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Review Article

Alternaria in Mexico: Morphological and molecular characterization, associated diseases, and management strategies

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ABSTRACT

Justification. Within the genus *Alternaria*, several phytopathogenic species stand out for causing diseases such as leaf spot and blight in hosts including fruit trees, cereals, vegetables, and ornamental plants, resulting in significant economic losses. Despite this issue, information on the genus *Alternaria* in Mexico is limited and scattered. Therefore, the objective of this review was to describe the current status of the genus *Alternaria* in Mexico through a compilation of published studies on the characterization of reported pathogenic species, the diseases they cause in plants, and the various control strategies employed.

Theoretical and experimental framework. Traditional identification of the genus *Alternaria* is based on morphological characteristics observed in culture; however, intra- and interspecific variability limits its accuracy. Consequently, molecular tools such as PCR, sequencing, and phylogenetic analysis are used to distinguish species and establish more precise evolutionary relationships. In Mexico, this genus affects more than 20 agricultural and ornamental hosts across 15 states, causing diseases in chrysanthemum, papaya, cacti, broccoli, pepper, and tomato, with incidences exceeding 40% in some crops. Its management requires an integrated approach combining accurate diagnosis, rational use of fungicides, strategies based on crop phenology and inoculum density, and sustainable alternatives such as biological control, plant extracts, microalgae, and nanoparticles, which have shown high efficacy and reduced environmental impact.

Conclusions and Perspectives. In Mexico, nine species have been reported affecting 23 cultivated hosts, although information gaps remain for ornamental, forest, and native species. The main challenges for their control stem from incorrect disease diagnosis, which limits the application of effective strategies.

Keywords: Phytopathogenic fungus, Diagnosis, Control, Leaf blight, Leaf spot

JUSTIFICATION

Phytopathogenic species of the genus *Alternaria* are of economic, environmental, agronomic, and phytopathological importance worldwide. They cause economically significant losses by inducing diseases known as leaf spot and blight in approximately 4,000 plant species of all ages. The main symptom consists of a dark lesion with concentric rings on the leaves of various hosts, including vegetables, fruit trees, cereals, cruciferous crops, and ornamental plants (Ogada *et al.*, 2021).

In addition, some *Alternaria* species produce secondary metabolites such as phytotoxins associated with pathogenicity, as well as mycotoxins including tenuazonic acid (TeA), alternariol (ALT), patulin, and alternariol monomethyl ether (AME), which can affect up to 50% of agricultural products and compromise food safety. These compounds are also difficult to remove during food processing, and even at low concentrations, mycotoxins exhibit carcinogenic, mutagenic, and cytotoxic activity. Furthermore, they are considered allergens and are associated with respiratory tract infections, causing asthma in humans (Patriarca, 2016; Bacha *et al.*, 2023; He *et al.*, 2024).

Given the negative effects that *Alternaria* species can have on plant health—and consequently on human health—it is essential to explore new management strategies for pathogenic species. However, information on this subject in Mexico is limited; therefore, the objective of this review was to describe the current status of the genus *Alternaria* in Mexico by compiling published studies on reported phytopathogenic species, the diseases they cause in plants, and the various control strategies available.

THEORETICAL AND EXPERIMENTAL FRAMEWORK

Bibliographic analysis. A systematic review of the scientific literature available at the time of writing was conducted to gather information on the characterization, associated diseases, and management strategies of *Alternaria* species in Mexico. Scientific articles in English and Spanish were searched using databases such as PubMed, Redalyc, Scopus, SciELO, and Google Scholar. The search included scientific publications from 1990 to 2025. The keywords used were "Alternaria" AND "identificación" AND "México", "Alternaria" AND "enfermedad" AND "México", and "Alternaria" AND "control" AND "México".

Morphological characterization of *Alternaria*. *Alternaria* was originally described by Nees in 1816, with the type species *A. tenuis*. The initial descriptions were compiled in the taxonomic key of Simmons (2007), in which 275 species were recognized. The fungus is characterized by colonies of gray, brown, or black coloration, with hyphae that are hyaline, brown, or olive; setae are absent, and stromata are rarely formed. Conidiophores are brown, solitary or in fascicles, bearing conidia that are ovoid, cylindrical, ellipsoid, or obclavate, olive to brown in color. They exhibit transverse septa and may or may not present longitudinal or oblique septa. On average, conidia measure 45(–70.5) × 6.5–15.5(–17) µm (Figure 1) (Watanabe, 2002; Simmons, 2007; Woudenberg *et al.*, 2013).

Morphological characterization of *Alternaria* begins with isolation and culturing on selective media such as Malt Extract Agar (MEA) and Sabouraud Agar, as well as non-selective media such as Potato Dextrose Agar (PDA), Potato Carrot Agar (PCA), Corn Meal Agar

(CMA), and V8 Agar (Rivas and Mhulhauser, 2014; Blagojevic *et al.*, 2020; Yessimseitova *et al.*, 2025). The macroscopic morphological characteristics considered for identification include colony color, colony margin, texture, and mycelial form. Microscopic characterization requires direct observation under light microscopy, focusing on the morphology of conidiophores, conidiogenous cells, and conidia; branching and arrangement of conidiophores; septation patterns; and chlamydospores. Morphometric characteristics are also essential, including conidial size, number of transverse and longitudinal septa, and the length of conidiophores and chlamydospores (Barnett and Hunter, 1998; Simmons, 2007).

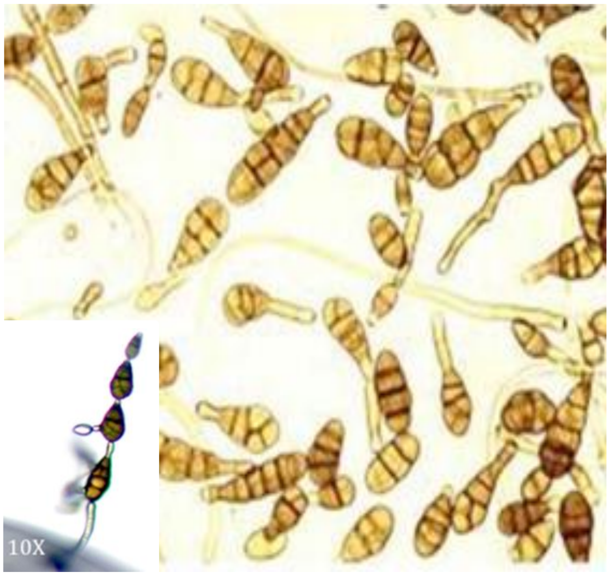

Figure 1. Conidia of *Alternaria alternata*. Taken from Montiel-Salero *et al.* (2022).

According to the morphological characteristics of this genus, species were previously classified into two categories—large-spored and small-spored—the latter including the section *Alternaria*, where *A. arborescens* and *A. alternata* are found (De Mers, 2022). The terms *formae speciales* and pathotypes have been adopted for some of these species; in the case of *A. alternata*, at least seven pathotypes have been described, each producing specific toxins depending on the host (Akimitsu *et al.*, 2014). Currently, morphological characteristics alone are insufficient for organism identification due to the difficulty in distinguishing species, which arises from intraspecific polymorphisms and interspecific similarities, compounded by their sensitivity to environmental variation (Ghoneem *et al.*, 2023).

Molecular characterization of *Alternaria*. Currently, DNA-based analytical techniques such as PCR and high-throughput sequencing, as well as multilocus gene amplification and phylogenetic analysis, are required for the molecular characterization of *Alternaria* species (Ghoneem *et al.*, 2023). The main multilocus genes used as molecular markers for species identification in *Alternaria* include the nuclear small subunit ribosomal RNA (SSU), the nuclear large subunit ribosomal RNA (LSU), the internal transcribed spacer (ITS), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), RNA polymerase II, the second largest subunit of RNA polymerase II (RPB2), elongation factor 1-alpha (TEF 1-alpha), major

Alternaria allergen (Alt A1), endopolygalacturonase (Endo PG), anonymous genetic region (OPA 102), calmodulin (CAL), and eukaryotic orthologous group (KOG) (Woudenberg *et al.*, 2015; Jayawardena *et al.*, 2019).

Molecular phylogeny is a valuable tool for resolving paraphyletic taxa within *Alternaria* clades; this implies that groups of species defined by morphological characteristics do not always correlate (He *et al.*, 2024). Therefore, various methods are used to determine phylogenetic relationships among species, such as Maximum Parsimony, Maximum Likelihood, and/or Bayesian Inference (Tovar-Pedraza *et al.*, 2024). Due to the challenge of distinguishing morphospecies based on gene sequences, whole-genome sequencing technologies can now be applied to identify genes that may serve as biomarkers for differentiating these species (Dang *et al.*, 2015). The National Center for Biotechnology Information (NCBI) currently lists two publicly available genomes of *Alternaria*: *A. brassicicola*, sect. *Brassicicola* (BioProject PRJNA34523), and *A. arborescens*, sect. *Alternaria* (BioProject PRJNA78243) (Woudenberg *et al.*, 2015).

***Alternaria* species complex.** The genera *Alternaria*, *Chalastospora*, *Crivellia*, *Embellisia*, *Nimbya*, *Stemphylium*, *Ulocladium*, *Undifilum*, and *Sinomyces* are included within the *Alternaria* species complex, as they are closely related; however, after taxonomic revision, all of these genera—except *Stemphylium*—have been placed in synonymy with *Alternaria*. This complex includes saprophytic, endophytic, and pathogenic species (Woudenberg *et al.*, 2013). Furthermore, due to taxonomic updates based on molecular studies, species formerly classified in *Chalastospora* have been reassigned to *Alternaria* (e.g., *Alternaria cetera* syn. *Chalastospora cetera*). The section *Chalastospora* is characterized by simple or branched conidiophores bearing brown, ellipsoid or ovoid conidia, lacking transverse septa and only rarely presenting longitudinal septa; conidia may occur singly or in chains (Woudenberg *et al.*, 2013). This section has been associated with nodular granulomatous dermatitis in domestic animals as well as plant species (Norris *et al.*, 2021).

The section *Crivellia* is characterized by primary conidiophores that may be straight or curved, simple or branched, bearing straight or curved conidia with transverse septa; microesclerotia or chlamydospores may also be present (Woudenberg *et al.*, 2013; Lawrence *et al.*, 2016). This section includes *A. penicillata*, the sexual state of *Brachycladium penicillatum*.

Within the section *Embellisia* is *A. embellisia*, the causal agent of bulb canker in garlic (*Allium sativum*). Conidiophores are described as simple or branched, bearing brown conidia with two to six transverse septa and one or two longitudinal septa, and chlamydospores occurring in pairs or chains (Delgado-Ortiz *et al.*, 2019). In the case of the genus *Nimbya*, it is included within the section *Alternantherae*, with species that are now placed under the genus *Alternaria* (e.g., *A. alternantherae* syn. *N. alternantherae*) (Woudenberg *et al.*, 2013). However, the section *Nimbya* also exists, within which *A. cypericola* is found; it presents branched, septate hyphae with straight or curved, ovoid to ellipsoid, brown conidia that are generally solitary but may form chains of two to three conidia. Conidiophores are macronematous, solitary, straight or slightly curved, septate, and brown. This species is associated with plants in the families Juncaceae and Cyperaceae (Ahmadpour *et al.*, 2021).

The genus *Stemphylium* is represented in various sections of the *Alternaria* species complex and is associated with diseases in crops such as onion, where it causes brown lesions on leaves, leading to defoliation and reduced productivity due to impaired photosynthesis (Hay *et al.*, 2021). This genus corresponds to the anamorphic state of *Pleospora* spp. (Simmons, 1985). The species *S. vesicarium* presents septate, branched, hyaline hyphae with smooth walls; conidiophores are solitary, simple, straight or slightly curved, smooth except for roughening at the apical cell; conidia are brown, oblong, oval, rounded at the apex, and verrucose (Kádasi *et al.*, 2024).

Ulocladium is a genus that, according to Kidd and colleagues (2022), includes saprophytic species that affect fruits and cause plant diseases, and only rarely affect humans. Colonies may range in color from black to olive or gray, with geniculate conidiophores producing multicellular conidia that are generally solitary, obovate, brown, and possess roughened walls. The species *U. atrum* has been tested as an antagonist of *Sclerotinia sclerotiorum*, demonstrating the ability to grow over the pathogen; however, it did not parasitize the sclerotia (Li *et al.*, 2003).

The section *Undifilum* includes endophytic species. The conidia present are ovate to elongate-ellipsoid, and the septa may be thick. This section shares some characteristics with *Embellisia*; however, it is distinguished by the formation of undulating, branching germ tubes and by the production of the toxic compound swainsonine (Woudenberg *et al.*, 2013). Species in this section may be found in *Astragalus* sp. and *Oxytropis sericea* (Cook *et al.*, 2009; Baucom *et al.*, 2012).

Distribution and main symptoms caused by *Alternaria* in Mexico

Several *Alternaria* species of agricultural and ornamental importance have been reported, causing diseases such as leaf spot and blight (Palemón-Alberto *et al.*, 2024). Among the affected species are onion (Reyes-Tena *et al.*, 2023), chrysanthemum (*Chrysanthemum morifolium*) (Domínguez-Serrano *et al.*, 2016), and papaya (*Carica papaya*) (Vásquez-López *et al.*, 2012). In cacti, *Alternaria* is associated with golden spot disease and black spot (Montiel-Salero *et al.*, 2022; Chavarría-Cervera *et al.*, 2024). At least 10 different *Alternaria* species are officially known in Mexico, affecting 23 economically important hosts distributed across 15 states (Table 1). However, knowledge of the fungus's broader distribution in crops of interest, as well as in alternate hosts, remains limited.

The importance of this fungus depends on the incidence and severity it can generate in different crops. For example, leaf spot caused by *Alternaria* in chrysanthemum crops has been reported with incidences of up to 30%, presenting symptoms as circular or oval lesions on the leaf margins, brown to black in color with yellow halos, along with other leaves turning completely yellow (Domínguez-Serrano *et al.*, 2016). In onion (*Allium cepa*) crops, leaf blight shows an incidence of 20% in summer, with symptoms consisting of brown and purple spots on the leaves, whereas in winter, incidence may reach up to 80%, with purple foliar spots and dry lesions. These symptoms affect bulb growth (Reyes-Tena *et al.*, 2023).

Table 1. Phytopathogenic *Alternaria* species reported in crops in Mexico.

Species reported	Host	Geographic area	Reference
A. alternata, *A. tenuissima*	*Chrysanthemum morifolium*	Yucatán	Dominguez-Serrano *et al*., 2016
A. limicola	*Citrus paradisi*, *C. aurantium, C. macrophylla* y *C. sinensis*	Colima	Palm & Civerolo, 1994
A. alternata	*Triticum* spp.	Sonora	Mata-Santoyo *et al*., 2018
A. tomato	*Helianthus annuus*	Yucatán	Poudel *et al*., 2019
A. alternata	*Fragaria×ananassa*	Guanajuato	Mariscal-Amaro *et al*., 2017
A. alternata	*Carica papaya*	Guerrero	Vásquez-López *et al*., 2012
A. tenuissima, A. alternata	*Brassica oleracea*	Guanajuato	Fraire-Cordero *et al*., 2010
A. alternata	*Opuntia matudae*	Hidalgo	Montiel-Salero *et al*., 2022
A. alternata	*Avena sativa*	Tlaxcala	Leyva-Mir *et al*., 2014
A. embellisia	*Allium sativum*	Coahuila	Delgado-Ortiz *et al*., 2019
A. alternata	*Brassica oleracea* var. *italica*	Guanajuato	Arratia-Castro *et al*., 2022
A. solani	*Solanum lycopersicum*	Chiapas	Quiroga-Madrigal *et al*., 2007
A. tenuissima	*Salix bonplandiana*	Estado de México	González-Díaz *et al*., 2011
A. chrysanthemi	*Chrysanthemum morifolium*	Yucatán	Villanueva-Couoh *et al*., 2004
A. alternata	*Jatropha curcas*	Sinaloa	Espinoza-Verduzco *et al*., 2012
A. alternata	*Solanum lycopersicum*	Sinaloa	Félix-Gastelum & Gálvez-Figueroa, 2002; Troncoso-Rojas *et al*., 2005
A. tenuissima	*Malus* x *domestica*	Chihuahua	Madrid-Molina *et al*., 2023
A. solani	*Capsicum chinense*	Yucatán	Cristóbal *et al*., 2006
A. alternata	*Allium cepa*	Michoacán	Reyes-Tena *et al*., 2023
A. alternata	*Ficus carica*	Morelos	Saavedra *et al*., 2020
A. alternata	*Opuntia ficus-indica*	Colima	Chavarría-Cervera *et al*., 2024
A. arborescens	*Capsicum pubescens*	Guerrero	Palemón-Alberto *et al*., 2024
Alternaria sp.	*Vaccinium* sp.	Michoacán	Mondragón-Flores *et al*., 2012
A. solani, A. alternata	*Capsicum annuum*	Chihuahua	Guigón-López *et al*., 2001
A. alternata	*Cyamopsis tetragonoloba*	Sinaloa	García-León e*t al*., 2024
Alternaria spp.	*Capsicum annuum*	Sinaloa	Guerrero-Santana & Vega-Camargo, 2024
A. burnsii, A. destruens	*Plumeria obtusa*	Sinaloa	Márquez-Licona *et al*., 2025
A. alternata	*Vaccinium corymbosum*	Sinaloa	Nuñez-García *et al*., 2025

Sinaloa is a major agricultural state with high production of crops such as maize, bean, pepper, and tomato, and it has documented problems caused by this fungus. Black mold on mature tomato fruits (*Solanum lycopersicum*) caused by *A. alternata* has been reported, with severity varying according to humidity conditions during fruit ripening. When prolonged periods of dew, rainfall, or high relative humidity occur, *A. alternata* conidia germinate in response to soluble nutrients present on the fruit surface. Disease symptoms range from small, light brown superficial lesions to sunken necrotic lesions, and a black layer of conidia develops on the infected tissue (a sign of the pathogen). This represents an economic loss for producers when disease incidence exceeds 8% (Félix-Gastélum and Gálvez-Figueroa, 2002). Additionally, *A. alternata* has been reported causing soft rot and sunken lesions in tomato fruits, as well as leaf spot in guar (*Cyamopsis tetragonoloba*) (Félix-Gastélum and Gálvez-Figueroa, 2002; García-León *et al.*, 2024). *Alternaria* spp. also cause leaf spot in sesame (García-Espinoza, 2022) and fruit rot in pepper (Guerrero-Santana and Vega-Camargo, 2024).

Alternaria not only affects foliage and fruits but can also cause inflorescence blight in *Jatropha curcas*, induced by *A. alternata* in Sinaloa, where small dark brown lesions coalesce into larger necrotic areas, leading to flower drop (Espinoza-Verduzco *et al.*, 2012). In chile (*Capsicum annuum*) nurseries and seeds, it induces early damping-off in Aguascalientes and Zacatecas, Mexico, in association with *Alternaria*, *Fusarium*, and *Rhizoctonia* (Velásquez-Valle *et al.*, 2007).

On the other hand, weeds are important as hosts of this fungus when they are found associated with or near economically relevant crops. For example, in Sinaloa, leaf blight (caused by *Alternaria* spp.) has been reported in wild tobacco (*Nicotiana glauca*), which grows along irrigation canals and drainage ditches. Symptoms on the leaves include irregular light to dark brown lesions. Severity increases when daily periods of leaf wetness range from 15 to 18 h and temperatures fluctuate between 14 and 28 °C. Species of *Alternaria* in the section *Alternata* are associated with leaf blight in tabaquillo (*Nicotiana trigonophylla*) and black nightshade (*Solanum nigrum*), while *Alternaria ricini* has been associated with leaf blight in wild castor bean (*Ricinus communis*) and foliar lesions in tabacón (*Nicotiana glauca*) and wild tobacco (Figure 2D–E) (Félix-Gastélum *et al.*, 2023).

Generally, this fungus exhibits characteristic symptoms; however, it has also been reported in association with other fungi. For example, black spot in prickly pear (*Opuntia ficus-indica*) is caused by a complex involving *Alternaria alternata*, *Corynespora cassiicola*, and *Neocytalidium dimidiatum*. Among these, *A. alternata* has shown incidences of up to 60%, with symptoms including softening of cladodes and circular to irregular black lesions (Figure 2C) (Chavarría-Cervera *et al.*, 2024). The same pathogen is responsible for golden spot disease, described in Mexico in *O. matudae* (xoconostle), producing lesions on cladodes characterized by yellowing or chlorosis near the areoles, which later develop into a golden spot that progresses to tissue necrosis (Figure 2A) (Montiel-Salero *et al.*, 2022).

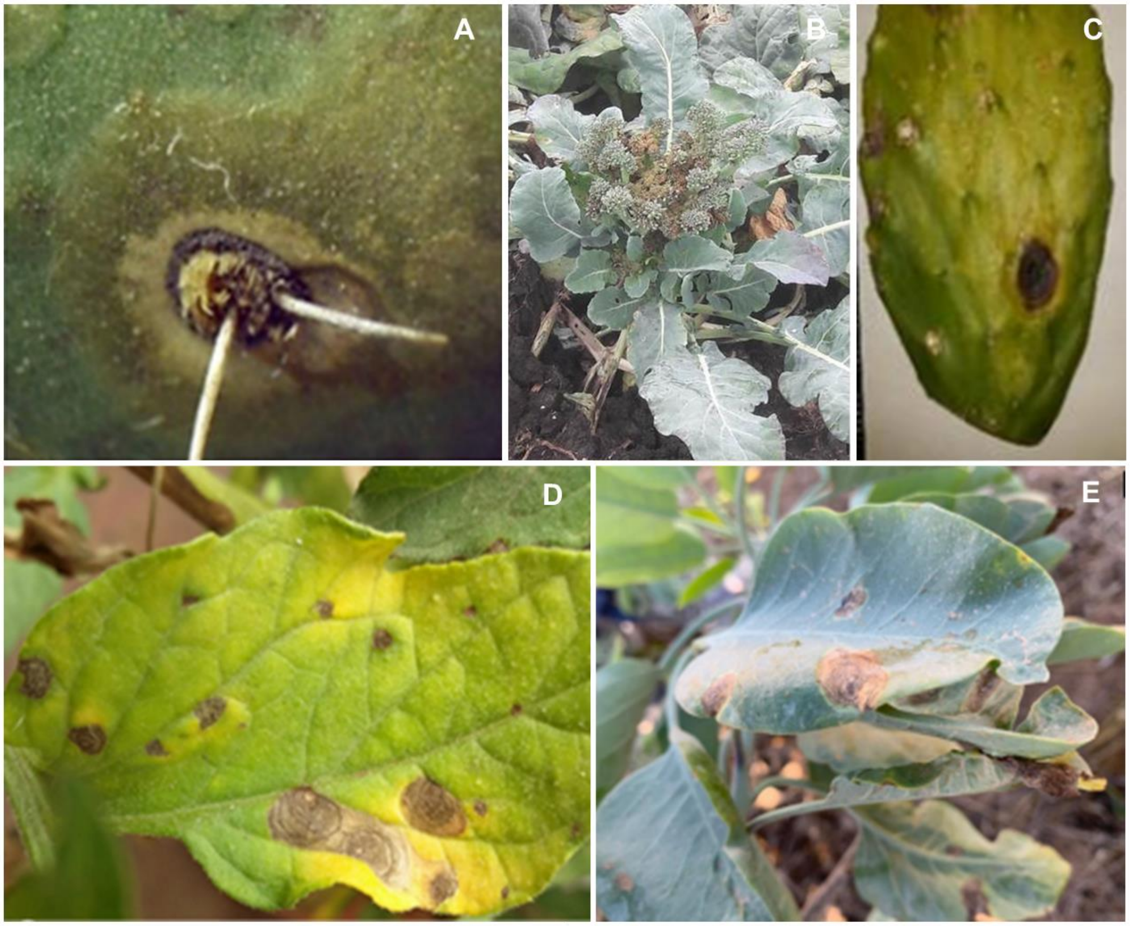

Figure 2. Diversity of diseases associated with *Alternaria* spp. A) Symptoms of golden spot in *Opuntia matudae* caused by *A. alternata* (Taken from Montiel-Salero *et al.*, 2022); B) Symptoms of broccoli floret rot caused by *A. alternata* (Taken from Arratia-Castro *et al.*, 2022); C) Symptoms of black spot in *Opuntia ficus-indica* caused by *A. alternata* (Taken from Chavarría-Cervera *et al.*, 2024); D) Symptoms caused by *Alternaria* sp. in wild tobacco; and E) in tobacco (*Nicotiana glauca*) (Taken from Félix-Gastélum *et al.*, 2023).

Another case of association with other fungi is floret rot in broccoli (*Brassica oleracea* var. *italica*), which reduces crop quality and yield. Under conditions of high relative humidity (70%) and temperatures of 30 °C, losses exceed 40% (Arratia-Castro *et al.*, 2022). *Alternaria tenuissima*, *A. alternata*, and *Fusarium oxysporum* were identified as the causal agents of the disease in the commercial varieties Marathon, Patron, and Monaco in Guanajuato (Fraire-Cordero *et al.*, 2010). Arratia-Castro *et al.* (2022) reported the association of *A. alternata*, *F. verticillioides*, and *F. oxysporum* as causal agents of broccoli floret rot (Figure 2B).

Management strategies

To establish control measures, it is necessary to diagnose the causal agent of the disease in order to implement management strategies appropriate for each crop. For integrated management, at least three approaches are typically applied: chemical, cultural, physical, and biological control. The latter includes the use of biological control agents, plant extracts, and microalgae. Although chemical control is the most effective option, its improper use has led to contamination of agroecosystems, in addition to posing public health risks due to the handling of these products (Zavaleta-Mejía, 1999; Zepeda-Jazo, 2018).

Chemical control. This is one of the methods most widely used by agricultural producers due to its high efficacy and rapid results. The main chemical groups used for the control of *Alternaria* spp. are triazoles, which include propiconazole. This systemic fungicide inhibits radial mycelial growth and conidial germination, as does the mixture of azoxystrobin + cyproconazole, belonging to the methoxyacrylate and triazole groups (Ramírez-Jiménez *et al.*, 2025). The combination of these two chemical groups has also been evaluated with azoxystrobin + epoxiconazole, which delays senescence in wheat plants, induces an increase in the antioxidant enzyme superoxide dismutase, and reduces O_2 levels (Wu and Tieddmann, 2001).

Among the carboxamides, Captan inhibits mycelial growth by interfering with cellular respiration, thereby hindering mycelial development; it also translocates to various tissues when applied to seeds or soil. Likewise, dithiocarbamates such as mancozeb modify and inactivate proteins involved in DNA translation and transcription (Zarate-Ramos *et al.*, 2022). Chloronitriles (chlorothalonil) reduce mycelial growth by competing with glyceraldehyde-3-phosphate for the active site of glyceraldehyde-3-phosphate dehydrogenase and by reducing fungal glutathione molecules to alternative forms. In addition, the degradation of this compound into byproducts that bind to target sites has been observed (Fairchild *et al.*, 2013).

Although in some cases fungicides with the same mode of action are applied to the same crop or pathogen, studies have shown that *Alternaria* species exhibit cross-resistance to mancozeb, tebuconazole, iprodione, fludioxonil, and cyprodinil in Greece (Malandrakis *et al.*, 2015), and to mancozeb and difenoconazole in China. This suggests that the use of non–site-specific fungicides may lead to reduced pathogen sensitivity and a greater capacity to cause disease, representing a risk to agricultural production (Yang *et al.*, 2019).

The systemic fungicide Amistar GS® (azoxystrobin) at 500 ppm is also used against *A. chrysanthemi*, reducing foliar damage intensity by 50% and being associated with lower infection rates compared with other synthetic fungicides (Villanueva-Couoh *et al.*, 2004). In postharvest fruits and *in vitro*, benzyl isothiocyanate has been used with favorable results at 0.1 mg mL^{-1} and 0.56 mg mL^{-1}, serving as an efficient controller in fruits without affecting quality (Troncoso-Rojas *et al.*, 2005). However, it is important to consider the timing of agrochemical applications during flowering or fruit development and the persistence of these compounds in fruits to avoid postharvest residues.

Similarly, *in vitro* evaluations have been conducted with Fosetyl-aluminum (800 ppm), Azoxystrobin (500 ppm), Imazalil (750 ppm), Prochloraz (450 ppm), Benomyl (500 ppm), and Thiabendazole (600 ppm). However, only Imazalil and Prochloraz demonstrated 100% effectiveness against *Alternaria* sp. (Herrera *et al.*, 2011). This suggests possible resistance of *Alternaria* species to certain agrochemicals. Therefore, studying the resistance acquired by *Alternaria* species in the country to commercially available products is necessary.

In Sinaloa, azoxystrobin was evaluated *in vitro* at doses of 7 and 10 ppm; although it inhibited up to 99.5% of conidial germination in *Alternaria alternata*, it did not reduce mycelial growth (Félix-Gastélum and Gálvez-Figueroa, 2002). Nevertheless, chemical control is not environmentally friendly, as it causes environmental contamination and poses health risks to consumers due to toxic residues in food, as well as to workers who are in direct contact with the chemicals (Rangel-Ortíz *et al.*, 2023). Therefore, the integration of additional management strategies is necessary.

Chemical control based on crop phenology. Although limited information exists in Mexico regarding prediction systems based on crop phenology, environmental variables, and inoculum density for initiating preventive applications of chemical fungicides against diseases caused by *Alternaria* species, studies from other countries provide insight into the efficient use of fungicides. In Mexico, stages of highest incidence and severity caused by *Alternaria* have been identified in onion crops; however, information on the practical application of these findings remains scarce (Reyes-Tena *et al.*, 2023). In Israel, periods of greatest susceptibility to *A. alternata* in apple cultivation were determined through the development of a phenology-based management strategy. Synchronizing fungicide applications with the stage of maximum fruit susceptibility proved effective for controlling *Alternaria* rot, allowing optimization of fungicide use, cost reduction, and minimization of resistance issues (Lior *et al.*, 2018).

On the other hand, inoculum load is an important factor to consider in preventive management with chemical fungicides. For example, inoculum load influences the severity of leaf spot caused by *A. brassicae* in cauliflower; therefore, effective disease management requires controlling the amount of inoculum in the soil, maintaining constant monitoring, and considering inoculum load as a key factor when interpreting the efficacy of chemical control (Sunitha and Jha, 2023).

Biological control. Various microorganisms have been evaluated as biological control agents against phytopathogenic fungi, with *Trichoderma* being the most extensively studied genus. In Mexico, the main species reported as biocontrol agents against phytopathogenic *Alternaria* species are *T. harzianum*, *T. asperellum*, and *T. viride* (Allende-Molar *et al.*, 2022). This genus employs several mechanisms to suppress the growth and development of phytopathogens: (1) antibiosis, through the production of secondary metabolites that alter the permeability of phytopathogen lipid membranes; (2) competition for space and nutrients, whereby its rapid growth enables it to colonize areas also contested by other microorganisms, even occupying pathogen attachment sites on the plant; (3) mycoparasitism, in which *Trichoderma* grows chemotropically toward the pathogen, adheres to and coils around it, and induces the production of extracellular lytic enzymes (chitinases, glucanases, and proteases) that degrade the pathogen's cell wall; and (4) induction of resistance, through activation of systemic resistance mechanisms that accelerate plant responses to phytopathogens by secreting proteins with enzymatic activity (Companioni *et al.*, 2019).

In vitro evaluation is the primary approach for preliminary testing of a biological control organism. Several antagonism assays have been conducted with different *Trichoderma* species. For example, *T. asperellum* was evaluated against *Alternaria* sp., showing effectiveness rates between 50 and 93% (Matas-Baca *et al.*, 2022), and *in vivo* evaluation of the same antagonist (100 mL) in apple trees demonstrated antagonistic capacity compared with the control (Madrid-Molina *et al.*, 2023). Its effectiveness is attributed to the enzymatic production of glucanases and chitinases, which play a role in defense responses against *Alternaria* spp. by degrading the pathogen's cell wall (Infante *et al.*, 2009; Camacho-Luna *et al.*, 2021). In recent years, numerous studies have focused on the use of biological control agents against a wide variety of phytopathogenic fungi; however, studies specifically targeting the control of *Alternaria* remain limited (Table 2).

Table 2. *In vitro* effectiveness of antagonistic microorganisms against *Alternaria* spp.

***Alternaria* spp.**	**Antagonistic species**	**Effective percentage (%)**	**Reference**
Alternaria solani	*Trichoderma harzianum*	62.9-73.8	Michel-Aceves *et al*., 2008
A. solani	*Trichoderma longibrachiatum*	44.2-67.8	Michel-Aceves *et al*., 2008
A. solani	*Trichoderma koningii*	81.3	Michel-Aceves *et al*., 2008
A. alternata	*Trichoderma asperellum*	56-62	Rios-Velasco *et al*., 2016
A. alternata	*Bacillus methylotrophicus*	63	Rios-Velasco *et al*., 2016
A. alternata	*Bacillus amyloliquefaciens*	64	Rios-Velasco *et al*., 2016
A. alternata	*Bacillus subtilis*	38.2-71.9	Ruiz-Sánchez *et al*., 2016
A. alternata	*Pseudomonas fluorescens*	47	Rodríguez-Romero *et al*., 2019

Bacillus subtilis is also among the bacterial species most widely used as biocontrol agents of phytopathogens. The commercial product Probacil® (1 × 10^8 cells per mL) has been tested in combination with salicylic acid against *A. solani* in tomato plants, resulting in reduced disease severity, increased plant growth, and higher fruit yield (Figure 2) (Espinosa-Vázquez *et al.*, 2019). *In vitro*, *B. atrophaeus* showed antagonism against *A. alternata*, with 33.7% spore germination, an effect attributed to the presence of lipopeptides. This strain was compared with *Brevibacterium frigoritolerans*, which did not exhibit sufficient inhibition; however, conidial germination was only 12% (Chacón-López *et al.*, 2021).

The effectiveness of biological control agents is attributed to the diversity of action mechanisms employed by these microorganisms, which are illustrated in Figure 3 (Martínez *et al.*, 2013; Álvarez-García *et al.*, 2020; Pedraza *et al.*, 2020). However, the use of microorganisms requires time for them to act effectively due to their growth rate, and rapid-action products are often needed for pathogen control. Additionally, the cost of biological control is higher than that of chemical or other types of control, prompting ongoing efforts to identify new alternatives for managing phytopathogens.

Other control alternatives. In addition to biological control, new alternatives have been explored, such as the use of plant extracts, essential oils, or biopolymers. In the case of biopolymers, this is an area with great potential and research is still expanding; however, chitosan has been shown to possess antifungal activity and to increase the production of peroxidase, catalase, and phenylalanine ammonia-lyase, thereby enhancing plant defense (Rodríguez-Guzmán *et al.*, 2019). When combined with biocontrol agents such as *P. fluorescens*, it inhibits up to 60.2% of mycelial growth and achieves 100% inhibition of conidial germination (Rodríguez-Romero *et al.*, 2019).

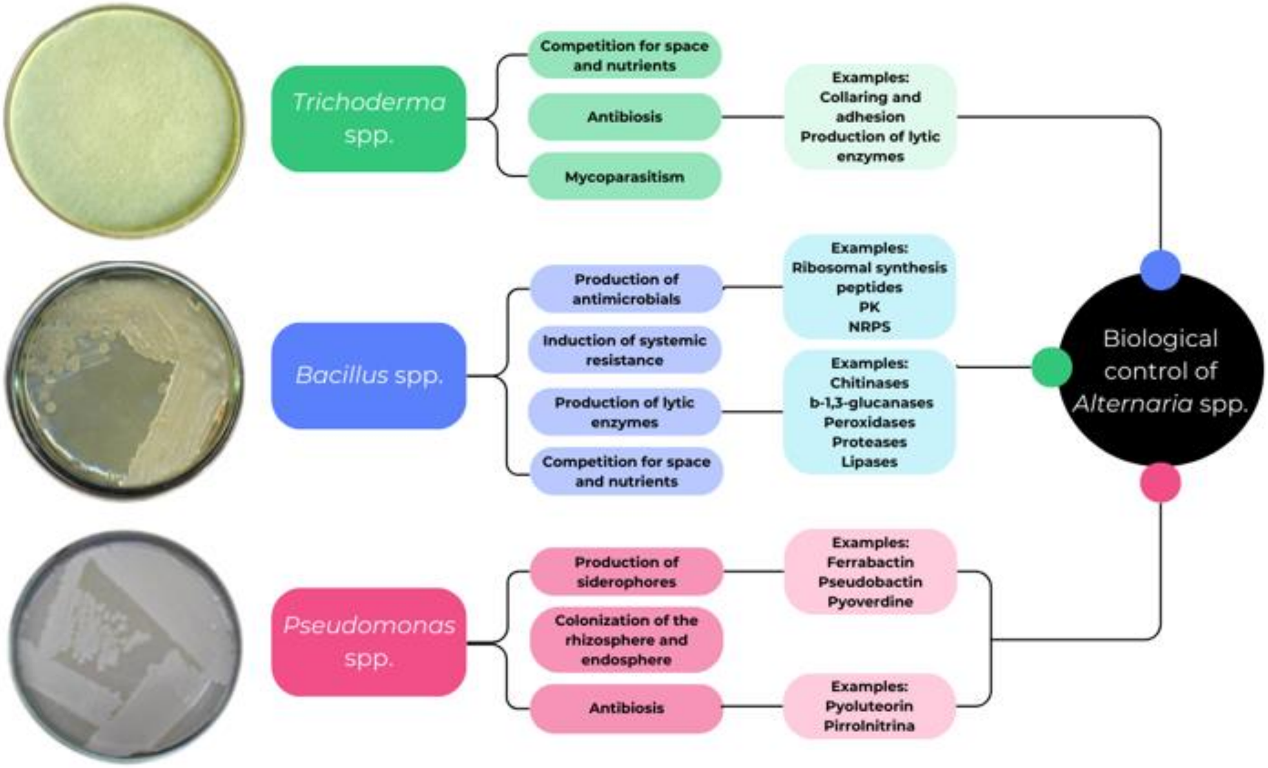

Figure 3. Mechanisms of action of the main biological control agents (PK: polyketides; NRPS: nonribosomal peptide molecules).

Plant extracts. Plant extracts represent a beneficial alternative as a preventive method. Acetone extract of chilemecate (*Salmea scandens*) at concentrations of 4 000 and 5 000 ppm has shown promising *in vitro* results and effectiveness on tomato fruits against *A. solani*. This activity is attributed to the presence of carboxylic acids, aldehydes, ketones, and aromatic compounds, which may act as antagonists (Salas-Marina *et al.*, 2021). Ethanol extract of mamey (*Pouteria sapota*) residues also exhibits inhibitory effects of up to 46.4% against *Alternaria* spp. (Rodríguez-Romero and Martínez-Ramírez, 2023). Essential oil of thyme (*Thymus vulgaris*) (1,000 ppm) displays *in vitro* antifungal activity against *A. citri*, the causal agent of citrus rot; its antagonistic effect is attributed to the presence of borneol, thymol, and carvacrol (Soto *et al.*, 2006).

Developing effective extract-based products against phytopathogens is challenging; however, continued evaluation of diverse extracts has yielded promising results, and these products are safe for consumers and the environment (Villa-Martínez *et al.*, 2015). Although they demonstrate good effectiveness, biopesticides require regulation by agencies such as the Secretaría de Salubridad y Asistencia (SSA), in coordination with the Secretaría de Agricultura y Desarrollo Rural (SADER) and the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), as permits must be issued for their production and manufacturing.

Microalgae. The use of microalgae has increased due to their low cost, ease of production, and versatile characteristics. They convert carbon dioxide into biomass, which is used to produce food for humans and animals, cosmetics, biofuels, wastewater treatment products, and plant biostimulants. Among the genera with the greatest commercial importance are *Chaetoceros*, *Chlorella*, *Dunaliella*, and *Isochrysis* (Ortiz-Moreno *et al.*, 2019). In a study conducted by Schmid and collaborators (2022), several microalgae were evaluated against different phytopathogens, including *A. alternata*. The microalgae tested were *Nannochloropsis* sp., *Phaeodactylum tricornutum*, *Scenedesmus obliquus*, *Chlorella vulgaris*, and *Spirulina* sp. It was determined that only *P. tricornutum* exhibited antagonistic activity against the fungi tested, with the exception of *A. alternata*.

Nanoparticles. Nanoparticles possess antimicrobial and antifungal activity, making them more efficient nanobiopesticides than traditional pesticides (Wang *et al.*, 2017). These particles can interact directly with the cell membranes of plant pathogens, causing structural alterations. Due to their small size, they are capable of penetrating the cell walls of bacteria and fungi, leading to membrane depolarization, loss of internal cellular contents, and ultimately cell lysis (Sirelkhatim *et al.*, 2015). This effect is attributed to the gradual release of zinc ions (Zn^{2+}) as ZnO NPs dissolve in the environment, which interferes with essential enzymatic processes, protein synthesis, and DNA replication, severely affecting microbial cells (Mishra *et al.*, 2025).

The application of zinc nanoparticles (ZnO) has been documented. Mishra *et al.* (2025) reported that mycogenic zinc oxide nanoparticles (produced using *Trichoderma harzianum* culture filtrate) inhibited the mycelial growth of *Alternaria brassicae* by 91.48% at 200 µg mL^{-1}, compared with chemically synthesized zinc nanoparticles at 200 µg mL^{-1} (79.62%) and Mancozeb at 0.2% (82.96%). Silver nanoparticles (AgNPs) also show potential antifungal activity; Ansari *et al.* (2023) suggest that silver nanoparticles can enhance the growth and yield of tomato plants while providing protection against *Alternaria solani*.

On the other hand, Cerna-Chávez *et al.* (2024) evaluated *in vitro* the inhibitory effect of silicon dioxide nanoparticles (SiO_2 NPs) and graphene nanoparticles (NPs-Graf), combined with extracts of *Bacillus amyloliquefaciens* (EcBa), on the mycelial development and reproductive structure formation of *A. alternata*. The treatment with silicon nanoparticles showed the strongest inhibitory effect, as it suppressed mycelial growth and reduced spore and sclerotia production by 84 to 100%.

In Mexico, studies on the use of nanoparticles against *Alternaria* species are limited. Hernández-López *et al.* (2018) developed α-pinene–loaded chitosan nanoparticles (P-CSNP) and a nano-structured edible coating (EC-PCSNP), and evaluated these nanoparticles on bell pepper (*Capsicum annuum*) inoculated with *A. alternata* under refrigeration to assess postharvest quality. They observed that the application of chitosan nanoparticles prevented the incidence and severity of the phytopathogen during 21 days of storage.

CONCLUSIONS AND PERSPECTIVES

The *Alternaria* species complex encompasses multiple species that pose risks to crops and ornamental plants, and, as producers of mycotoxins, represent a potential threat to human health. Its taxonomy is complex, and phylogenetic analyses are continually evolving. *Alternaria* spp. have been extensively studied for their economic importance; in this review, 10 species are detailed across 23 crops distributed in different states of Mexico, demonstrating the genus's strong adaptability to diverse environmental conditions. *Alternaria* can cause up to 80% damage in affected crops, underscoring the importance of studying these organisms. However, it is likely that additional cultivated hosts remain unreported, as well as other plant species that may act as pathogen reservoirs, such as ornamental plants and native species, which, because they do not generate direct economic impact, receive little attention from the scientific community despite their potential for significant ecological impact.

Given the importance of developing control strategies against *Alternaria* spp., chemical control remains one option; however, these products can have negative consequences for consumers and may also indirectly affect beneficial soil microorganisms. Furthermore, proper disease management could reduce the ability of pathogens to generate resistant structures and remain latent in the soil.

The use of preventive methods, such as biological and natural products, along with agricultural practices like crop rotation and disinfection of machinery and materials, can reduce pathogen incidence and severity. Biological control as a strategy against phytopathogens is a favorable approach for improving soil quality, which has a positive impact on plant health. Although these methods generally act in the short and medium term, they offer greater long-term benefits. Among the examples discussed in this review that are most commonly used in agriculture, *Trichoderma* spp. and *Bacillus* spp. stand out—not only as effective antagonists but also for their ability to fix essential elements for crops, promote plant growth, and induce systemic resistance to pathogens (González-León *et al.*, 2022). These effects have been demonstrated in various *in vitro* and *in vivo* studies targeting the control of *Alternaria* spp. (Ríos-Velasco *et al.*, 2016), yielding promising results with direct applicability for growers (González-Chingate *et al.*, 2020). Additionally, other natural alternatives have been explored, such as plant extracts, microalgae, essential oils, and chitosan, as these produce compounds that confer antagonistic activity while preserving soil microbiota.

The application of biological and organic control methods to manage *Alternaria* spp., or any other phytopathogen, presents challenges due to the incorrect diagnosis of pathogens. Moreover, gaps remain in the available information on reported species and in common agricultural practices. Therefore, it is essential to emphasize the use of preventive strategies in agronomy involving biological or natural products, as these approaches would yield better outcomes for plant health and, consequently, human health.

The *Alternaria* species complex undergoes constant taxonomic revisions and includes pathogenic species that cause economic losses in agricultural crops. Officially, nine species have been reported in 23 cultivated hosts; however, gaps persist across various crops, as well as in ornamental, forest, and native species. Difficulties in achieving proper control of diseases caused by *Alternaria* spp. and other pathogens often arise from incorrect disease diagnosis. This review outlines the types of control strategies, providing examples from Mexico, and summarizes current advances in alternative approaches to chemical control, including antagonism assays using beneficial microorganisms such as *Trichoderma* spp., *Bacillus* spp., *Brevibacterium* spp., and *Pseudomonas fluorescens*, which are widely studied and viable as biological control agents due to their beneficial interactions. Additionally, natural control options—such as chitosan, plant extracts, and microalgae—show antagonistic activity against *Alternaria* spp. Finally, the emerging use of nanoparticles offers preventive potential for disease management.

Limitations

This review is limited to studies published in English and Spanish, which may exclude relevant literature in other languages, as well as the availability of complete and accessible scientific articles.

Conflict of interest

The authors declare that there is no conflict of interest.

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Author contributions

NMEM. Study conception, data analysis/interpretation, manuscript preparation, editing, and review. **JDLM.** Data analysis/interpretation, manuscript preparation, editing, and review. **ESV.** Data analysis/interpretation, manuscript preparation, editing, and review. **LMC**. Data analysis/interpretation, manuscript preparation, editing, and review. **IRB.** Study conception, data analysis/interpretation, manuscript preparation, editing, and review.

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