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Seed extracts as an effective strategy in the control of plant pathogens: Scalable industry bioactive compounds for sustainable agriculture

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ABSTRACT

With a growing global population, maintaining sufficient agricultural production is crucial. However, agriculture faces numerous challenges today, particularly due to the undeniable impacts of climate change, which are expected to intensify pest and disease pressures. The traditional approach to combat these phytopathological issues has relied on synthetic chemical pesticides. While their use has indeed increased productivity, it is also evident their detrimental and cumulative effects on the environment, and the current negative perception of the population toward these chemicals. In response, governments are prompting the search for alternatives to synthetic pesticides, through different policies, such as the strategy From Farm to Fork in the European Union, which aims to reduce the use of chemical pesticides by 50% by 2030, among other measures. At this point, seed extracts with biocidal activity are emerging as a viable option for the control and management of various pathogenic agents, such as harmful bacteria, fungal and oomycete pathogens, and plant-parasitic nematodes. Nevertheless, it is worth mentioning that most of the studies have been only conducted under highly controlled conditions. Thus, this line of research should be still more deeply developed, including proofs under field conditions, in order to become the extensive and widespread use of these bio-products a reality. In this review, we compile the main studies focused on the use of these compounds for phytosanitary purposes, describing and analysing the key metabolites, their composition, extraction processes and the mechanisms involved in their antagonistic effects. Additionally, we analyse the primary factors contributing to the limited adoption of these extracts in the field, such as the scarcity of studies under real conditions or the possible impact on non-target organisms, and discuss future prospects for their development.

1. Introduction

Plant pathogens and pests can have significant impacts on agriculture, leading to substantial losses. However, they also play a crucial role in natural ecosystems by regulating the mortality and dispersal of dominant plant species (Tedersoo et al., 2019). In agricultural systems, these groups pose significant challenges to food security, affecting production, distribution, economic access, as well as the quality and nutritional value of crops (Savary et al., 2019). Globally, pathogens, pests, and weeds account for annual losses rang-

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ing from 20% to 40% of agricultural productivity. Among these losses, pathogens contribute to approximately 10%–15%, while insect pests account for 18%–25% (Poveda, 2021; Mohammad-Razdari et al., 2022). The extent of these losses can vary depending on the crop species. For major staple crops, estimated losses caused by plant pathogens and pests are approximately 28% for wheat, 41% for rice and maize, 21% for potato, and 32% for soybean (Savary et al., 2019). The main microorganisms that cause diseases in crops include viruses, bacteria, fungi, oomycetes, and nematodes (Mohammad-Razdari et al., 2022).

The primary approach employed globally for pest and pathogen control in agriculture is the utilization of chemical pesticides, amounting to nearly 3 billion kg of pesticides and an annual budget of approximately 40 billion USD (Sharma et al., 2020). The extensive use of these agrochemicals has resulted in approximately 64% of agricultural land worldwide being at risk of severe contamination with various pollutants, with South Africa, China, India, Australia, and Argentina being the most affected countries (Tang et al., 2021). Chemical pesticide contamination negatively impacts water, soil, crops, and subsequently, the food supply, leading to significant environmental damage and the loss of biodiversity (Tudi et al., 2021). Furthermore, direct exposure to these chemical contaminants poses serious health risks to farmers and consumers, including neurological dysfunction, cancer, diabetes, respiratory disorders, and reproductive disorders (Rani et al., 2021). In the pursuit of more sustainable and environmentally friendly alternatives to chemical pesticides for combating plant pathogens, various strategies are being developed, including the utilization of phytochemicals. In recent years, there has been a significant increase in both research and industry interest in the development of new bio-pesticides based on microorganisms, plants, algae, and other sources (Gwinn, 2018). Interestingly, even residual biomass collected from beaches (Poveda and Díez-Méndez, 2022) or freshwater bodies (Poveda, 2022) can be utilized as resources for obtaining such products.

Plants serve as an important reservoir of phytochemicals with diverse applications in numerous fields, including health, cosmetics, food, dyes, etc. The main groups of compounds produced by plants are secondary metabolites, which encompass terpenes, phenolics, flavonoids, alkaloids, and sulfur-containing compounds (Naboulsi et al., 2018). These plant extracts can be obtained through various methodologies, such as Soxhlet extraction, maceration, or hydrodistillation. These extraction processes commonly involve the use of water and/or various organic solvents such as hexane, acetone, methanol, ethanol, and others (Naboulsi et al., 2018).

So far, a significant number of plant phytochemicals with substantial biocidal potential have been identified for use against pathogens (Naboulsi et al., 2018) and plant pests (Lengai et al., 2020). For post-harvest treatments, plant extracts derived from the neem tree (*Azadirachta indica*), chinaberry (*Melia azedarach*), and marigold (*Tagetes* spp.) are commonly employed for disease control (Anjum-Malik et al., 2016). Another group of plants that deserves special attention due to their high phytochemical content are the cruciferous plants, among which glucosinolates (GSLs) are prominent. These sulfur-rich secondary metabolites possess potent antimicrobial properties against fungi, oomycetes (Poveda et al., 2020a; Eugui et al., 2023) and plant-parasitic nematodes (Eugui et al., 2022). Currently, the application of these phytochemical-rich extracts is primarily carried out through essential oils, although other types of extracts are gaining interest (Basaid et al., 2021).

Among different plant parts, seeds serve as a significant source of phytochemicals, as they possess inherent protective mechanisms against pathogens and pests to ensure maximum viability and species propagation (Lundgren, 2009). Consequently, the objective of this review is to collect and collate the current state-of-art on seed extracts and their utilization as antimicrobials against plant pathogens, with the aim of contributing to the development of a more sustainable agriculture.

2. Seed extracts: extraction, composition and uses

Seeds have multiple applications not only in agriculture, food, and ecosystem restoration but also in the pharmaceutical, chemical, and energy industries. Their significance is so profound that seeds are considered a crucial element in achieving the United Nations Sustainable Development Goals: 1 (no poverty), 2 (zero hunger), 3 (good health and well-being), 13 (climate action), 14 (life below water), and 15 (life on land). Hence, the conservation of agricultural and wild biodiversity in germplasm banks is essential (Mattana et al., 2021). However, seeds remain largely unexplored in many aspects.

Currently, the seeds of various crops are receiving special attention as superfoods due to the presence of phytochemicals that hold particular interest for human health, such as chia, flax, or hemp seeds (Cox et al., 2022). Moreover, these phytochemicals have diverse industrial uses and applications. For instance, fatty acids and lipids are utilized in the cosmetic industry and serve as renewable (non-petroleum-based) raw materials. Other bioactive compounds synthesized and accumulated in seeds are of significant interest to the chemical, pharmaceutical, and pesticide industries since, due to its cytotoxic activity, they can be used as fungicides, insecticides, herbivore repellents and herbicides (Powell, 2009). Prior to their application, phytochemicals must be extracted. This process can be performed by various methods: cold solvent extraction, Soxhlet extraction, ultrasonic extraction, microwave extraction, and supercritical fluid extraction. Different solvents can be utilized, such as water, methanol, ethanol, ethyl acetate, acetone, isopropanol or hexane, and are considered an essential part of these procedures (Knez-Hrnčić et al., 2019).

The composition of seed extracts can vary significantly depending on the plant species and the extraction method employed. According to a recent publication (Corso et al., 2021), the primary groups of secondary metabolites found in these extracts are phenylpropanoids, particularly anthocyanins, flavonols, flavan-3-ols, and proanthocyanidins. These metabolites are associated with seed longevity and dormancy, as they act as effective scavengers of reactive oxygen species (ROS). Alkaloids, another common group of secondary metabolites, are frequently present in seed extracts and are primarily involved in seed defense against herbivores and pathogens. Some well-studied alkaloids found in seeds include caffeine, theobromine, daturine, lupanine, and physostigmine. Additionally, GSLs and terpenoids, especially monoterpenoids, diterpenoids, and tetraterpenoids, are commonly found in seeds of many plants and serve as defense mechanisms against pathogens. However, several of these compounds are also valued for their gastronomic interest, such as carvone, limonene, and α-phellandrene, or for their pharmaceutical applications, such as taxol, artemisinin, and ginkgolides (Corso et al., 2021).

The wide range of diverse nature compounds present in seed extracts allows multiple applications across various industries. For example, seed extracts have been used in bioremediation processes, such as the removal of contaminating dyes in the textile industry (Radini et al., 2018; Guo et al., 2020) and even in the treatment of drinking water (García-Fayos et al., 2016). Seed extracts also find application in the manufacture of photovoltaic cells (Maurya et al., 2019) and as corrosion inhibitors (Bahlakeh et al., 2019). In the food industry, seed extracts are utilized as potent preservatives due to their antimicrobial and antioxidant properties (Perumalla and Hettiarachchy, 2011; Kaur et al., 2015).

The high antioxidant capacity of phytochemicals in seed extracts, primarily attributed to their abundant phenolic compounds, flavonoids, and tannins, has garnered significant interest in the pharmaceutical industry. Extracts derived from various sources, including *Moringa oleifera* (Jahan et al., 2018), faba bean (Choudhary and Mishra, 2019), fennel (Kalleli et al., 2019), camelina (Kumar et al., 2017), arecanut (Wang et al., 2021) and cress (Al-Sheddi et al., 2016), have demonstrated therapeutic potential. For instance, grape seed extracts have been found to suppress the activity of ATP-binding cassette (ABC) transporters, contributing to overcoming chemoresistance in colorectal cancer cells and providing benefits against many diseases, such as cardiovascular disease, hypertension, microbial infections, etc. (Ravindranathan et al., 2019). Camu-camu seed extracts exhibit chromosome-protective effects (Do Carmo et al., 2019), while açai seed extracts induce cell cycle arrest and apoptosis in human lung carcinoma cells (Martinez et al., 2018). Other extracts have been utilized in the prevention and treatment of various diseases, including diabetes (Tiji et al., 2021), obesity (Piragine et al., 2021), neurodegenerative disorders such as Alzheimer's (Dehghanian et al., 2017), renal diseases (Seo et al., 2017), pulmonary fibrosis (Javadi et al., 2015), wound healing (Izadpanah et al., 2019), immunosuppression (Sharma et al., 2017), anti-inflammatory effects (Adam et al., 2016) and protection against hazardous chemical contaminants (Abdel-Kawi et al., 2016; Evcimen et al., 2018).

Furthermore, due to their insecticidal properties, several seed extracts have been utilized as larvicides against mosquitoes transmitting diseases to humans and animals, including *Culex quinquefasciatus* (Rawani et al., 2009) or *Aedes aegypti* (Marimuthu et al., 2012). Neem seed extracts have also been employed to combat pests, such as house dust mites, poultry mites, harvest mites, cat fleas, bed bugs, cockroaches, and raptor bugs, as well as beetles that attack food supplies (Schmahl et al., 2010). Additionally, although some reviews have already focused on the application of the extracts of specific seeds, such as *Jatropha curcas* (Ratnadass and Wink, 2012) and *Annona squamosa* (Mondal et al., 2018) for controlling agricultural pests, the extensive research conducted on this topic might deserve a specific review article in this area to compile, describe and analyse the multiple results obtained.

3. Antimicrobial capacity of seed extracts

Seed extracts represent a newly emerging alternative as a source of antimicrobial agents. Moreover, they offer a new alternative in the fight against multi-resistant microorganisms (Ahmad Sowhini et al., 2020). The way in which these extracts act as antimicrobials is difficult to generalize since each seed presents a unique combination of metabolites and bioactive molecules. However, the main groups of phytochemicals described as antimicrobial in these extracts include alkaloids, tannins, phenols and flavonoids. Examples of these compounds are thymol, linalool, carvone, eugenol, farnesol, geraniol, or catechins (Ahmad Sowhini et al., 2020).

Concerning viruses, various phytochemicals found in seed extracts have been identified as potent antiviral agents by targeting viral envelopes (Chen et al., 2014). For instance, *Poncirus trifoliata* seed extracts have shown effective antiviral activity against influenza virus (Heo et al., 2018); *Sambucus nigra* extracts have exhibited activity against bronchitis virus (Chen et al., 2014); and grapefruit seed extract in nasal spray solution has demonstrated efficacy against SARS-CoV-2 (Go et al., 2020).

A significant number of studies have been conducted on the antibacterial properties of seed extracts. These phytochemicals exhibit various mechanisms of action against bacteria, including direct toxicity by affecting membranes, nuclei, and other targets, as well as inhibiting the formation of biofilms, which are responsible for bacterial virulence (Delimont and Carlson, 2020). The most studied bacteria in these investigations are *Enterococcus faecium*, *E. faecalis*, *Staphylococcus aureus*, *S. epidermidis*, *Bacillus cereus*, *B. subtilis*, *Salmonella typhi*, *S. enterica*, *Pseudomonas aeruginosa*, *Shigella flexneri*, and *Escherichia coli*. These bacteria were treated with seed extracts from *Trigonella foenum-graecum* (Goyal et al., 2018; Radini et al., 2018; Altinkaynak et al., 2019), black cumin (Topcagic et al., 2017), grape (Zhu et al., 2014), avocado (Rodríguez-Sánchez et al., 2019), rocket (Khoobchandani et al., 2010), coffee (Dhand et al., 2016), or *Pongamia pinnata* (Rajput et al., 2021).

Regarding non-plant pathogenic fungi, the majority of studies have focused on the yeast *Candida albicans*. Notably, the use of coumarins extracted from apple seeds has demonstrated significant antimicrobial activity (Mohammed and Mustafa, 2020). In the case of animal and human parasites, numerous successful cases of effective antimicrobial activity have been reported using various seed extracts against different pathogenic organisms. For instance, seed extracts from *Nigella sativa* have shown effectiveness against the malarial parasite *Plasmodium berghei* (Abdulelah and Zainal-Abidin, 2007). Additionally, extracts from pumpkin (Marie-Magdeleine et al., 2009) and chinaberry tree (Kamaraj et al., 2010) have demonstrated activity against different nematode parasites, such as *Haemonchus contortus*. Seed extracts have also found to have practical applications as antimicrobials in food protective films. For example, terebinth seed extracts have been included in chitosan films (Kaya et al., 2018), and grape seed extracts have been used in pea starch films for pork loins (Corrales et al., 2009).

4. Seed extracts against plant pathogens

Seed extracts have been recognized as potent bioactive agents *in planta* applications. For instance, the application of seed extracts has been found to activate plant defensive responses, even in the absence of biotic stress, due to the presence of elicitors, such as defense hormones (Poveda, 2020). In the case of table grapes during postharvest, the application of grapefruit seed extracts has been shown to enhance the activity of defense-related enzymes, including superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), without the presence of plant pathogens (Xu et al., 2009).

Other forms of utilizing phytochemicals present in seeds for plant pathogens control is through seed meals or oilseed cakes. Seed meals of brassicaceous plants (Zasada et al., 2009; Radwan et al., 2012; Curto et al., 2016; Wang and Mazzola, 2019), chamomile or castor bean (Radwan et al., 2012) have been recognized as effective biological control methods against fungi (*Rhizoctonia solani*, *Ilyonectria destructans*, *Mortierella alpina*), oomycetes (*Phytium ultimum*) and nematodes (*Meloidogyne incognita*, *Pratylenchus penetrans*). Oilseed cakes, which are the residues obtained after oil extraction from seeds through expelling or solvent extraction, have shown to control several pathogenic fungi (*Phyllosticta phaseolina*, *Fusarium oxysporum*) and plant-parasitic nematodes (*M. incognita*, *M. javanica*, *Rotylenchulus reniformis*, *Tylenchorhynchus brassicae*, *Helicotylenchus indicus*) when directly applied to the soil, due to the residual presence of bioactive phytochemicals (Tiyagi and Alam, 1995; Tiyagi et al., 2002; Yang et al., 2015).

The use of seed extracts against plant pathogens is discussed in the subsequent sections categorized by pathogen group: bacteria, fungi, oomycetes and nematodes. Additionally, Fig. 1 provides an infographic summarizing the information gathered from these subsections.

4.1. Bacterial pathogens

All studies conducted on the antimicrobial activity of seed extracts against plant pathogenic bacteria are listed in Table 1. Several seed extracts have demonstrated *in vitro* antibacterial activity. For example, methanolic extracts from *Urtica* spp. seeds have shown activity against *Clavibacter michiganensis* subsp. *michiganensis* and *Xanthomonas vesicatoria* (Körpe et al., 2013), while extracts from *Eugenia jambolana* have shown activity against *Xanthomonas campestris* (Uma et al., 2012). Although the specific molecules responsible have not been determined yet, antibacterial proteins, such as plant lipid transfer proteins, have been identified in seed extracts. These proteins have exhibited antimicrobial properties by binding to cell membranes and altering their permeability (Amador et al., 2021). Isolated proteins from onion seeds have been applied *in vitro* and demonstrated significant inhibition of growth in pathogenic bacteria, such as *Erwinia carotovora* and *Pseudomonas syringae* pv. *tabaci* (Cammue et al., 1995).

Various antibacterial metabolites have been isolated from seed extracts as well. Lignans, which are phenylpropanoids, primarily act as antimicrobials in plants by interfering with the adhesion and colonization of pathogens in tissues through the disruption of metabolic pathways (Zálešák et al., 2019). Methanolic extracts of *Myristica fragrans*, rich in lignans, have exhibited *in vitro* antibacterial activity against bacteria such as *Agrobacterium tumefaciens*, *Acidovorax konjaci*, *Burkholderia glumae*, and *P. syringae* pv. *lachrymans* (Cho et al., 2007). Caffeine, another antibacterial secondary metabolite identified in seed extracts, is present in methanolic extracts of *Trigonella foenum-graceum*. It has shown the ability to inhibit various virulence factors of the pathogenic bacterium *Pseudomonas aeruginosa in vitro*, including protease, elastase B, pyocyanin production, chitinase, exopolysaccharides, and swarming motility (Husain et al., 2015).

To our knowledge, only two studies have investigated the *in planta* effects of seed extracts against pathogenic bacteria (Li et al., 2014; Musyimi et al., 2022). In the first study, the application of *Clausena lansium* seed extracts to tobacco plants reduced the incidence of the disease caused by *Ralstonia solanacearum* up to 96%. This reduction was attributed to the presence of the secondary metabolite lansiumamide B in the extracts, which exhibited antimicrobial effects up to 40 times greater than antibiotics such as streptomycin (Li et al., 2014). The second study demonstrated that seed extracts of *M. oleifera* were able to reduce by half the severity of *R. solanacearum* as well, when applied in plants of tomato in this case (Musyimi et al., 2022).

4.2. Fungal pathogens

Most studies conducted using seed extracts as antifungals against plant pathogenic fungi are listed in Table 2. Many of them describe this antifungal activity, but without identifying the specific phytochemical involved, either *in vitro*, postharvest, or *in planta*.

Several proteins with *in vitro* antifungal capacity against plant fungal pathogens have been isolated from seed extracts. Similarly to their antibacterial effects, plant lipid transfer proteins act against fungi by modifying membrane permeability (Amador et al., 2021). Onion and wheat seed extracts containing these proteins have shown high *in vitro* antifungal activity against various pathogens, such as *Alternaria brassicola*, *Ascochyta pisi*, *Botrytis cinerea*, *Colletotrichum lindemuthianum*, *Fusarium culmorum*, *F. oxysporum*, *Nectria haematococca*, *Phoma betae*, and *Verticillium dahliae* (Cammue et al., 1995; Dubreil et al., 1998). Wheat seed extracts have also yielded peptides called puroindolins, which accumulate in the endosperm and exhibit antifungal activity by binding to membranes, disrupting them, forming ion channels, and disrupting intracellular nucleic acid binding and metabolism (Morris, 2019). These proteins have shown potent antifungal activity against *A. brassicola*, *A. pisi*, *B. cinerea*, *F. culmorum*, and *V. dahliae in vitro* (Dubreil et al., 1998).

Another group of proteins isolated from seed extracts with antifungal activity are the 2S albumin proteins. These proteins are essential for seed providing amino acids and nutrients during germination and seed defense. Their antifungal mechanism involves permeabilization of the plasma membrane (Souza, 2020). These 2S albumins have been identified in acetic acid:acetone extracts from *Taraxacum officinale* seeds and have been implicated in inhibiting the growth and germination of pathogenic fungi such as *Helminthosporium sativum*, *P. betae*, and *Verticillium albo-atrum* (Odintsova et al., 2010).

Certain antifungal proteins are specific to particular plant species, such as *Momordica charantia* seeds, which contains α-momorcharin protein. This protein has been described as a potent antifungal agent, causing cell deformation with irregular budding, loss of cell wall integrity, rupture of the fungal cell membrane, DNA fragmentation, and disruption of macromolecular synthesis and organelle functions (Villarreal-La Torre et al., 2020). *M. charantia* seed extracts have been shown to possess antimicrobial activity against *Fusarium solani*, with α-momorcharin causing cell deformation with irregular sprouting, loss of cell wall integrity, and rupture of the fungal cell membrane (Wang et al., 2016).

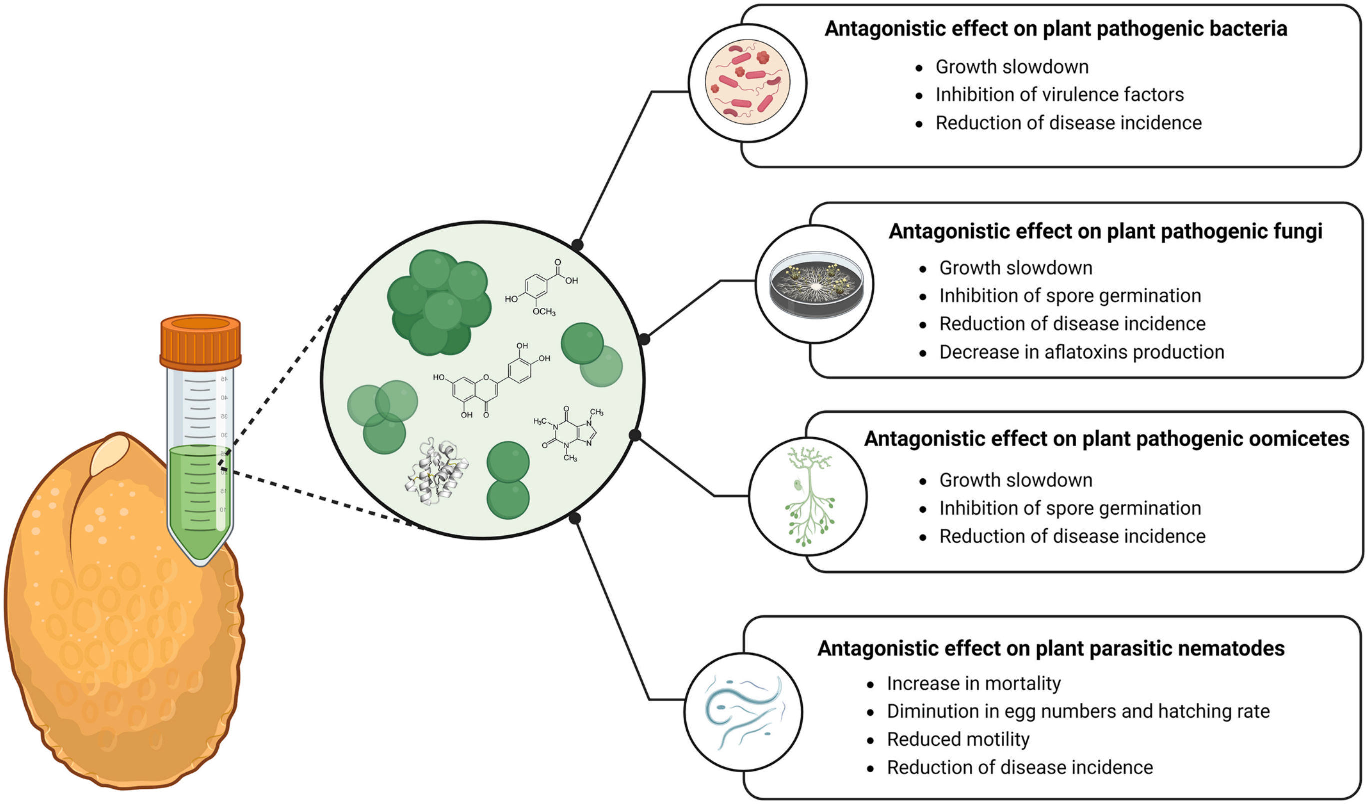

Fig. 1. Summary infographic on the use of seed extracts in the control of plant pathogens.

Table 1
Use of seed extracts in the control of plant pathogenic bacteria.

BACTERIA	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Acidovorax konjaci	*Myristica fragrans*	Methanol	50 mg/L	*In vitro*	–	Inhibition of bacterial growth	Lignans (metabolites)	Cho et al. (2007)
Agrobacterium tumefaciens	*M. fragrans*	Methanol	20 mg/L	*In vitro*	–	Inhibition of bacterial growth	Lignans (metabolites)	Cho et al. (2007)
	Seabuckthorn	Dimethylsulfoxide	10 μl per plate	*In vitro*	–	Inhibition of bacterial growth	Not identified	Gupta et al. (2011)
Burkholderia glumae	*M. fragrans*	Methanol	40 mg/L	*In vitro*	–	Inhibition of bacterial growth	Lignans (metabolites)	Cho et al. (2007)
Clavibacter michiganensis subsp. *michiganensis*	*Urtica dioica* *U. pilulifera*	Methanol	1024 μg/ml	*In vitro*	–	Inhibition bacteria growth	Not identified	Körpe et al. (2013)
	Corchorus olitorius	Methanol Acetone	8–128 μg/ml	*In vitro*	–	Inhibition of bacterial growth	Vanillic acid	Iseri et al. (2022)
Pectobacterium carotovorum (syn. *Erwinia carotovora*)	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of bacterial growth	Plant lipid transfer proteins	Cammue et al. (1995)
Pseudomonas aeruginosa	*Trigonella foenum-graceum*	Methanol	125–1000 mg/ml	*In vitro*	–	Inhibition of virulence factors	Caffeine (metabolite)	Husain et al. (2015)
P. syringae pv. *lachrymans*	*M. fragrans*	Methanol	50 mg/L	*In vitro*	–	Inhibition of bacterial growth	Lignans (metabolites)	Cho et al. (2007)
P. syringae pv. *tabaci*	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of bacterial growth	Plant lipid transfer proteins	Cammue et al. (1995)
Ralstonia solanacearum	*Clausena lansium*	Not indicated	125 mg/L (*in vitro*) 100 mg/kg of soil (*in planta*)	*In vitro* Growth chamber (*in planta*)	Tobacco	Inhibition bacteria growth (*in vitro*) Reduced disease incidence (*in planta*)	Lansiumamide B (metabolite)	Li et al. (2014)
	Moringa oleifera	Methanol	2.5–15%	*In vitro* *In planta*: greenhouse	Tomato (*in planta*)	Inhibition of bacterial growth (*in vitro*) Reduce disease incidence (*in planta*)	Not identified	Musyimi et al. (2022)
Xanthomonas campestris	*Eugenia jambolana*	Methanol	100 μL	*In vitro*	–	Inhibition bacteria growth	Not identified	Uma et al. (2012)
X. vesicatoria	*U. dioica* *U. pilulifera*	Methanol	1024 μg/ml	*In vitro*	–	Inhibition bacteria growth	Not identified	Körpe et al. (2013)

Regarding secondary metabolites, seed extracts contain numerous compounds with antifungal activity. These metabolites can be analysed in combination or individually. In seed extracts, we find a complex mixture of phytochemicals rather than a single compound. For example, methanolic extracts from *Cichorium intybus* seeds containing alkaloids, flavonoids, tannins, steroids, saponins, and anthraquinones have been shown to significantly reduce the production of mycotoxins (aflatoxins) by the stored grain pathogens *Aspergillus flavus* and *A. niger* (Mehmood et al., 2012).

Terpenes and their derivatives have been recognized as potent antimicrobial agents, acting through mechanisms such as cell membrane disruption, modulation of efflux pumps, inhibition of virulence factors, alteration of oxidative phosphorylation, inhibition of oxygen uptake, or suppression of biofilm development (Mahizan et al., 2019). Several studies have demonstrated that the presence of different terpenes and/or their derivatives in seed extracts can inhibit up to 95% of the *in vitro* growth of various pathogenic fungi. Monoterpenes, sesquiterpenes, and triterpenes (along with their derivatives, such as saponins) have been identified as the phyto-

Table 2
Use of seed extracts in the control of plant pathogenic fungi.

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Alternaria spp.	*Cynara scolymus* *Aloe vera*	Acetic acid	20%	*In vitro*	–	Inhibition of fungal growth	Not identified	Dellavalle et al. (2011)
A. alternata	*Myristica fragrans*	Methanol	92 mg/L	*In vitro*	–	Inhibition of fungal growth	Lignans (metabolites)	Cho et al. (2007)
	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Al-Hazmi (2013)
	Filipendula ulmaria	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
A. brassicola	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	Wheat	Diethylether:ethanol	300 µg/ml	*In vitro*	–	Inhibition of fungal growth	Puroindolines and nonspecific lipid transfer protein (proteins)	Dubreil et al. (1998)
A. tenuissima	*F. ulmaria*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
Alternaria sp.	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
	Foeniculum vulgare	Essential oil	26 µg/ml	*In vitro*	–	Inhibition of fungal growth	Not identified	Barkat and Bouguerra (2012)
Ascochyta pisi	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	Wheat	Diethylether:ethanol	300 µg/ml	*In vitro*	–	Inhibition of fungal growth	Puroindolines and nonspecific lipid transfer protein (proteins)	Dubreil et al. (1998)
Aspergillus flavus	*Melia azedarach*	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)
	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
	Cashew	Ethanol	10 µl per plate	*In vitro*	–	Inhibition of fungal growth	Triterpenoids (metabolites)	Kannan et al. (2009)
	Jatropha curcas Castor oil plant	Essential oil	1 ml per plate (*in vitro*) 1 ml per tuber fragment (postharvest)	*In vitro* Postharvest	Yam tubers (postharvest)	Inhibition of fungal growth (*in vitro*) Reduce disease incidence (postharvest)	Not identified	(Anjorin et al. (2011a))
	Cichorium intybus	Methanol	10 mg/ml	*In vitro*	–	Reduced funagl aflatoxins production	Alkaloids, flavonoids, tannins, steroids, saponins and anthraquinones	Mehmood et al. (2012)
	Baobab	Essential oil	0.5–100 ml per tube	*In vitro*	–	Reduced funagl aflatoxins production	Not identified	El-Nagerabi et al. (2013)
	Abelmoschus esculentus	Aqueous	50 µl per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Jayaseelan et al. (2013)

(*continued on next page*)

Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
	Moringa oleifera	Methanol	100 mg/ml	*In vitro*	–	Inhibition of fungal growth	Not identified	Ayirezang et al. (2020)
	Aframomum melegueta	Water	25%	*In vitro*	–	Inhibition of fungal growth	Not identified	Gyasi et al. (2022)
A. niger	Cabbage Cauliflower Cress Turnip	Water	0.2 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Abdel-Mallek (1995)
	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
	Fennel	Essential oil	15 µl per plate	*In vitro*	–	Inhibition of fungal growth	Monoterpenes y sesquiterpenes	Anwar et al. (2009)
	Cashew	Ethanol	10 µl per plate	*In vitro*	–	Inhibition of fungal growth	Triterpenoids (metabolites)	Kannan et al. (2009)
	Pipper nigrum *Trachyspermum ammi*	Water	20%	*In vitro*	–	Inhibition of fungal growth	Not identified	Avasthi et al. (2010)
	Pawpaw	Water	2%	*In vitro*	–	Inhibition of fungal growth	Not identified	Obinna and Abikoye (2010)
	A. esculentus	Aqueous	50 µl per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Jayaseelan et al. (2013)
	C. intybus	Methanol	10 mg/ml	*In vitro*	–	Reduced funagl aflatoxins production	Alkaloids, flavonoids, tannins, steroids, saponins and anthraquinones	Mehmood et al. (2012)
	Hop	Methanolic	0.15 mg/ml	*In vitro*	–	Inhibition of fungal growth	Catechin and epicatechin (metabolites)	Alonso-Esteban et al. (2019)
	M. oleifera	Methanol	100 mg/ml	*In vitro*	–	Inhibition of fungal growth	Not identified	Ayirezang et al. (2020)
	A. melegueta	Water	25%	*In vitro*	–	Inhibition of fungal growth	Not identified	Gyasi et al. (2022)
A. parasiticus	Baobab	Essential oil	0.5–100 ml per tube	*In vitro*	–	Reduced funagal aflatoxins production	Not identified	El-Nagerabi et al. (2013)
Blumeria graminis (syn. *Erysiphe graminis*)	Peanut *Cecropia obtusifolia* Soybean *Penstemon multiflorus* Pea *Cryptolepis sinensis*	Methanol	250 mg/L	*In vitro*	–	Inhibition of fungal growth	Not identified	Lee et al. (1998)
	M. fragrans	Methanol	50 mg/L	Greenhouse (*in planta*)	Barley	Reduced disease incidence	Lignans (metabolites)	Cho et al. (2007)
Botrytis cinerea	Wheat	Diethylether:ethanol	300 µg/ml	*In vitro*	–	Inhibition of fungal growth	Puroindolines and nonspecific lipid transfer protein (proteins)	Dubreil et al. (1998)

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Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
	Peanut *C. obtusifolia* Soybean *P. multiflorus* Pea *C. sinensis*	Methanol	250 mg/L	*In vitro*	–	Inhibition of fungal growth	Not identified	Lee et al. (1998)
	Senna tora	Chloroform	2 g/L leaves spray	Greenhouse (*in planta*)	Cucumber	Reduced disease incidence	Emodin, physcion and rhein (metabolites)	Kim et al. (2004)
	M. fragrans	Methanol	100 mg/L (*in vitro*) 50 mg/L (*in planta*)	*In vitro* Greenhouse (in *planta*)	Tomato	Inhibition of fungal growth (*in vitro*) Reduced disease incidence (*in planta*)	Lignans (metabolites)	Cho et al. (2007)
	Grapefruit	Commercial product	0,5% (v/v) per plate (*in vitro*) and fruits immersion (postharvest)	*In vitro* Postharvest	Grapefruit	Inhibition of fungal germination and growth (*in vitro*) Reduce disease incidence (postharvest)	Not identified	Xu et al. (2007)
	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
	Pomegranate	Methanolic	500–1500 ppm per plate	*In vitro*	–	Inhibition of fungal germination and growth	Not identified	Tehranifar et al. (2011)
Cladosporium cucumerinum	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Cochliobolus sativus (syn. *Bipolaris sorokiniana*)	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Al-Hazmi (2013)
	Chenopodium album	Hexane:ethyl acetate	200 µl per plate	*In vitro*	–	Inhibition of fungal germination	Not identified	Semina et al. (2016)
	F. ulmaria *Nigella sativa*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
Colletotrichum sp.	*A. melegueta*	Water	25%	*In vitro*	–	Inhibition of fungal growth	Not identified	Gyasi et al. (2022)
C. coccodes	*M. fragrans*	Methanol	50 mg/L	*In vitro*	–	Inhibition of fungal growth	Lignans (metabolites)	Cho et al. (2007)
C. gloeosporioides	*M. fragrans*	Methanol	50 mg/L	*In vitro*	–	Inhibition of fungal growth	Lignans (metabolites)	Cho et al. (2007)
	Papaya	Ethanol	20 mg/ml	*In vitro*	–	Inhibition of fungal growth	Triterpenes and saponins (metabolites)	Chávez-Quintal et al. (2011)
C. lindemutkianum	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
Corynespora cassiicola	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Diaporthe phaseolorum	*M. azedarach*	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)

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Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Drechslera hawiinesis	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
Erysiphe graminis	*S. tora*	Chloroform	2 g/L leaves spray	Greenhouse (*in planta*)	Barley	Reduced disease incidence	Emodin, physcion and Rhein (metabolites)	Kim et al. (2004)
Fusarium sp.	Cashew	Ethanol	10 µl per plate	*In vitro*	–	Inhibition of fungal growth	Triterpenoids (metabolites)	Kannan et al. (2009)
F. culmorum	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	Wheat	Diethylether:ethanol	300 µg/ml	*In vitro*	–	Inhibition of fungal growth	Puroindolines and nonspecific lipid transfer protein (proteins)	Dubreil et al. (1998)
	F. ulmaria *Plantago major* *Elytrigia elongata*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
F. moniliforme	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
F. nivale	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
F. oxysporum	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	M. azedarach	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)
	M. fragrans	Methanol	100 mg/L	*In vitro*	–	Inhibition of fungal growth	Lignans (metabolites)	Cho et al. (2007)
	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Al-Hazmi (2013)
	F. ulmaria *Chenopodium album*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
	Ricinus communis	Water	5–15%	*In vitro*	–	Inhibition of fungal growth	Not identified	Das and Sarma (2022)
	M. oleifera	Water	500 mg/ml	*In vitro*	–	Inhibition of fungal growth	Not identified	Ibiam et al. (2022)
F. oxysporum f.sp. *lycopersici*	Avocado	Water	1.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Leontopoulos et al. (2022)
F. oxysporum f.sp. *melonis*	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)

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Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
F. semitectum	Neem Black cumin Asafoetida	Hexane	0.1–0.5%	*In vitro*	–	Inhibition of fungal growth	Not identified	Sitara et al. (2008)
F. solani	*M. azedarach*	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)
	Fennel	Essential oil	15 µl per plate	*In vitro*	–	Inhibition of fungal growth	Monoterpenes y sesquiterpenes	Anwar et al. (2009)
	Momordica charantia	Protein extraction buffer	1 mg/ml	*In vitro*	–	Inhibition of fungal growth	α-momorcharin (protein)	Wang et al. (2016)
	F. ulmaria	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
F. verticilloides	*M. azedarach*	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)
	Castor oil plant	Essential oil	1 ml per plate (*in vitro*) 1 ml per tuber fragment (postharvest)	*In vitro* Postharvest	Yam tubers (postharvest)	Inhibition of fungal growth (*in vitro*) Reduce disease incidence (postharvest)	Not identified	Anjorin et al. (2011)
	A. melegueta	Water	25%	*In vitro*	–	Inhibition of fungal growth	Not identified	Gyasi et al. (2022)
Fusarium spp.	Papaya	Ethanol	20 mg/ml	*In vitro*	–	Inhibition of fungal growth	Triterpenes and saponins (metabolites)	Chávez-Quintal et al. (2011)
Helminthosporium sp.	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Al-Hazmi (2013)
H. sativum	*Taraxacum officinale*	Acetic acid:acetone	250 µg/ml	*In vitro*	–	Inhibition of fungal germination and growth	2S albumins (proteins)	Odintsova et al. (2010)
Macrophomina phaseolina	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Magnaporthe oryzae (syn. *Pyricularia oryzae)*	Neem	Oil extract	1 ml per plate (*in vitro*) 0.1% (leaves spraying)	*In vitro* Greenhouse (*in planta*)	Rice	Inhibition of fungal growth (*in vitro*) Reduction of disease incidence and severity (*in planta*)	Not identified	Amadioha (2000)
	M. fragrans	Methanol	50 mg/L (*in vitro*) 50 mg/L (*in planta*)	*In vitro* Greenhouse (in *planta*)	Rice (*in planta*)	Inhibition of fungal growth (*in vitro*) Reduced disease incidence (*in planta*)	Lignans (metabolites)	Cho et al. (2007)
Monosporascus cannonballus	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Mucor spp.	Pawpaw	Water	2%	*In vitro*	–	Inhibition of fungal growth	Not identified	Obinna and Abikoye (2010)
Nectria kaematococca	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)

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Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Neofusicoccum parvum	*Sinapis arvensis*	Water	10%	*In vitro*	–	Inhibition of fungal growth	Phenols and aromatic amines (metabolites)	Khatami et al. (2015)
Neonectria ditissima (syn. *N. galligena*)	Neem	Methanol	1000 ppm	*In vitro*	–	Inhibition of fungal growth	6-deacetylnimbin	Govindachari et al. (1998)
Penicillium chrysogenum	Cabbage Cauliflower Cress Turnip	Water	0.2 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Abdel-Mallek (1995)
P. funiculosum	Hop	Methanol	0.15 mg/ml	*In vitro*	–	Inhibition of fungal growth	Catechin and epicatechin (metabolites)	Alonso-Esteban et al. (2019)
P. italicum	Pomegranate	Methanolic	500–1500 ppm per plate	*In vitro*	–	Inhibition of fungal germination and growth	Not identified	Tehranifar et al. (2011)
P. ochrochloron	Hop	Methanolic	0.15 mg/ml	*In vitro*	–	Inhibition of fungal growth	Catechin and epicatechin (metabolites)	Alonso-Esteban et al. (2019)
P. verrucosum var. *cyclopium*	Hop	Methanolic	0.15 mg/ml	*In vitro*	–	Inhibition of fungal growth	Catechin and epicatechin (metabolites)	Alonso-Esteban et al. (2019)
Pestalotiopsis mangiferae	Neem	Methanol	1000 ppm	*In vitro*	–	Inhibition of fungal growth	6-deacetylnimbin	Govindachari et al. (1998)
Phaeosphaeria nodorum (syn. *Stagonospora nodorum*)	*F. ulmaria* *C. album*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
Phoma betae	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	T. officinale	Acetic acid:acetone	250 µg/ml	*In vitro*	–	Inhibition of fungal germination and growth	2S albumins (proteins)	Odintsova et al. (2010)
Puccinia graminis f.sp. *tritici*	*A. esculentus*	Aqueous	50 µl per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Jayaseelan et al. (2013)
P. triticina (syn. *P. recondita* f. sp. *tritici*)	Peanut *C. obtusifolia* Soybean *P. multiflorus* Pea *C. sinensis*	Methanol	250 mg/L	*In vitro*	–	Inhibition of fungal growth	Not identified	Lee et al. (1998)
	M. fragrans	Methanol	50 mg/L	Greenhouse (in *planta*)	Wheat	Reduced disease incidence	Lignans (metabolites)	Cho et al. (2007)
Rhizoctonia solani	*S. tora*	Chloroform	2 g/L leaves spray	Greenhouse (*in planta*)	Rice	Reduced disease incidence	Emodin, physcion and Rhein (metabolites)	Kim et al. (2004)
	M. fragrans	Methanol	90 mg/L (*in vitro*) 50 mg/L (*in planta*)	*In vitro* Greenhouse (in *planta*)	Rice (*in planta*)	Inhibition of fungal growth (*in vitro*) Reduced disease incidence (*in planta*)	Lignans (metabolites)	Cho et al. (2007)
	Fennel	Essential oil	15 µl per plate	*In vitro*	–	Inhibition of fungal growth	Monoterpenes y sesquiterpenes	Anwar et al. (2009)

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Table 2 (*continued*)

FUNGI	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Rhizopus spp.	Pawpaw	Water	2%	*In vitro*	–	Inhibition of fungal growth	Not identified	Obinna and Abikoye (2010)
R. oryzae	Seabuckthorn	Dimethylsulfoxide	10 µl per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Gupta et al. (2011)
R. stolonifer	Cabbage Cauliflower Cress Turnip	Water	0.2 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Abdel-Mallek (1995)
	Pomegranate	Methanolic	500–1500 ppm per plate	*In vitro*	–	Inhibition of fungal germination and growth	Not identified	Tehranifar et al. (2011)
Sclerotinia sclerotiorum	*M. azedarach*	Ethanol	5–25 mg/ml	*In vitro*	–	Inhibition of fungal growth	Vanillin, 4-hydroxy-3-methoxycinnamaldehyde and pinoresinol (metabolites)	Carpinella et al. (2003)
	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Thilaeviobsis sp.	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Al-Hazmi (2013)
Tilletia indica	Seabuckthorn	Dimethylsulfoxide	10 µl per plate	*In vitro*	–	Inhibition of fungal growth	Not identified	Gupta et al. (2011)
Ulocladium sp.	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)
Verticillum albo-atrum	*T. officinale*	Acetic acid:acetone	250 µg/ml	*In vitro*	–	Inhibition of fungal germination and growth	2S albumins (proteins)	Odintsova et al. (2010)
V. dahliae	Onion	Protein extraction buffer	300 mg/ml	*In vitro*	–	Inhibition of fungal growth	Plant lipid transfer proteins	Cammue et al. (1995)
	Wheat	Diethylether:ethanol	300 µg/ml	*In vitro*	–	Inhibition of fungal growth	Puroindolines and nonspecific lipid transfer protein (proteins)	Dubreil et al. (1998)
	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of fungal growth	Not identified	Sarpeleh et al. (2009)

chemicals responsible for inhibiting the growth of pathogenic fungi, such as *Fusarium* spp., *Aspergillus* spp., *R. solani*, and *Colletotrichum gloeosporioides* (Anwar et al., 2009; Kannan et al., 2009; Chávez-Quintal et al., 2011). In a specific case, the limonoid 6-deacetylnimbin has been identified as the single terpene responsible for the antifungal activity of neem seed extracts. This triterpene, found in the methanolic extract of neem seeds, can inhibit up to 70% of the *in vitro* growth of fungal plant pathogens such as *Neonectria ditissima* and *Pestalotiopsis mangiferae* (Govindachari et al., 1998).

Furthermore, seed extracts contain various types of flavonoids, which are potent antimicrobial phytochemicals acting through mechanisms such as membrane disruption, inhibition of biofilm formation, inhibition of cell envelope synthesis, inhibition of nucleic acid synthesis, or inhibition of the electron transport chain and ATP synthesis (Górniak et al., 2019). Some flavonoids, such as catechin and epicatechin, have been identified in hop seed extracts and have been associated with the *in vitro* growth inhibition of important plant pathogens such as *Penicillium funiculosum*, *P. ochrochloron*, *P. verrucosum* var. *cyclopium*, and *A. niger* (Alonso-Esteban et al., 2019).

In terms of *in planta* studies, there is limited research on the application of seed extracts for controlling pathogenic fungi. However, there is one notable study conducted with lignans in various plant species and with different pathogens. In this study, the antifungal capacity of lignans against a wide range of fungi has been demonstrated, including *A. alternata*, *Blumeria graminis*, *Colletotrichum coccodes*, *C. gloeosporioides*, *F. oxysporum*, *B. cinerea*, *Magnaporthe oryzae*, and *R. solani*, *in vitro*. However, when these lignan-rich extracts from *Myristica fragrans* seeds were applied *in planta*, they only resulted in disease reduction caused by *B. cinerea* on tomato (7% reduction), *M. oryzae* on rice (100% reduction), *Puccinia triticina* on wheat (93% reduction), and *R. solani* on rice (75% reduction) (Cho et al., 2007).

4.3. Oomycete pathogens

The studies performed on the use of seed extracts as a biological control strategy against oomycete plant pathogens are compiled in Table 3. Many *in vitro* studies have investigated the inhibitory effects of seed extracts on the growth and germination of oomycete

Table 3
Use of seed extracts in the control of plant pathogenic oomycetes.

OOMYCETES	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Phytophthora drechsleri	Wild rue	Water	200 µl	*In vitro*	–	Inhibition of oomycete growth	Not identified	Sarpeleh et al. (2009)
P. infestans	*S. tora*	Chloroform	2 g/L leaves spray	Greenhouse (*in planta*)	Tomato	Reduced disease incidence	Emodin, physcion and rhein (metabolites)	Kim et al. (2004)
	Myristica fragrans	Methanol	50 mg/L	Greenhouse (*in planta*)	Tomato	Reduced disease incidence	Lignans (metabolites)	Cho et al. (2007)
	Psoralea corylifolia	Methanol	5%	In seedlings	Tomato	Reduced disease incidence	Furanocoumarins (metabolites)	Shim et al. (2009)
	Taraxacum officinale	Acetic acid:acetone	250 µg/ml	*In vitro*	–	Inhibition of oomycete growth	2S albumins (proteins)	Odintsova et al. (2010)
	Nigella sativa	Methanol	Not indicated	*In vitro*	–	Inhibition of oomycete growth	Different proteins	Oshchepkova et al. (2013)
	Terminalia bellerica *Psoralea corylifolia*	Acetone Methanol Hexane	500 ppm	*In vitro*	–	Inhibition of oomycete growth	Not identified	Rani et al. (2015)
	Filipendula ulmaria *N. sativa*	Hexane Ethyl acetate	2–10%	*In vitro*	–	Inhibition spore germination	Not identified	Pushkareva et al. (2017)
P. megakarya	*Thevetia peruviana*	Methanol	12.5–50 ml/L	*In vitro*	–	Inhibition of oomycete growth	Not identified	Ambang et al. (2010)
Pythium aphanidermatum	Neem	Methanol	1000 ppm	*In vitro*	–	Inhibition of oomycete growth	6-deacetylnimbin	Govindachari et al. (1998)
	Bitter kola	Water	150 ml per plate	*In vitro*	–	Inhibition of oomycete growth	Not identified	Suleiman and Emua (2009)
	Neem	Ethanol	0.5 ml per plate	*In vitro*	–	Inhibition of oomycete growth	Not identified	Al-Hazmi (2013)
P. ultimum	*M. fragrans*	Methanol	50 mg/L	*In vitro*	–	Inhibition of oomycete growth	Lignans (metabolites)	Cho et al. (2007)

zoospores. However, most of the specific phytochemicals responsible have not yet been identified. These studies include seed extracts from plants, such as neem, bitter kola, wild rue, *Terminalia bellerica*, *Filipendula ulmaria*, *N. sativa*, or *Thevetia peruviana*, against pathogenic oomycetes including *Phytophthora drechsleri*, *P. infestans*, *P. megakarya*, or *Pythium aphanidermatum* (Sarpeleh et al., 2009; Suleiman and Emua, 2009; Al-Hazmi, 2013; Rani et al., 2015; Pushkareva et al., 2017).

Several proteins isolated from seed extracts have been described to possess oomyceticidal, as well as antifungal, capacity, such as 2S albumins against *P. infestans* (Odintsova et al., 2010). Additionally, numerous secondary metabolites present in seed extracts have been identified as antifungal agents with oomyceticidal activity, including lignans against *P. infestans* and *P. ultimum* (Cho et al., 2007), and 6-deacetylnimbin against *P. aphanidermatum* (Govindachari et al., 1998).

Coumarins, which are phenylpropanoids widely known as iron-mobilizing compounds secreted by roots, have gained significant interest due to their antimicrobial activity in recent years. These secondary metabolites penetrate the cell walls and membranes of microorganisms, causing severe damage to cytosolic organelles and genetic material (Stringlis et al., 2019). The use of methanolic extracts from *Psoralea corylifolia* seeds has been shown to reduce disease incidence in tomato seedlings caused by *P. infestans*. These extracts primarily contained the furanocoumarins psoralen and isopsolaren (Shim et al., 2009).

4.4. Plant-parasitic nematodes

The use of seed extracts against plant-parasitic nematodes has shown numerous successful cases, from laboratory to field studies, which are compiled in Table 4. However, many of these studies did not identify the specific phytochemicals responsible for the nematicidal capacity of these extracts. *In vitro* experiments have demonstrated that water and methanolic extracts from marigold and neem seeds can cause mortality of *Heterodera schachtii* juveniles up to 15% (Riga et al., 2005) and *M. incognita* up to 80% (Elbadri et al., 2008). Aqueous extracts of castor bean applied to tomato plants have been shown to reduce gall formation, egg masses, and juvenile populations of *Meloidogyne* spp., leading to improvements in plant growth, such as increased height and fresh shoot weight (Tibugari et al., 2012; Adomako and Kwoseh, 2013; El-Nagdi and Youssef, 2013). Moreover, the application of aqueous extracts directly onto plant-parasitic nematodes had no effect, indicating that the extracts primarily affect nematodes within the plant (El-Nagdi and Youssef, 2013). In field studies, the application of aqueous extracts from baker tree and neem seeds significantly reduced the disease caused by *M. incognita* in tomato plants, resulting in a notable reduction in nematode population density, root-knot index, and significant increases in yield per plant and total yields (Taye et al., 2012).

In response to attack by plant-parasitic nematodes, plants accumulate nematicidal defense proteins locally and systemically, including chitinases, glucanases, and proteases (Poveda et al., 2020b). For instance, exudation extracts rich in various defense-related proteins, such as β-1,3-glucanase, chitinase, lectin, trypsin inhibitor, and lipoxygenase, have been obtained through the maceration of soybean seeds. The application of these extracts *in vitro* to *M. incognita* caused a reduction in egg hatching and 100% mortality in second-stage juveniles. Additionally, their application to tobacco plants resulted in a 90% reduction in gall numbers. These findings suggest that the exuded proteins play a direct role in plant defense against soil pathogens, including nematodes, during seed germination (Rocha et al., 2015).

On the other hand, the nematicidal activity of GSLs has been widely described, primarily in the form of their hydrolysis products, the isothiocyanates. These phytochemicals act against nematodes by exerting direct toxicity, reducing nematode movement, reproduction and egg hatching, while also increasing populations of nematophagous bacteria and saprophytic nematodes in the soil (Eugui et al., 2022). *In vitro* application of seed extracts rich in isothiocyanates from rapeseed, turnip, papaya, *Lepidium sativum*, or *Brassica carinata* has resulted in juvenile mortality rates of 90–100% for nematodes with different life habits, such as *H. schachtii* (cyst-forming endoparasite), *M. incognita* (gall-forming endoparasite), or *Xiphinema americanum* (ectoparasite) (Lazzeri et al., 1993; Jing and Halbrendt, 1994; Nagesh et al., 2002).

Other secondary metabolites present in seed extracts have also shown promising *in vitro* results against plant-parasitic nematodes, including transanethole, estragole, linalool, α-terpineol, azadirachtin, or colchicine. The essential oil of anise seeds contains secondary metabolites of great gastronomic interest, some of which may possess nematicidal activity. It has been observed that the presence of secondary metabolites such as transanethole, estragole, linalool, and α-terpineol in this essential oil can significantly reduce the egg hatching of *M. incognita* (Ibrahim et al., 2006). Colchicine is a widely known secondary metabolite with antimitotic properties, often used in genetic studies and crop breeding, such as seedless watermelon (Hassan et al., 2020). It has also been described to have nematicidal potential when present in extracts from *Gloriosa superba* seeds, resulting in 40% mortality and a 50% reduction in motility of *M. incognita* juveniles (Nidiry et al., 1993).

One of the most extensively studied metabolites with nematicidal properties is azadirachtin, which has been proposed as a biorational tool in integrated nematode management programs (Khalil, 2013). Azadirachtin is a specific metabolite found in neem seeds and is available in various formulations. One commercial product derived from neem seed extracts was able to completely inhibit the mobility *in vitro* of *Meloidogyne* spp. (Gravanis et al., 2011). Additionally, when applied to tomato plants, these commercial azadirachtin-rich products reduced the number of egg masses formed by *M. javanica* on the roots. Furthermore, when a split-root system was used, the systemic effect of azadirachtin was observed, indicating that it can activate plant defenses systemically and/or be actively transported by the roots (Javed et al., 2007). The use of neem seed extracts containing azadirachtin and other tetranortriterpenoids (such as salannin, desacetylsalannin, nimbin and desacetylnimbin) has shown efficient results in the control of plant-parasitic nematodes both *in vitro* and *in planta*. These neem seed extracts caused more than 98% mortality of juveniles *in vitro* and, in the soybean-*Heterodera glycines* interaction, they resulted in an 84% reduction in the number of females and a 90% reduction in the number of eggs (Silva et al., 2008).

Table 4
Use of seed extracts in the control of plant parasitic nematodes.

NEMATODES	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
Heterodera glycines	Neem	Water Methanol	1000 mg/ml	*In vitro* Greenhouse (*in planta*)	Soybean	Increased mortality rates of nematode juveniles (*in vitro*) Reduced egg hatch (*in vitro*) Reduced female and egg number (*in planta*)	Tetranortriterpenoids	Silva et al. (2008)
H. schachtii	Rapeseed *Lepidium sativum* Turnip *Brassica carinata*	Methanol	1% + 0.3 units of myrosinase enzyme	*In vitro*	–	Increased mortality rates of nematode juveniles	Isothiocyanates (metabolites)	Lazzeri et al. (1993)
	Marigold	Water	Not indicated	*In vitro*	–	Increased mortality rates of nematode juveniles	Not identified	Riga et al. (2005)
Meloidogyne spp.	Neem	(comercial producto)	5–10 %	*In vitro*	–	Reduced juveniles mobility	Azadirachtin (metabolite)	Gravanis et al. (2011)
	Castor bean	Water	10–40% (*in vitro*) 20–60% (*in planta*)	*In vitro* Greenhouse (*in planta*)	Tomato	Increased mortality rates of nematode juveniles (*in vitro*) Reduced egg hatch (*in vitro*) Reduced disease incidence (*in planta*)	Not identified	Adomako and Kwoseh (2013)
M. hapla	Neem	(comercial product)	2000–10000 ppm	*In vivo*	Carrots	Reduced gall and egg numbers	Not identified	Douda et al. (2010)
M. incognita	*Argemone mexicana*	Water	5 ml	*In vitro*	–	Reduced nematodes motility	Triglyceride (lipid)	Saleh et al. (1987)
	Gloriosa superba	Methanol	5%	*In vitro*	–	Increased mortality rates of nematode juveniles Reduced nematodes motility	Colchicine (metabolite)	Nidiry et al. (1993)
	Papaya	Methanol	25 ppm	*In vitro*	–	Increased mortality rates of nematode juveniles	Benzyl isothiocyanate (metabolite)	Nagesh et al. (2002)
	Parkia biglobosa	Ethanol	5 ml per plant at 1000 ppm	Greenhouse	Tomato	Reduced disease incidence and juveniles population	Not identified	Bawa et al. (2014)

(*continued on next page*)

Table 4 (*continued*)

NEMATODES	SEED	EXTRACT TYPE	DOSAGE	TYPE OF EXPERIMENT	CROP	EFFECT	METABOLITES/MOLECULES INVOLVED	REFERENCES
	Anise	Essential oil	1 mg/L	*In vitro*	–	Reduced egg hatch	Transanethole, estragole, linalool and α-terpineol (metabolites)	Ibrahim et al. (2006)
	Neem	Methanol	500 ppm	*In vitro*	–	Increased mortality rates of nematode juveniles	Not identified	Elbadri et al. (2008)
	Baker tree Neem	Water	5% in irrigation water	In field	Tomato	Reduced nematode population and disease incidence	Not identified	Taye et al. (2012)
	Castor bean	Water	0.1 g/ml in irrigation	Greenhouse	Tomato	Reduced galls and egg masses Reduced juveniles population	Not identified	El-Nagdi and Youssef (2013)
	Soybean	Acetate buffer	60–500 mg of protein/L	In vitro Greenhouse (*in planta*)	Tobacco (*in planta*)	Increased mortality rates of nematode juveniles (*in vitro*) Reduced egg hatch (*in vitro*) Reduced disease incidence (*in planta*)	β-1,3-glucanase, chitinase, lectin, trypsin inhibitor and lipoxygenase (proteins)	Rocha et al. (2015)
	Solanum stramonifolium	Water	100 μg/ml	*In vitro*	–	Increased mortality rates of nematode juveniles number (*in planta*)	Not identified	Costa et al. (2022)
M. javanica	Neem	(commercial product)	0.05–0.1% w/v in roots immersion	Growth chamber	Tomato	Reduction of egg masses per root	Azadirachtin (metabolite)	Javed et al. (2007)
	Castor bean	Water	10 ml	Greenhouse	Tomato	Reduced gall formation	Not identified	Tibugari et al. (2012)
Radopholus similis	Neem	Organic, watery and essential oil extracts	10–50 μl/mg (in plates) 10–50 μl/ml of soil (*in planta*)	*In vitro* Geenhouse (*in planta*)	Plantain	Nematode death (*in vitro*) Lower incidence of disease (*in planta*)	Alkaloids, saponins, triterpens and steroids (metabolites)	Kosma et al. (2011)
Xiphinema americanum	Rapeseed	Methanol	3–13%	*In vitro*	–	Nematode death	Isothiocyanates (metabolites)	Jing and Halbrendt (1994)

5. Conclusions and future perspectives

In the current context, there are several important factors that support the use of biological products to combat pathogens affecting major crops in agricultural systems. Contemporary societies, particularly in highly developed countries, are increasingly aware of the detrimental effects of chemical biopesticides on the environment, which jeopardizes the sustainability of ecological systems. As a result, there is a growing demand that urges governments to impose stricter regulations on the use of such products. Several governments, including the European Union, have responded to these demands by incorporating them into their policies. In this regard, the EU has implemented the Farm to Fork Strategy as part of its European Green Deal, which aims to reduce the use of chemical pesticides by 50% by 2030, among other measures. Consequently, many companies are currently investing significant resources in finding environmentally friendly alternatives that meet these requirements.

Moreover, as people fulfill their basic needs, there is an increasing desire for healthier food produced in systems that respect nature, the environment and wildlife, whenever possible. Many individuals are even willing to pay a little extra for these products. Companies have recognized this shift in consumer preferences and are increasingly offering new food products labeled as healthy, organic or bio, as they have observed that these products are more appealing to consumers. Additionally, the widespread use of synthetic chemical products derived from non-renewable resources is becoming increasingly challenging and expensive. Firstly, these resources are becoming scarcer, making their acquisition more complicated. Furthermore, they are often controlled by a few countries that completely dominate the prices. The ongoing global inflationary crises have underscored the importance for countries to have access to their own resources.

Among the various alternatives, this review demonstrates that seed extracts from several plant species can be highly effective in controlling plant pathogens. Numerous examples have been included, showcasing their antagonistic effects on a wide range of phytopathogens. However, despite the multitude of studies highlighting their positive effects, the extensive and widespread use of these bio-products is still far from becoming a reality. Most of the studies mentioned here have been conducted *in vitro* or under highly controlled conditions. Field studies are scarce and often yield contradictory results, indicating that their actual effectiveness in real-world conditions may be limited. Consequently, more fundamental research is still required to precisely understand the underlying mechanisms responsible for the observed results. This knowledge will aid in the development of products that are effective under practical field conditions and applicable to a wide range of crops and pathogens.

Another important aspect to consider is that, similar to synthetic pesticides, these biological products could also have a negative impact on beneficial organisms. Although several studies have confirmed the safety of these extracts on various animal and fungal species, they should still undergo a battery of tests to evaluate their safety for other different groups of organisms, just like their synthetic chemical counterparts.

In conclusion, this review has demonstrated that seed extracts possess tremendous potential as environmentally friendly alternatives to synthetic pesticides for combating phytopathogens, as they have exhibited clear antagonistic effects against numerous harmful organisms. However, in most cases, widespread and extensive use of these bio-products has yet to be achieved, as the promising results observed in the laboratory often fail to be replicated in the field under real conditions. A comprehensive understanding of the mechanisms underlying the observed effects *in vitro* could facilitate the development of new procedures to enhance their effectiveness and optimize their utilization in the field. Governments, research centers and companies must continue to invest efforts and resources to make their practical use a reality.

CRediT authorship contribution statement

Tamara Sánchez-Gómez: Investigation, Writing – original draft, Writing – review & editing. **Óscar Santamaría:** Writing – review & editing. **Jorge Martín-García:** Writing – review & editing. **Jorge Poveda:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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