Plant Pathol. J. 41(2) : 121-139 (2025)
https://doi.org/10.5423/PPJ.RW.07.2024.0108
eISSN 2093-9280

The Plant Pathology Journal
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Review Open Access

Exploring the Perilous Nature of *Phytophthora*: Insights into Its Biology, Host Range, Detection, and Integrated Management Strategies in the Fields of Spices and Plantation Crops

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(Received on July 19, 2024; Revised on January 29, 2025; Accepted on February 1, 2025)

The horticultural crops, including spices and plantation crops, are known for their enormous benefits, contributing to the country's economy. However, *Phytophthora*, a genus of Oomycetes class, poses a threat to spice and plantation crops by infecting and damaging them, resulting in yield losses, economic hardship for farmers, and food security concerns, thereby threatening the sustainability of spice and plantation crops. Moreover, *Phytophthora* has greater adaptation systems in varying environmental conditions. Therefore, eradicating or controlling *Phytophthora* is a highly challenging process due to the longevity of its infective propagules in soil. Early detection and curative measures would be more effective in managing this destructive pathogen. Additionally, molecular detection using innovative methods such as polymerase chain reaction, reverse transcription polymerase chain reaction, recombinase polymerase amplification, and loop-mediated isothermal amplification would offer reliable and rapid detection. Furthermore, integrated disease management strategies, combining cultural, physical, chemical, and biological methods, would prove highly beneficial in managing *Phytophthora* infections in spices and plantation crops. This review provides a comprehensive overview of the diversity, symptomatology, pathogenicity, and impact of *Phytophthora* diseases on prominent spice and plantation crops. Finally, our review explores the current disease reduction strategies and suggests future research directions to address the threat posed by *Phytophthora* to spices and plantation crops.

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Handling Editor : Junhyun Jeon

Keywords **:** biological, IDM, LAMP, *Phytophthora*, RT-PCR, yield losses

The spices and plantation crops have long been recognized for their enduring benefits over centuries. Spices were esteemed as some of the most valuable trade items in the ancient and medieval world (Vasanthi and Parameswari, 2010). The global spice production stands at around 13.1 million tonnes. In addition to spices, plantation crops play a pivotal role in soil conservation, ecosystem preservation, and employment generation within the agriculture sector (Chowdappa et al., 2014). According to estimates from 2022-2023, the total production of plantation crops in India alone is expected to be around 16.05 million tonnes (Ministry of Agriculture and Farmers Welfare, 2022-2023). However, significant concerns surrounding these crops include high production costs, small-scale cultivation, poor quality standards, and competition for land (Herath, 2002).

The spices and plantation crops encounter various biotic and abiotic stresses (Vinod, 2011). These crops are susceptible to a range of fungal, bacterial, and viral diseases, leading to significant reductions in yield. Major spice crop diseases include wilt, root rot, blight, mildew, and leaf spots. In contrast, plantation crops are impacted by rot diseases, causing substantial declines in crop production and yield. *Phytophthora* species have become a significant concern among the major fungal diseases affecting spice and plantation crops due to their highly destructive impact. Based on epidemiological prowess and virulence, *Phytophthora* species is considered one of the most destructive genera in temperate and tropical regions, causing annual damages in billions (Drenth and Guest, 2004).

The *Phytophthora* genus is known to infect a variety of spices and plantation crops. The *Phytophthora* taxonomy has undergone many evolutions during the study. Based on nuclear and mitochondrial characteristics, 12 well defined clades have been recognized till now (Brasier et al., 2022). The twelve-clade internal transcribed spacer (ITS) phylogeny is a phylogenetic tree constructed based on sequence data from the ITS region. This framework provides a structured way to classify and understand the diversity within the genus. An abundance of *Phytophthora* species is noticed in forest soils, streams, and canopies. Still, more natural ecosystems and new species are yet to be described (Hansen et al., 2012).

The emergence of new genotypes and global migration has increased the risk of spreading *Phytophthora* species. Interspecific hybridizations have a remarkable impact on the genome characteristics of this oomycete pathogen. These genera do not seem to synthesize sterols, which makes the fungicidal treatments ineffective (Avila-Quezada and Rai, 2023). According to global data, the notorious *Phytophthora* species remain significant obstacles to horticulture forestry and agriculture (Abad et al., 2023), leading to substantial yield losses. Detailed information about different *Phytophthora* species infecting major spices and plantation crops is unavailable. Therefore, the main aim of this review is to understand the nature, biology, geographical distribution, host range, symptomology, and complexity of the perilous pathogen, their timely detection using advanced molecular tools, and also the integrated disease management (IDM) strategies to combat the awful phytopathogen-*Phytophthora* infecting spices and plantation crops.

Phytophthora-as Soilborne Pathogen and Its Disease Cycle

Phytophthora, a member of the oomycete, is considered a threat which has revisited the 21st century (Guha Roy, 2015). It is considered the world's most historic and economically significant genus in plant pathology. *Phytophthora* members, are considered severe threats to agriculture as well as horticulture causing diseases in hundreds of crops. Similarly, the spices and plantation crops are highly susceptible to this genus, which remains persistent for many years. The first *Phytophthora* species identified was *Phytophthora infestans* (De Bary, 1876)—the pathogen responsible for late blight in potatoes, having a significant history dating back to the mid-19th century when it caused the Great Irish Famine in 1845. The impact of the epidemic was so catastrophic and sound. This famine, on average, killed more than one million people (Turner, 2005). Till today, the late blight of potatoes remains a destructive disease leading to an annual loss of potatoes. Likewise, *Phytophthora* spp. remain a persisting pathogen in the fields of spices and plantation crops extending its damage at greater levels. Some common pathogenic effects of *Phytophthora* are leaf blights, collar rot, root rot, stem canker, and fruit rots. This genus consists of both necrotrophic and biotrophic species parasitizing a wide range of host plants, substantially leading to losses in millions worldwide. *Phytophthora*, also known as the "Plant Destroyer," has more than 200 identified species, with additional species being identified each year.

The soil serves as a favorable habitat for various microorganisms, including fungi, bacteria, viruses, algae, and protozoa (Lucas, 2006). The ability of some microorganisms to infect plants are so-called soilborne pathogens, and they tend to complete their entire life cycle in soil or a part of their life cycle in the aerial parts. According to the research studies and economic impact, soilborne pathogens seem to affect crops worldwide, and their control is quite complex (Lucas and Sarniguet, 1998). Since the spice and plantation crops are perennial in nature, the pathogen survives as resting spores in the soil for many years serving as primary source of inoculum causing infections when the environmental conditions favor.

Successful disease establishment of these pathogens occurs only after the completion of the disease cycle. For an infection to be successful, first, the pathogen makes contact with the plant and gets itself attached to the surface of the host. This is followed by penetration, wherein the nutrients required for efficient growth and sporulation are driven (Hardham, 2001). The disease cycle occurs *viz*. the following stages: (1) Initial contact with the host, (2) Encystment of the zoospore and plant surface adhesion, (3) Spore germination and penetration into the host, (4) Colonization of the host plant, (5) Nutrient acquisition from the host, and (6) Sporulation.

Systematic Position and Classification – *Phytophthora* species

The water moulds *Phytophthora* though tend to resemble the members of fungi, they are placed in the Kingdom Chromista and the Phylum Oomycota (Beakes and Sekimoto, 2009). The genus *Phytophthora* has been widely acknowledged as taxonomically 'difficult' (Brasier, 1983), as many of the characters used for species identification are plastic, highly influenced by the environment, show overlap between species, and have an unknown genetic basis. The higher classification levels have led to the placement of this genus in the order Perenosporales, class Perenosporomycete, and the family Perenosporaceae (Abad et al., 2023). *Phytophthora* classification was based on morphology (Waterhouse, 1963). Advancements in DNA sequencing paved the way for the classification based on molecular phylogeny. Later, the progress made by Cooke et al. (2000) led to the first molecular phylogenic classification of 51 species, wholly based on the sequences of ITS regions placed into eight well defined clades (Clade 1 to 8) followed by two potentially distant clades (Clade 9 and 10).

Further evolutions led to species classification based on the nuclear and mitochondrial genes (Kroon et al., 2004). Later, Blair et al. (2008) made phylogenetic sequences based on seven genetic markers. Rahman et al. (2015) paved way for the addition of eleventh clade (Clade 11) which was followed by Jung et al. (2017) who proposed the addition of the twelfth clade (Clade 12) using multigene phylogeny.

Bourret et al. (2018) proposed some additional clades from 13 to 16, where the provisional *Phytophthora* species has been placed in these clades. At present, the genus *Phytophthora* comprises a total of 266 described species spread across 17 phylogenetic clades with additional clades under the inclusion process (Abad et al., 2023).

Pathogen Biology and Life Cycle

Phytophthora is primarily soil and water-inhabiting oomycetes and exhibits a range of pathogenic natures, from hemi-biotrophic to necrotrophic, forming zoosporic sporangia. *Phytophthora* species are distinguishable from the higher fungi, through distinct features, like the occurrence of coenocytic hyphae with subtle constrictions at the base of their branches forming right angles (Brasier et al., 2022). Additionally, they produce sporangiophores containing laterally biflagellate zoospores enclosed within the sporangium (Ho, 2018). Furthermore, the genus is characterized by a spherical oospore with a limited periplasm in the globose oogonium.

Phytophthora species can exhibit either homothallic characteristics, producing abundant sexual organs within single cultures, or heterothallic traits, necessitating pairing in dual cultures with compatible A1 or A2 mating types. The oospore is typically spherical and hyaline, although it may sometimes appear yellowish. Usually, only one antheridium is present per oogonium, and the presence of the amphigynous antheridium remains a distinct and unique feature of *Phytophthora* in the monotypic genus (Tabor and Bunting, 1923).

Most *Phytophthora* spores are asexual spores with specialized hyphae known as the sporangiophores. They are branched and bear many numbers of multinucleate spores called sporangia or zoosporangia (Bartnicki-Garcia and Wang, 1983). The sporangia have a distinct ability to germinate using two different pathways via direct and indirect germination (Situ et al., 2022). Higher temperatures favor direct germination, where hyphae formation occurs through the sporangial wall (Judelson and Blanco, 2005). Indirect germination is highly favored in cooler temperatures. Environmental conditions play a crucial role in the survival and spread of *Phytophthora* species in the spice and plantation crop fields. The continuous wet, humid and damp conditions facilitate rapid movement of zoospores, increasing plant susceptibility, while also enhancing the pathogen's ability to survive as resting spores in soil for many years

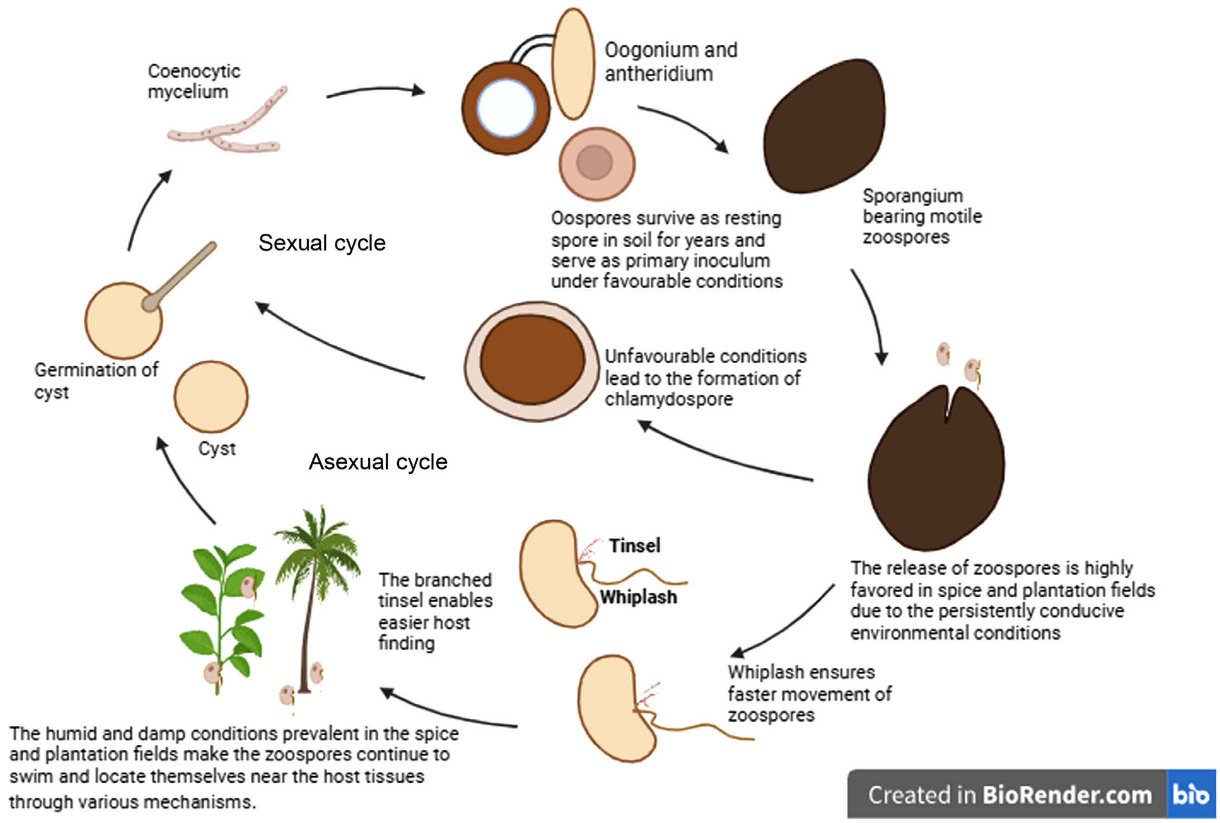

Fig. 1. Life cycle of *Phytophthora* species infecting spices and plantation crops. *Phytophthora* completes its life cycle viz. sexual and asexual phases. In case of asexual reproduction, the cycle begins through zoospore-favorable conditions ensure fast movement and successful infection- zoospores enter the encystment phase at low temperature- germination of encysted zoospore giving rise to infective hyphae- In sexual phase amphigynous type of reproduction takes place-giving rise to diploid oospores.

under unfavourable conditions.

Further colonization in the host plants takes place through the help of natural openings. The escape of wall less zoospores take place as a result of the dissolution of the sporangium. The zoospores freed by the turgor pressure (Ambikapathy et al., 2002) continue to swim and locate themselves near the host tissues through various mechanisms. Both homothallic and heterothallic mating systems are noticed in the oomycetes. The thick-walled oospore peculiar to Oomycetes helps in sexual reproduction. The sexual cycle is initiated by forming both male and female gametangia (Fabritius et al., 2002), and antheridium makes pairing. This results in synchronous meiosis wherein the fertilization tube is developed between the antheridium and oogonium, and then a single haploid nucleus is transferred from the male to the female. The oospore's maturation results in a multi-layered thick wall, making it an effective resting structure (Judelson, 2009). The schematic representation of the life cycle of *Phytophthora* species infecting spice and plantation crop is depicted in Fig. 1.

Host Range of *Phytophthora* Species

Phytophthora species show more significant variations in their degrees of host specificity (Drenth and Sendall, 2001). They seem to have a broader host range, causing remarkable damage to crop hosts worldwide. For example, *Phytophthora fragariae* var. *rubi* attacks only one host, whereas *P. cinnamomi* can infect as many as 1,000 hosts at varying adaptations (Erwin and Ribeiro, 1996). Some *Phytophthora* species attack the broad host range using certain enzymes (Brasier, 1983). In contrast, some host-specific species interact specifically in a gene-for-gene system with the host's resistance genes. Since the genus is widespread globally, it affects almost all crops worldwide, including spices and plantation crops. Table 1 shows the list of *Phytophthora* species with their broad host range and geographical distribution.

Table 1. List of *Phytophthora* species and their host range and geographical distribution

Phytophthora sp.	Host range	Geographical distribution	Reference
P. alni	Alders	Sweden, Latvia, Germany, Austria, Italy, Hungary, Europe	Trzewik et al. (2021)
P. brassicae	Brassicaceae	Europe, North America	Hermansen and Hoftun (2005)
P. cactorum	Wide host range	Cosmopolitan	Hudler (2013)
P. capsici	Wide host range	Cosmopolitan	Lamour et al. (2012)
P. cinnamomi	Wide host range	Southern Hemisphere	Hardham and Blackman (2018)
P. citricola	Wide host range	Cosmopolitan	Portz et al. (2011)
P. fragariae	Strawberry	Asia, Australia, New Zealand, Europe, North America	Adams et al. (2020)
P. ilicis	*Illex* spp.	Europe, North America	Scanu et al. (2014)
P. infestans	Solanaceous crops, Tomato, etc.	Cosmopolitan	McLeod et al. (2024)
P. lateralis	Cuppreasceae family	Cosmopolitan	Sniezko et al. (2020)
P. litchi	Litchi	Asia, Europe	Zhang et al. (2021)
P. meadii	Wide host range	Asia, Australia, Europe, Pacific Islands	Dang et al. (2021)
P. megakarya	Cocoa, Irvingia	Africa, Asia	Morales-Cruz et al. (2020)
P. melonis	Cucurbitaceae and Anacardiaceae	Asia	Hashemi et al. (2020)
P. palmivora	Wide host range	Cosmopolitan	Misman et al. (2022)
P. porri	*Allium* spp. *Alnus* spp.	USA, Japan, Netherlands, Europe	Parthasarathy et al. (2016)
P. phaesoli	*Phaseolus* spp.	Africa, Asia, Europe, North and South America, Caribbean islands	Santamaria et al. (2018)
P. quercina	*Quercus* spp.	Asia, Europe, and US	Dorado et al. (2023)
P. ramorum	Wide host range	Europe, North America, USA	Beltran et al. (2024)
P. sojae	Fabaceae	Australia, North America, South America, Asia, New Zealand	Dorrance (2018)
P. syringae	Wide host range	Africa, Australia, Asia, North America, South America, Europe	Harris and Xu (2003)
P. tropicalis	Wide host range	Pacific Islands, North America, Europe	Chávez-Ramírez et al. (2021)
P. ulginosa	*Quercus* spp.	Europe	Mora-Sala et al. (2019)
P. uniformis	*Alnus* spp.	France, Spain, Belgium, Slovenia, USA	Redondo et al. (2017)
P. vignae	Fabaceae and Rosaceae	Asia, Australia	Sun et al. (2021)

Symptomology and Impact of *Phytophthora* on Spices and Plantation Crops

Phytophthora species produce a variety of symptoms depending upon their virulence and environmental conditions. Some common symptoms of *Phytophthora* species include root rot, collar rot, tree cankers, leaf blight, tuber and corm rot, bud rot, and fruit rot (Drenth and Sendall, 2001). They also tend to pose various below and aboveground symptoms, such as rotting of feeder roots, which results in blackening and decay, and some aboveground symptoms, such as pale green leaves, wilting, dieback of shoots, etc. The spices and plantations are highly targeted by *Phytophthora* species, mainly during the monsoon seasons causing severe disasters. *Phytophthora* infections remain a persistent threat to the spice and plantation crops, causing yield losses from 10-100%, leading to severe economic imbalance and impacting the global market system. This genus represents a diverse group of plant pathogens that epitomize global biosecurity issues (Scott et al., 2019).

The various symptoms produced, and the damages caused by *Phytophthora* species in various spice and plantation crops along with their yield losses have been tabulated (Table 2).

Table 2. Devastating impact of *Phytophthora* species and yield losses in key spice and plantation crops

Sl. no.	Name of the spice/plantation crop	Causal organism	Disease name	Symptomatology	Yield loss (%)	Reference
1	Black Pepper	*P. capsici*	Foot rot	The disease initiates as dark, water-soaked lesions at the stem base leading to yellowing, wilting defoliation and dieback. In severe cases, the entire vine rots, collapses and dies.	25-30	Thomas and Naik (2017)
2	Cardamom	*P. meadii*	Capsule rot (Azhukal)	The disease starts with discoloured, water-soaked lesions on capsules and leaves leading to rotting and shredding. Infected capsules turn brown emitting a foul smell and shed prematurely. In advanced stages, it spreads to panicles and tillers, causing complete plant decay and death.	30-40	Thomas et al. (2022)
3	Chilli	*P. capsici*	Phytophthora root rot	Almost all stages of crop get affected *viz.*, damping off, stem blight, fruit rot, leaf blight root rot eventually leading to complete death of the plant.	80-100	Shah et al. (2013)
4	Cinnamon	*P. cinnamomi*	Stripe canker	Brown to black lesions which turn into vertically striped cankers on the bark region followed by gummy exudations, yellowing and wilting leading to dieback, rotting and death of the infected plant	10-40	Andrade-Hoyos et al. (2023)
5	Nutmeg	*P. meadii*	Fruit rot	In the immature nuts the symptom appear as splitting and rotting of fruits which drop prematurely. In the mature nut it causes discolouration of the rind leading to rotting. As the infection advances the mace rots completely emitting a foul smell.	20-35	Sumbula and Matthew (2015)
6	Vanilla	*P. meadii*	Bean rot	The infection starts from the bean tip and extends to the stalk, causing water-soaked, dark brown, and soft beans. In dry conditions, beans shrivel, while in moist conditions, they shed. Whitish pustules develop, leading to rotting, foul odour eventual bunch fall.	23-57	Jithya Dhanesh (2008)
7	Areca nut	*P. meadii/P. palmivora*	Fruit and bud rot	Fruit rot disease manifests as water-soaked lesions on immature nuts later turning black soft and shrivelled, emitting a foul odour and fall off prematurely. Similarly, the bud rot disease begins with yellowing and wilting of the central spindle leaf followed by rotting and foul odour. As the disease progress it leads to collapse of the crown and eventual death of the palm.	10-90	Balangouda et al. (2021)
8	Betel vine	*P. parasitiaca*	Foot and root rot	Water-soaked lesions, rotted base, yellowing and wilting of vines as the infection advances it results in the death of vines.	30-100	Datta et al. (2011)
9	Cocoa	*P.palmivora/ megakarya*	Black pod	The fungus affects almost all stages leading to blackened, dried and mummified pods. The infected pods emit a fishy odour.	10-30	Merga (2022)
10	Oil palm	*P. palmivora*	Bud rot	Chlorosis of the younger leaves followed by necrosis affecting the meristem, collapsing of spear leaf and complete death of the plant	27-90	Moreno-Chacón et al. (2013)
11	Coconut	*P. palmivora*	Bud rot	Young palms are more susceptible, yellowing of leaves, rotting, withering, crown rots and turn slimy emitting a foul smell and the palm eventually dies.	7-21	Prathibha et al. (2023)
12	Rubber	P. palmivora	Abnormal leaf fall	Dull grey to brown spots on leaves, fruits rot, Premature leaf shedding, rotting and foul odour.	38-56	Krishnan et al. (2019)

Molecular Detection and Characterization

Phytophthora activity may vary widely depending on environmental conditions or the availability of host systems, ranging from dormancy to rapid increases in density over a short period. Therefore, a more rapid and sensitive method would ensure timely detection and management. Over the last 15 years, DNA sequence analysis has significantly advanced our comprehension of the diversity and phylogenetic relationships within the *Phytophthora* genus. Molecular diagnostics are widely used for faster and more precise species identification. In order to ensure the exact identification of *Phytophthora* species, various DNA-based identification methods have been explored (Kroon et al., 2012). Nucleic acid-based tools are more sensitive, rapid, and reliable for detecting *Phytophthora* in some essential crops (Cissin et al., 2016; O'Brien et al., 2009) both at the genus and species levels. Various molecular methods were emphasized for successfully detecting and identifying *Phytophthora* species. These methods include protein electrophoresis, determination of isozyme pattern, Direct sequencing of ITS, and polymerase chain reaction (PCR)-based fingerprinting.

For example, the PCR has been a significant molecular taxonomy and detection breakthrough. The advantages of PCR lie in its high specificity, sensitivity, and rapidity compared to traditional methods. PCR has been widely used for the detection of fungal plant pathogens based on the ITS regions of ribosomal DNA (rDNA) (Grote et al., 2002; Willits and Sherwood, 1999). Conventional and closed tube nested PCR was more effective for detecting and identifying *Phytophthora* at the species level. Grote et al. (2002) highlighted the usage of nested PCR as it enables the detection of the pathogen at lower levels and can also be used as a warning tool for the detection and diagnosis at earlier stages. Real-time PCR has the potential to quantify target DNA (Livak and Schmittgen, 2001) accurately. This method proved efficient as it could sense the quality of the DNA within a short span and help produce disease-free plantlets (Huang et al., 2010). Some studies have shown that endonuclease restriction analysis of ITS-restriction fragment length polymorphism (ITS-RFLP) and amplified fragment length polymorphism possess higher levels of resolving power for distinguishing between and within species (O'Neil et al., 1997). A novel and new assay named recombinase polymerase amplification (RPA) performed under isothermal conditions had more significant advantages, including minimal assay time. RPA assays specific to the *Phytophthora* genus were developed by Miles et al. (2015), and the detection limit was found to be 200 to 300 fg. Loop-mediated isothermal amplification (LAMP) is an emerging technique for detecting plant pathogens with higher levels of accuracy using species-specific primers. LAMP is widely known for its low resource utilization and sensitivity (Notomi et al., 2000) (Table 3). Portraying the novel molecular tools used for the detection of *Phytophthora* species in a wide array of spices and plantation crops is given below.

Management Strategies to Combat *Phytophthora*

Phytophthora, a dreadful pathogen, needs a combination of management strategies to avoid crop damage and yield loss. Understanding pathogens' genomic makeup, virulence factors, and epidemiology forms the groundwork for crafting tailored approaches to combat biotic diseases in spices and plantation crops (Scortichini, 2022). IDM, which holistically combines cultural, physical, chemical, and biological control strategies rather than using a single component, was more effective and sustainable (Khoury and Makkouk, 2010). This section provides the current approaches for *Phytophthora* management, including cultural, chemical, genetic, and biological control.

Cultural management. The cultural control method would be the only economically viable method for some crops in the developing country (Khoury and Makkouk, 2010). In order to reduce the incidence of *P. capsici* in chili, cultural practices such as raised beds, mulching, proper irrigation management, and moisture-based forecasting models would ensure reductions in the severity of the disease (Sanogo and Ji, 2013). In black pepper, phytosanitary measures would help reduce the primary inoculum and manage the foot rot disease. Shade regulation can be done to reduce humidity. The vines infected by foot rot symptoms will be uprooted and burnt earlier. Crop rotation with non-host species can be adopted to manage the field's oospores (Babadoost, 2016). Adequate cultural practices favoring the plant and disfavoring the pathogen help reduce the disease severity. According to Granke et al. (2012), a slight angle of inclination of the beds in the rainy season is recommended for proper drainage. Khan et al. (2020) suggested phytosanitary measures such as removing and destroying affected parts and wound dressing with tar to manage the infection. Good drainage is the prime factor in minimizing *Phytophthora* in cinnamon crops. In oil palms, proper drainage and avoidance of overhead irrigation have reduced *P. palmivora* infections (Martínez, 2009). Covering the bunches with polythene effectively prevented foot rot disease in areca nut. Covering the bunches before the monsoon resulted in

Table 3. Molecular tools used for detecting wide range of *Phytophthora species* in spices and plantation crops

Methodology	*Phytophthora* species	Primer	Sequence (5′–3′)	Reference
PCR	*P. capsici*	Pc1F	GTATAGCAGAGGTTTAGTGAA	Lan et al. (2013)
		Pc1R	ACTGAAGTTCTGCGTGCGTT	
PCR	*P. megakarya*	Pmeg ITS_F/R	TGCTCGAAAAGTAAAGCTTGC/AGGAAAAAC-GCCCAATAAGC	Ali et al. (2016)
	P. palmivora	Ppal ITS_F/R	AAAAGCGTGGCGTTGCT/AATCATACCACCACAGCT-GAA	
	P.capsici/ P.citrophthora	Pcap/cit ITS_F/R	TCGAAAAGCGTGGTGTTG/GCCACAGCAG-GAAAAGCATA	
	P.citrophthora	Pcit ITS_F/R	GGGTGTTGCTTGGCATTTT/CACAAAAACCGCAAGA-CACTT	
Nested PCR	*P.nicotianae*	PNIC1	CAATAGTTGGGGGTCTTATT	Grote et al. (2002)
		PNIC2	GTATACCGAAGTACACATTAAG	
	P. capsici	PC-1	GTCTTGTACCCTATCATGGCG	Farhana et al. (2013)
		PC-2	CGCCACAGCAGGAAAAGCATC	
	P. capsici	Pc1F	GTATAGCAGAGGTTTAGTGAA	Lan et al. (2013)
		Pc2R	GACGTTTTAGTTAGAGCACTG	
RT-PCR	*P. capsici*	Phyto_qPCR_F	CTGAACAGGCGCTTATTGAATG	Pandian et al. (2018)
		Phyto_qPCR_R	GAGATGCGCACCGAAGTGCA	
RFLP	*P. meadii*	ITS1 and 4	TCCGTAGGTGAACCTGCGG CCTCCGCTTATTGATAT-GC and restriction enzymes such as *Hinf I*, *Msp I*, *HaeIII*, and *RsaI* were used.	Chowdappa et al. (2003)
AFLP	*P. meadii*	Six AFLP Primers from A-F	A (GACTGCGTACATGCAGGT), B (GACTGCGTA-CATGCAGGA), C (GACTGCGTACATGCAGGC), D (GACTGCGTACATGCAGAC), E (GACTGCGTACATG-CAGAG), and F (GACTGCGTACATGCAGCG)	Chowdappa et al. (2003)
AFLP	*P. capsici*	EcoRI, MseI	GACTGCGTAC CAATTC GATGAGTCCTGAGTAA	Bowers et al. (2007)
RPA	*P. capsici*	PC-YR-FP	CAGATTGTAAGCAACCAAAGTTCAAGACGTTT	Jeevalatha et al. (2021)
		COM-YR-RP	TACGAACCTATCGATCTCATGCAGCCACTG	
	P. tropicalis	PT-YR-FP	AAGCTCCAGATTGTAAG CACTTGTTA TCCATC	Jeevalatha et al. (2021)
		COM-YR-RP	TACGAACCTATCGATCTCATGCAGCCACTG	
LAMP	*P. capsici*	F3	GCTGCGGCGTTTAAAGGA	Dong et al. (2015)
		B3	AGTGCACACAAAGTTCCCAA	
		FIP	ACCCACAGCAGGAAAAGCATT-GAGTGTTCGATTC-GCGGTA	
		BIP	GGCTTGGCTTTTGAATCGGCTT-TGGATCGACCCTC-GACAG	
LAMP	*P. palmivora*	AVM2-F3	CAGGGAACAGTTGTTTGGA	Maizatul-Suriza et al. (2024)
		AVM2-B3	CTGGCTTGGTCGAAGATG	
		AVM2-FIP	CGCCGTCGTCAGCATCTTACGATG TCAATGTGGGTG	
		AVM2-BIP	TCTCTGGAGTACGAGAGTGAC GTCGTCTTGCTC-GAATGTG	
		AVM2-LF	TGACTCCGATGGCAACTTC	
		AVM2-LB	CATCGTCGCTTATCATCTCCT	

PCR, polymerase chain reaction; RT-PCR, reverse transcription polymerase chain reaction; RFLP, restriction fragment length polymorphism; AFLP, amplified fragment length polymorphism; RPA, recombinase polymerase amplification; LAMP, loop-mediated isothermal amplification.

100% control of this disease (Chowdappa et al., 2000). For the effective management of *Phytophthora* infection in cocoa plantations, cultural practices such as nutrient management, canopy pruning, and field hygiene were found to be highly successful (Peter and Chandramohan, 2014). As wet weather and excess moisture favor pathogen availability, ensuring adequate drainage prevents soil inoculum build-up. The selection of fields with low pathogen inoculum and good drainage is the first line of defense against this pathogen. Before chemical control methods, phytosanitary measures such as removing decayed materials, thinning, pruning, etc., were more efficacious in managing *Phytophthora* diseases.

Genetic control. Genetic resistance holds a pivotal role in plant disease management. Most cellular pathogens, such as fungi, bacteria, and oomycetes, use the effector and toxin proteins to enter the cytoplasm. In the case of oomycetes, they tend to enter the host cells directly (Tyler, 2011). *P. capsici*, being a pathogen with a broad host range, has developed resistance over time. Saltos et al. (2022) interpreted that some genotypes, such as Nathalie, ECU 12831, ECU 9129, and ECU 1296, showed effective resistance against root and crown rot diseases. Race-specific resistance (Sy et al., 2008) and Syndrome-specific resistance (Sy et al., 2005) has been reported in chili peppers. Using recurrent selection, has ensured polygenic resistance in the elite materials (Thabuis et al., 2004). Reeves et al. (2013) recognized a resistance gene (*Ipcr*) inhibiting *P. capsici*. Grafting was evident in conferring genetic resistance (Gisbert et al., 2010). Jang et al. (2012) reported that grafted pepper plants significantly resisted *P. capsici* and *R. solanacearum*. In chili crops, the genotypes were evaluated for resistance against *P. capsici*, which causes root rot. The evaluation concluded that a significant dominant gene associated with a few minor gene-controlled resistance. The genotype IHR 3575 was resistant against the virulent isolate PC-IIHR1 (Kumar et al., 2021). Mohammadbagheri et al. (2022) stated that, in characterizing the resistance for root and crown rot, the five new genotypes such as 11BlockyP-YToran, 19OrnP-PBI, 23CherryP-Orsh, 32OrnP-China, and 37ChilP-Paleo were found resistant against *P. capsici*. In *Capsicum annum*, 45 physiological races showing resistance using different R genes against *Phytophthora* root rot and blight were reported. McGregor et al. (2011) reported the various sources of resistance, such as Criollo de Morelos 334 (CM334), PI 201232, PI 201234, PI 201237, and PI 640532 from Mexico, followed by AC2258 from Central America, and perennial from India showing resistance to *P. capsici*. *Piper colubrinum*, a wild species of black pepper, was found resistant to *P. capsici*, causing rot diseases. The resistance is due to the hypersensitive response on recognition of the entry of the pathogen (Suraby et al., 2020).

Rachana et al. (2024) elucidated the use of coconut resistant gene analogues (*CnRGAs*) in formulating resistant breeding strategies against *P. palmivora* which causes bud rot in coconut. Cooley et al. (2000) identified the gene *RPP8* to exhibit resistance against *P. parasitica.*

Similarly, the stacking of three resistant gene's namely *RB*, *Rpi-blb2*, and *Rpi-vnt1.1* proved highly successful in managing the late bight of potatoes which showed extreme resistance (Ghislain et al., 2019). The R genes including *R1, R2, R3a*, and *R3b* identified from the wild species of *S.demissum* exhibited race-specific resistance, aiding in the management of late blight disease in potato crops (Kim et al., 2012). The *R8* gene found in the transgenic potatoes also tend to exhibit a broad spectral activity against *P. infestans* enabling long-term resistance (Jiang et al., 2018).

Similarily, The *Rps11* gene provides resistance against *P. sojae*, serving as a promising source of resistance ensuring improved production and protection of soybean (Ping et al., 2016). The novelty of three resistance genes, namely *Rps3a*, *Rps* 3c, and *Rps* 4 was found to be effective in managing *Phytophthora* root rot in soybean crop (McCoy et al., 2022). So far, 33 *Rps* genes have been discovered in different soybean cultivars (Zhong et al., 2019) showing evident results in the management of *Phytophthora* root rot. Lucas (1975), reported the R genes *Php* and *PhI* to confer complete resistance to *P. nicotianae* otherwise known as race 0. Similarly, Drake et al. (2015) found the *Wz* gene to be highly effective in managing black shank disease caused by *P. nicotianae.* Mapping studies revealed the quantitative trait loci (QTL) *Phn 7.1* to confer partial resistance against *P.nicotianae.* Future developments by combining both *Ph* and *Wz* genes in the genetic backgrounds could ensure slow adaptation to the pathogen, thereby contributing to improved cultivars, that are highly effective against black shank disease (Jin et al., 2022).

The resistance to black pod disease is primely oligogenic, and the genotypes of the F1 generation (TSH 1188 9 × CCN 51) could ensure increased resistance to black pod disease in future breeding programs (Barreto et al., 2015). Mucherino Muñoz et al. (2021) identified 20 QTL involved in resistance against *Phytophthora* species and suggested the involvement of the candidate genes 164 from CRIOLLO genome and 160 from the MATINA genome in the recognition and activation of defense responses. Baruah et al. (2024) studied the seven genotypes for their resistance to *P. palmivora* where the genotypes CCN51, Sca6, and Pound 7 exhibited resistance post-penetration which would ensure better management strategies against black pod rot disease of cocoa.

Apart from this, the usage of enzymes such as cellulose synthase 1, ATPases, mitogen-activated protein kinases, and Nep-1-like proteins, which tend to play an essential role in *Phytophthora* metabolism, can be employed for managing the pathogenesis of *Phytophthora* (Avila-Quezada and Rai, 2023).

Chemical management. For decades, fungicides have been essential in controlling plant diseases (Khoury and Makkouk, 2010). Chemicals are widely recommended for *Phytophthora* control, but their effectiveness varies depending on the incidence and severity, particularly during high-disease pressure in the wet season. At weekly intervals, copper-based fungicides and systemic fungicides such as metalaxyl are recommended for managing *Phytophthora* diseases. In black pepper, nursery treatment by spraying either with 1% Bordeaux mixture and soil drenching with 0.2% copper oxychloride or spray cum drenching with metalaxyl-mancozeb 0.125% or a spray with potassium phosphonate 0.3% at timely intervals is highly recommended to avoid the incidence and spread of *Phytophthora* species (Anandraj and Susheela Bhai, 2015; Kumar et al., 2012). For managing *Phytophthora* in cardamom through chemical means, spraying with 1% Bordeaux mixture or drenching with 0.2% copper oxychloride effectively destroyed the soil inoculum. Also, other chemicals like Fosetyl-aluminium 0.2% or potassium phosphonate can be sprayed @ 500-750 ml/clump. For effective management of *Phytophthora* species in Vanilla, spraying with 1% Bordeaux mixture and soil drenching with 0.25% copper oxychloride can be employed, depending on the disease severity. Spraying potassium phosphonate 0.4% was also effective in reducing the disease incidence. In tree species, spraying with 1% Bordeaux mixture before the onset of monsoon season effectively prevents disease development. The fungicidal application was found to be a prophylactic measure for managing *Phytophthora* diseases (Anandaraj and Suseela Bhai, 2015). Spraying of Bordeaux mixture (1%) and removing fallen nuts reduced the incidence of *Phytophthora* in areca nut. Naik et al. (2019) also found that applying a 1% Bordeaux mixture before the onset of monsoon drastically reduced the Koelroga disease in areca nut plantations. Sagaff et al. (2022) reported that using copper oxychloride mixed with mineral oil reduced the severity of abnormal leaf fall disease in rubber.

The application of fungicides had a better impact when used within an IDM strategy. New generation fungicides were eco-friendly, with minimal doses compared to conventional fungicides. Some of the new generation fungicides such as famoxadone, fenamidone, fluopicolide, zoxamide, iprovalicarb, benthiavalicarb, mandipropamid cyazofamid, and ethaboxam were found effective in managing *Phytophthora* species and other related oomycetes through various modes of action (Thind, 2009). Fluopicolide is a recently developed acyl picolide fungicide with a unique mode of action that is highly effective against a wide range of oomycetes. The study by (Shin et al., 2010) showed evident results in managing *Phytophthora* blight in pepper as fluopicolide served as a potent inhibitor of mycelial growth, zoospore release, and germination. Rini and Remya (2020) found that the new generation fungicide fenamidone 10WDG, along with mancozeb, resulted in the management of *P. capsici* in black pepper. Patil et al. (2023) evaluated the new generation fungicides against *P. meadii* in areca nut and concluded mandipropamid as an alternative control measure for fruit rot disease.

Biological management. *Phytophthora species* infection poses considerable challenges to spice and plantation crop production globally. Traditional disease mitigation strategies, which often depend on chemical fungicides, are increasingly unsustainable due to environmental concerns and the development of resistance by pathogenic isolates. The alternative approach is to explore the effect of fungal and bacterial antagonists, which opens an avenue for *Phytophthora* management. Management of diseases using biological control agents (BCAs) seems to come from a combination of mechanisms, which includes the production of enzymes and antibiotics that play crucial roles in impeding the growth and progression of plant pathogens (Kumar et al., 2019). BCAs can suppress diseases in an eco-friendly and more sustainable manner (Yuliar et al., 2015). BCAs employ either direct or indirect methods to combat pathogenic organisms. Direct mechanisms involve actions like parasitism, antibiosis, or competition, while indirect mechanisms include inducing systemic resistance (Raymaekers et al., 2020). Biological control of plant diseases has evolved as a natural method of pathogen control by using beneficial microbes for sustainable crop production and protection (Avila-Quezada and Rai, 2023).

Fungal antagonists. The usage of fungal BCAs has rapidly increased as they have higher reproductive rates and are more target-specific. They can survive as saprophytes in the absence of host plants (Thambugala et al., 2020). Among the fungal BCAs identified so far, *Trichoderma* species appears to be one of the effective BCAs as it has a broader range of action to the soil and foliar pathogens.

Trichoderma is found to be a potent BCA as it uses complex modes of action such as parasitism, competition, production of antibiotics, and hyper-parasitism to combat pathogenic organisms (Mukhopadhyay and Kumar, 2020).

In black pepper, the fungal BCAs such as *Trichoderma* species and arbuscular mycorrhizal fungi were effective against foot rot disease. Vithya et al. (2018) reported that the CKT isolate of *T. harzianum* is a promising BCA-suppressing foot rot incidence. The secondary metabolites of the *Trichoderma species* inhibit the growth of pathogens. Coffee husk-based *Trichoderma* formulations have been reported effective in managing the foot rot of pepper. In betel vines, the combined applications of *T. harzianum* mixed with 500 kg oil cake applied at quarterly intervals were found effective against *Phytophthora* infection, and minimum incidence was observed (Dasgupta et al., 2011).

The native species of *Trichoderma*, such as *T. harzianum* and *T. hamatum*, exhibited greater antagonism against *Phytophthora* (de Ita et al., 2021). It was also reported that four isolates of *Trichoderma* species demonstrated antifungal activity and reduced the mycelial growth of the pathogen. In nutmeg crops, soil application of *Trichoderma* was practical (Sumbula and Mathew, 2015). The application of *T. harzianum* pellets @ a dosage of 2 g/100 ml suspension effectively inhibited the growth of *Phytophthora* in cocoa seedlings (Sriwati et al., 2019). The delayed occurrence and prevention were noticed in the cocoa plants by applying *Trichoderma* species. In areca nut, three native species of *Trichoderma* effectively controlled *P. meadii* under *in vitro* conditions. Among the species tested, *T. virens* showed maximum inhibition at 62.5%. The bioactive compounds from *A. flavipes* showed potent inhibitory activity against several species of *Phytophthora* (El-Sayed and Ali, 2020).

Bacterial antagonists. Bacteria play a pivotal role in the management of *Phytophthora* (Avila-Quezada and Rai, 2023). Bacterial BCAs have gained importance as they are effective against various fungal and bacterial pathogens that cause damage to crops worldwide. The bacterial BCAs use various modes of action, which can be classified into direct and indirect, to suppress the growth of pathogens. The bacterial BCAs use different mechanisms such as antibiosis, siderophore production, competition for space and nutrition, parasitism, biofilm formation, and induction of host resistance to combat the fungal and bacterial pathogens (Haidar et al., 2016). The volatile organic compounds produced by the bacterial agents play significant roles in host plant interactions (De Vrieze et al., 2015). For example, the bacterial strains NH7, NH27, NH32 and NH46 identified as *Enterobacter cloacae*, *Streptomyces flaveus*, *Klebsiella pneumoniae*, and *Bacillus amyloliquefaciens* exhibited strong antagonistic activity against *P. capsici* along with the production of chitinolytic enzymes aiding in successful disease management (Nguyen et al., 2022).

In chili crop, the rhizosphere organisms was isolated and tested for their antagonism. Among the 15 isolates obtained, eight were found to be potential. The strains were tested under greenhouse conditions, showing significant disease suppression against *P. capsici* with increased plant growth characteristics (Hyder et al., 2020). In pepper, the bacterial isolates obtained from the rhizosphere, phyllosphere, and endosphere showed maximum ability to reduce the disease severity. The biocontrol efficacy tested ranged from 0.7% to 92.3%. The bacterial BCA, such as *Bacillus cereus* and *Chrysobacterium* species, helped manage *Phytophthora* blight (Yang et al., 2012). Trihn et al. (2019) screened the bacterial BCA, *Bacillus velezensis* RB.DS29 to exhibit strong antifungal activities against *Phytophthora* along with plant growth promotion in black pepper. Similarly, the bacterial agents including *B. cereus*, *B. polymyxa*, and *B.licheniformis* emerged as potential BCAs in managing *P. meadii* causing fruit rot of arecanut (Shalini and Rajashekhar, 2006). In cardamom, the two bacterial strains *Pseudomonas fluorescens* (*Pf 51*) and *Bacillus subtilis* (*Bs*) showed more significant levels of inhibition, such as 40.2% and 39.7% against *P. meadii* (Sivakumar et al., 2015) also reported the compatible nature of *P. fluorescens* and *B. subtilis* and concluded the effectiveness in disease suppression.

Latha et al. (2023) emphasized that soil and crown applications of *B. subtilis* @10 g/l of water, applied at two intervals, effectively reduced the incidence of *Phytophthora* in coconut. The bacterial agent *Pseudomonas fluoresecnes* showed evident results against *P. palmivora* under *in vitro* and could aid in better disease management (Aruna and Motha, 2020). Thomas et al. (2011) identified 44 *Bacillus* species from the rhizospheric region and six *Pseudomona*s species from the rhizosphere that exhibited antagonistic activity against *P. palmivora*, making them potential bacterial BCAs. Similarily, the bacterial BCA, *Paenibacillus polymyxa* NMA1017 exhibited significant effectiveness in managing *P. tropicalis* causing black pod rot of cocoa, establishing it as potential BCA (Chávez-Ramírez et al., 2021; Wu et al., 2015) reported that compounds such as volatiles, siderophores produced by the bacteria, flagellin, and lipopeptides tend to engender induced systemic resistance against some fungal species.

Endophytes as potential BCAs. The endophytic bacteria obtained from the roots, stem, and leaves of the wild relative of black pepper *Piper colubrinum* was found effective and resistant against *P. capsici*. The growth was significant when the cuttings were bacterized (Irabor and Mmbaga, 2017; Kollakkodan et al., 2021) stated that endophytic bacteria, such as *Bacillus* species, were effective in controlling *P. capsici* and promoting bell pepper plant growth (Adama et al., 2020) stated that the cocoa tree naturally has endophytic bacteria, which can be used as potential antagonists against *P. palmivora* and *P. megakarya.* The bacterial endophytic isolates obtained from the healthy parts of the cocoa plant were screened for their antagonistic activity under *in vitro* conditions where *P. aeruginosa* and *C. proteolyticum* showed 100% inhibition against *P. palmivora* (Alsultan et al., 2019).

The antagonistic potential of bacterial endophytes against *P. meadii* was screened under *in vitro* conditions wherein six isolates were found virulent, among which EIL-2 showed maximum inhibition of 62.5% (Abraham et al., 2013). It was reported that the antagonism displayed against *P. meadii* may be used to control *Phytophthora* disease *in vivo.* The fungal endophytic *Trichoderma* strains were tested for their potential antagonism and efficacy where the strains of *T. harzianum* KUFA0436 and KUFA037 showed disease suppression by 43% and 48% (Sirikamonsathien et al., 2023). Dang et al. (2023) identified the endophytic isolates including *Penicillium citrinium*, *Xylaria curta*, and *Clonostachys rosea* to pose strong antagonistic activities against *Phytophthora* spp. which could serve as effective BCA against root rot disease in cinnamon.

Microbial consortia of potent BCAs. Despite the limited availability of BCAs, the fungal BCA such as Trichoderma species and the bacterial agents such as *Bacillus* species and *Pseudomonas species* have been proven effective in managing *Phytophthora* in spice and plantation crops by various researchers. The development of microbial consortia of *T. harzianum*, *P. fluorescens*, and *B. megaterium* reduced the severity of the disease along with the overall growth and development of palms (Naik et al., 2019).

In cardamom plants, the combined application of antagonistic organisms through rhizome and soil treatments reduced the capsule infection by 60% (Sivakumar et al., 2012). For managing foot rot of black pepper, combined applications of *T. asperellum*, *P. fluorescens*, and AMF are recommended when planting in the nursery and main field. The combination of BCAs has proven to be very effective against the growth and development of *Phytophthora* species because of the synergistic activities of the antagonists, which enhances their efficacy (Manasfi et al., 2018).

Integrated approaches. The combined applications of neem cake amended with *Trichoderma* 1 kg/vine showed increased microflora populations and reduced root infections. In nutmeg, the combination of treatments, such as a spray with 1% Bordeaux mixture and soil application with *T. viride*, showed progressive results in disease reduction (Sumbula and Mathew, 2015). The combined applications of potassium phosphonate with *T. harzianum* reduced foot rot incidence in black pepper. Since the actual disease of small cardamom solely depends on weather parameters, an IDM strategy involving plant sanitation, such as removal of diseased plant parts and shade regulation before the onset of monsoon, followed by chemical and biological methods such as the application of prophylactic fungicidal spray and soil application of *Trichoderma* species before the rainy season would be more helpful in managing this disease (Thomas and Suseela, 1995).

In cinnamon crops, the combination of cultural practices such as removal and destruction of the infected plant parts, shade lopping to ensure sunlight, availing proper drainage followed by chemical control measures viz., spraying of 1% Bordeaux mixture and soil drenching with copper oxychloride 0.25% reduced the incidence and spread of disease. In tree species, phytosanitary measures such as removing the infected and fallen nuts along with a prophylactic spray of 1% Bordeaux mixture help prevent the disease's survival and spread (Anandaraj and Susheel Bhai, 2015). For managing black pod disease in cocoa, applying copper oxychloride followed by metalaxyl + mancozeb and suitable cultural practices showed good, reliable results in disease control (Peter and Chandramohan, 2014). Application of lime @ 200 kg/ha during pre-monsoon season followed by the application of 1% Bordeaux mixture as a foliar spray with suitable cultural practices such as removal of fallen nuts, ensuring proper drainage, and removal of excessive branches in the intercrops showed evident results in managing *Phytophthora* in areca nut fields (Balanagouda et al., 2021). The ultimate goal of IDM lies in achieving both efficient disease control and the mitigation of plant diseases, along with minimizing detrimental effects.

Conclusion and Future Prospects

Phytophthora infections pose an extreme threat to the sustainability and profitability of spices and plantation crop cultivation. Early detection of this dreadful pathogen using novel molecular methods offers an advantage in reducing inoculum and spread, resulting in lesser damage to spices and plantation crops. Adopting multi-pathed approaches in detection and management prove a holistic strategy in combating the devastating effects of *Phytophthora* pathogens in the fields of spice and plantation crops. This includes accurate diagnostics to avoid primary sources of infection, the use of disease-resistant planting materials, soil health and fertility improvement, the employment of novel biological agents, effective fungicides, and the utilization of pathbreaking new generation molecules against the *Phytophthor*a species improving the production and protection of spices and plantation crops. Gaining a deeper understanding of the biology and pathogenicity mechanisms of *Phytophthora* species will ensure effective mitigation, reducing their impact on spices and plantation crops while enhancing their durability.

Furthermore, given that phytopathogens pose a threat globally, more attention is warranted as they are highly detrimental to spices and plantation crops worldwide. Identifying and addressing research gaps is essential. Prospects include timely pathogen detection using novel molecular tools, such as Pyrosequencing, for rapid and accurate quantification. Eco-friendly management strategies can contribute to reduced yield losses. Additionally, ensuring biocides is vital as alternatives to harmful fungicides and enhancing the future use of bio-capsules for low-volume applications and eco-friendly management. The advancement of nascent nanotechnological approaches holds promise for early detection diagnosis and management in their preliminary stages, ensuring crop safety and security. The widespread adoption of recent advancements in metabolomics, proteomics, and transcriptomics along with effective integrated disease management strategies holds high significance in saving the spice and plantation crops from the alarming danger of *Phytophthora* species worldwide.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

Acknowledgments

The authors thank Department of Plant Pathology, Agricultural College and Research Institute, Madurai and Department of Plant Protection, Horticultural College and Research Institute, Periyakulam, Tamil Nadu Agricultural University for the valuable support provided.

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