and Pospiviroid Rev for viroids of the *Pospiviroid* genus (Bostan *et al.*, 2004). For retrotranscription, the M-MLV RT (Promega®) enzyme was used for 1 h at 42 °C, and subsequently, at 95 °C for 3 min to denature the enzyme; PCR was carried out with 30 cycles of 30 s at 92 °C, 30 s at 62 °C and 90 s at 72 °C with a final extension of 10 min at 72 °C; for viruses of the *Begomovirus* genus, primers AV494 and AC1048 were used (Wyatt and Brown, 1996) with the following amplification conditions: 35 cycles of 1 min each at 92 °C, 20 s at 60 °C and 30 s at 72 °C. The amplified products were separated and visualized by 1% agarose gel electrophoresis with GelRed® Nucleic Acid Stain 10,000X, Biotium, as an intercalating agent.

**Identification of whitefly.** In order to identify the whitefly species, a PCR (GoTaq® Flexi DNA Polymerase, Promega®) was carried out with oligonucleotides LCO1490 and HCO2198 (Folmer, 1994), which amplify a ~710 bp fragment of the mitochondrial gene of

subunit I of cytochrome C oxidase (mtCOI). Likewise, in order to find out whether the whiteflies were begomovirus carriers, the four samples composed of five adults were analyzed using PCR under the conditions mentioned earlier for these viruses. The amplified fragments were purified using Wizard® SV Gel and PCR Clean-Up System (Promega®) following the manufacturer's instructions and nine pospiviroid and eight begomovirus samples were sequenced in MacroGen®. The obtained sequences were compared with those in GenBank® and incorporated into this database.

**Phylogenetic analysis.** For the *Begomovirus* genus, the phylogenetic tree was created in MEGAX, using the Neighbor-Joining method and the Tajima-Nei model, with 1,000 Bootstrap replications. As an external group, the alfalfa leaf curl virus (*Capulavirus medicaginis*) was used. For the case of the *Pospiviroid* genus, the phylogenetic tree was created using the Tamura 3-parameter model, and *Coleus blumei* viroid 1 (*Coleviroid alphacolei*) was used as an external group.

## RESULTS AND DISCUSSION

**Gathering plant material and whitefly.** The main symptoms observed in the collected leaves were mosaic, inter-venial chlorosis, leaf deformation and necrosis, blistering and roughness (Figure 1). These symptoms have been associated with infections caused by begomoviruses and viroids in tomato crops (Garzón *et al.*, 2002; Holguín *et al.*, 2004; Hammond, 2017; Škorić, 2017).

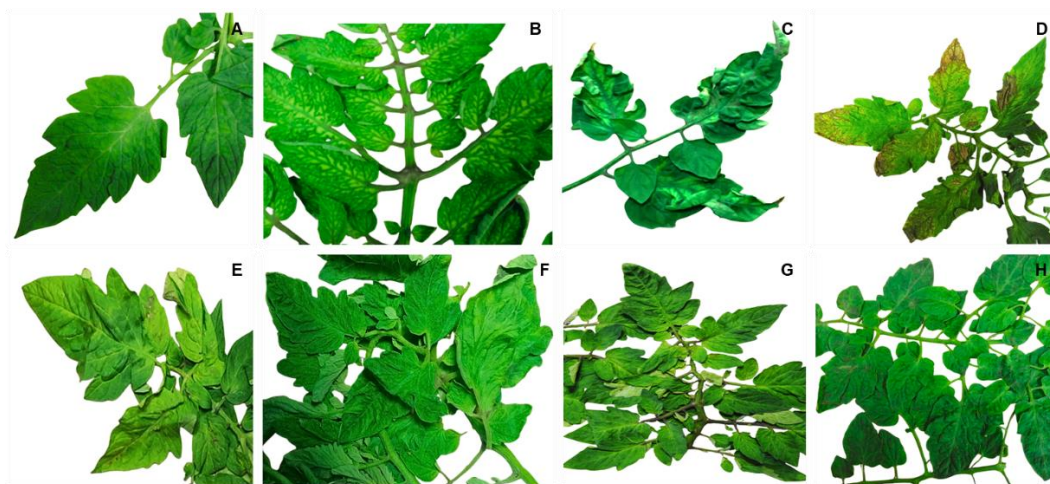


**Figure 1.** Symptoms observed in tomato plants associated with begomoviruses. **A.** Mosaic; **B.** Interveinal chlorosis; **C.** Leaf deformation; **D.** Necrosis; **E.** Chlorosis with blistering; **F.** Chlorosis with leaf deformation; **G.** Chlorosis with rugosity; **H.** Rugosity with mild mosaic.

**Detection of viruses and viroids.** In the two years of sampling, a total of 347 plants were analyzed (211 with and 136 without symptoms) and all were negative to the ImmunoStrips® tests for the viruses analyzed. Regarding the PCR tests, out of the 211 samples with symptoms, 97 were only positive to *P. machoplantae*, 83 samples only to *B. solanumseveri* and 31 samples were positive for both pathogens (co-infection). In addition, out of the 136 samples that showed no symptoms, 75 turned out positive to the viroid (asymptomatic plants) and 61 turned out negative to the infection by the viroid or begomovirus (healthy plants).

The fragments amplified by RT-PCR (~200 bp) and PCR (~550 bp) for the *Pospiviroid* and *Begomovirus* genus (Figure 2A, 2B), had a similarity of 100% with *Pospiviroid machoplantae* and between 97.24 and 97.83% with different isolates of *Begomovirus solanumseveri* (accession number MK3235269, MK 325270, MK325268, KC479066 and KX51835), respectively. For the case of the analyzed whiteflies, the expected product was obtained for begomovirus and its sequences had an identity of 99% with two *B. solanumseveri* isolates (accession numbers: PX582709 and PX582710).

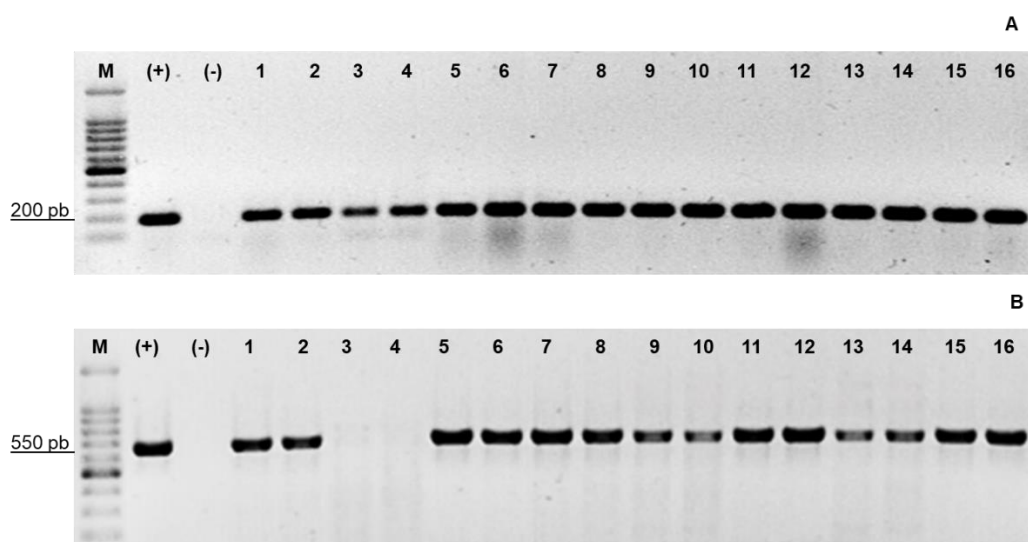


**Figure 2.** 1% agarose gel electrophoresis of PCR products. **A.** RT-PCR products obtained using universal primers for viroids of the genus *Pospiviroid* (~200 bp). Lane M: 100 bp molecular marker (Promega®); Lane (+): positive control (sample positive for *Pospiviroid machoplantae*); Lane (-): negative control (water); Lanes 1-16: processed samples; **B.** PCR products obtained using universal primers for viruses of the genus *Begomovirus* (~550 bp). Lane M: 100 bp molecular marker (Promega®); Lane (+): positive control (sample positive for *Begomovirus abelsmoschusmexicoense*); Lane (-): negative control (water); Lanes 1-16: processed samples.

In this study, out of the total of plants analyzed (347) with DNA amplification in the thermocycler, 49.56% turned out positive to the viroid, which may be due to the ease with which these pathogens are mechanically transmitted (Hadidi *et al.*, 2022), with their leaves and stems being the most important sources of inoculum, due to the cultural practices carried out in this crop, from the production of seedlings, transplanting, pruning and staking, among others, that can be crucial in the mechanical transmission of viroids, along with contaminated tools (Flores *et al.*, 2021; Škorić, 2017). Out of the samples that turned out positive to the viroid, 56.4% displayed symptoms and 43.6% were asymptomatic, possibly due to differences in the viroid load during inoculation or detection, as well as to the different moments in which the infection could have taken place, since it is generally established that this is more efficient in young plants than in adult plants. The presence of asymptomatic plants, positive for the viroid, is a factor that can contribute in important ways to its spreading, since its asymptomatic condition can go unnoticed, and this is perhaps the reason some control practices (desinfesting tools, for example) are carried out less strictly.

On the other hand, 23.9% of samples were positive for *B. solanumseveri*, whose transmission is not mechanical, but it is efficient, due to the *Bemisia tabaci* species complex (Polston *et al.*, 2014). This percentage is lower than for plants positive to the viroid,

probably due to the control of insects performed in the greenhouse in which this study was conducted.

The results of this investigation show, for the first time, the natural co-infection (8.9% of plants with symptoms) of the tomato planta macho viroid with the severe tomato curl begomovirus. Co-infections have been proven to appear frequently and naturally, giving rise to infections that can be synergistic or antagonistic (Chávez-Calvillo *et al.*, 2016; Kwon *et al.*, 2023). In some coinfections, an asymmetric antagonism is observed, due to the competition between the pathogens to become established in the plant, frequently leading to one of them accumulating in a higher concentration (Mascia and Gallitelli, 2016). This aspect must be studied to understand what takes place in the planta macho viroid/tomato severe curl virus. On the other hand, most cases of viral diseases report low percentages of co-infection regarding the number of plants infected with individual viruses (Ling and Zhang, 2009; González-Pérez *et al.*, 2024), similar to the results in this investigation.

This investigation involved the sampling and analysis of 136 asymptomatic samples and negative controls. However, part of them turned out positive for the viroid. Asymptomatic infections caused by these pathogens have been documented in several cases (Hammond, 2017; Owens and Verhoeven, 2017; Rodríguez *et al.*, 2017) as in citrus fruits in which, using biological trials and RT-PCR (Palacios and Figueroa, 2024), the co-infection of the exocortis viroid (*Pospiviroid exocortiscitri*) as found, along with cachexia viroid (*Hostuviroid impedihumuli*) in citrus fruits, both in plants with and without symptoms (Palacios and Figueroa, 2023). Citrus exocortis viroid can be found from the nursery, commonly without symptoms, and after four years, symptoms begin to manifest themselves (Duran-Vila, 2004) possibly, among other factors, to the citrus species and the pattern used. Likewise asymptomatic plants have been reported in viral infections, both in co-infections involving the potato yellow vein virus (*Crinivirus flavisolani*) and potato virus Y (*Potyvirus yituberosi*), and in single infections with potato virus X (*Potexvirus ecspotati*) (García and Franco-Lara, 2015) in the potato crop (*Solanum tuberosum* and *Solanum phureja*). Finally, no specific symptoms associated with the presence of the virus, the viroid or the co-infection were observed, which could be due to different factors, including the order in which pathogens infect and the inoculum load that affects the type and the expression of symptoms (González-Jara *et al.*, 2005; Tatineni *et al.*, 2010; Wintermantel *et al.*, 2008).

**Identification of whitefly.** The whitefly adults collected in the Moëricke traps belonged to the *Bemisia tabaci* species, according to the molecular analysis of the mitochondrial gene (mtCOI) and its sequence had an identity of 99% with this species. The sequences of the samples of this investigation were registered in the GenBank with accession numbers PX565212 and PX565213.

**Phylogenetic analysis.** Nine sequences were recorded in the GenBank (accession numbers OL409105 to OL409113) of the gene of the coat protein that had a 99% similarity with the *Begomovirus solanumseveri* (Figure 3A), which were broadly related with isolates from the State of Mexico (accession number MK325270) and from Ixcaquixtla, Puebla (accession number KC479066 y KC479065), the latter of which have an identity of 98% with an isolate of the Guatemala severe tomato leaf curl (accession number AF130415) (Hernández *et al.*, 2013; Zuñiga-Romano *et al.*, 2019). Seven sequences that amplified with the universal oligonucleotides for viroids of the *Pospiviroid* genus (accession numbers

OL409098 to OL409104), had a similarity of 100% with a *Pospiviroid machoplantae* (accession number MW960968) isolate from de Ixmiquilpan, Hidalgo, and they formed a group, along with *Mexican papita viroid* and *P. machoplantae* (Figura 3B) isolates, taken from wild solanaceae collected in Aguascalientes, Mexico, and from tomato cv. Rutgers tissue from Chapingo, State of Mexico, respectively (Kiefer *et al.*, 1983; Martínez-Soriano *et al.*, 1996). Although for many years *Mexican papita viroid* and *P. machoplantae* were considered different species, later studies proved that they are the same species, currently accepted and named as *Pospiviroid machoplantae* (Verhoeven *et al.*, 2011; Zerbini *et al.*, 2023).

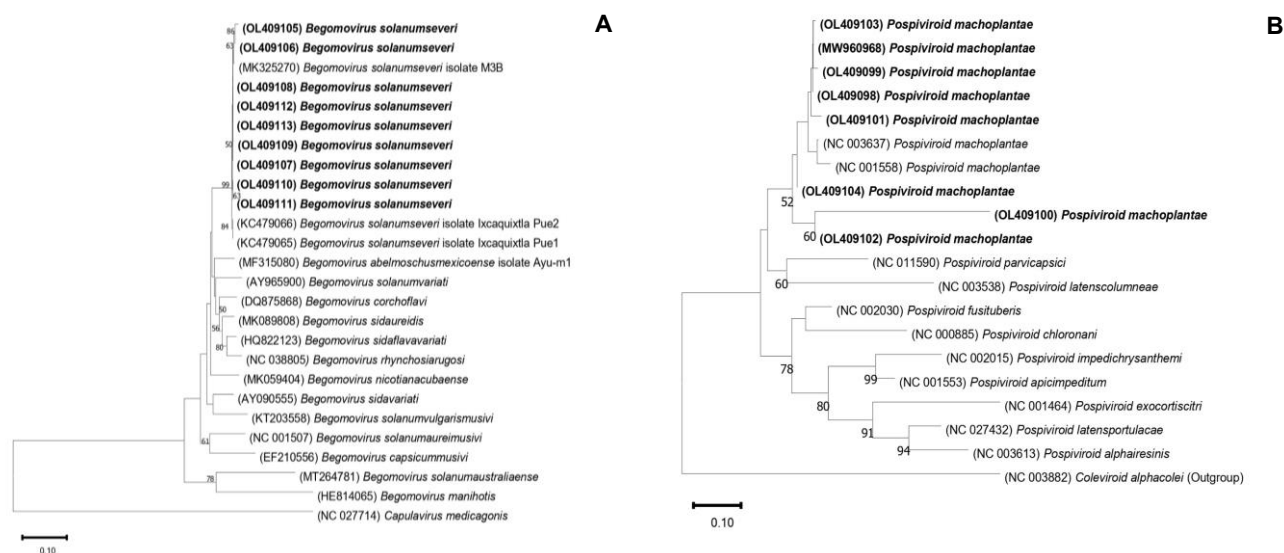


**Figure 3.** Phylogenetic tree constructed using the Neighbor-Joining method based on partial sequences of *Begomovirus solanumseveri* and *Pospiviroid machoplantae* from the isolates obtained in this study. **A.** For *B. solanumseveri* the Tajima-Nei model was used with 1,000 bootstrap replicates in the MEGAX program, and *Capulavirus medicaginis* was used as the outgroup; **B.** For *P. machoplantae* the Tamura 3-parameter model was used with 1,000 bootstrap replicates in the MEGAX program, and *Coleviroid alphacolei* was used as the outgroup.

## CONCLUSIONS

The symptoms of mosaic, intervenial chlorosis, leaf deformities and necrosis, blistering and roughness in tomato plants were associated to *Pospiviroid machoplantae*, *Begomovirus solanumseveri* or the coinfection of both pathogens. No symptom was found to be associated with any of the pathogens found or with their co-infection. *Bemisia tabaci* is the species of whitefly found in tomato crops as a possible carrier of the begomovirus. The asymptomatic condition observed solely in the infection of the planta macho viroid must be studied in order to understand the implications it can have in its spreading, distribution and management within the greenhouse. This is the first report of the natural co-infection of tomato planta macho viroid with tomato severe leaf curl virus in tomato.

**Conflict of interest.** The authors declare to have no conflict of interest regarding the research, authorship and/or publication of this Article.

**Acknowledgements.** To the Consejo Nacional de Ciencia y Tecnología (National Science and Technology Council - CONACYT) for the scholarship granted to the main author. To the Colegio de Postgraduados' Graduate Program in Phytosanitary Sciences-Plant Pathology, for the opportunity to pursue graduate studies.

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