






Root rot pathogens of *Cinnamomum cassia* in Vietnam

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Abstract

A study was conducted to determine the pathogens causing root rot, wilt and dieback disease of *Cinnamomum cassia* (Chinese cinnamon or cassia) in Vietnam, in nurseries and plantations in the Yen Bai, Quang Ninh, Thanh Hoa and Quang Nam provinces, and streams in the Yen Bai province. Pathogens were identified using morphology and internal transcribed spacer (ITS) sequence analysis. The 204 isolates obtained included 125 *Phytophthora* isolates and 79 from other oomycete genera. There were 112 isolates of *P. cinnamomi*, four *P. heveae*, two *P. virginiana*, three *P. multibullata* and four *P. x vanyenensis*. The pathogenicity and virulence of 16 *P. cinnamomi*, two *P. heveae*, two *P. multibullata* and four *P. x vanyenensis* isolates were assessed using lesion size after under-bark inoculation of *C. cassia* stems, and root damage following inoculation of 4-month-old *C. cassia* seedlings. The most virulent isolate from both assessments was a *P. cinnamomi* from the Quang Nam plantation. Isolates of *P. cinnamomi* showed a wide range of virulence, with isolates from healthy trees or seedlings showing the lowest virulence. Isolates of *P. x vanyenensis*, *P. multibullata* and *P. heveae* showed moderate or low pathogenicity. This study showed that although *P. cinnamomi* is the most common pathogen associated with dieback disease in Vietnamese *C. cassia* plantations, other *Phytophthora* species may also cause this disease. Knowledge of the presence of these soil- and waterborne pathogens will encourage improved soil and water hygiene in nurseries and implement measures to prevent the spread of the pathogens in plantations.

KEYWORDS

disease survey, nursery disease, *Phytophthora*, plantations, virulence

1 | INTRODUCTION

The genus *Phytophthora* is one of the most destructive plant pathogens in temperate and tropical regions. Various diseases are caused by different species, affecting roots, shoots or fruits (Abraham et al., 2015), and have resulted in significant economic losses in agriculture and agroforestry. Many *Phytophthora* species

have spread beyond their original geographical regions, primarily due to international trade, and climate change is also altering their distribution (Derevnina et al., 2016; Fisher et al., 2012). In Vietnam, the tree crops known to be affected by *Phytophthora* include avocado, pepper, durian, cocoa, rubber, bananas, citrus fruits, apples, plums and longan (Nguyen et al., 2015; Thanh et al., 2004; Thanh & Trung, 1999; Tri et al., 2016; Truong et al., 2008). The

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Phytophthora species reported from these hosts are *P. colcasiae*, *P. infestans*, *P. mekongensis*, *P. nicotianae*, *P. palmivora*, *P. prodigiosa*, and *P. tropicalis*, as well as several unnamed species (Puglisi et al., 2017; Thanh et al., 2004). *Phytophthora* species that cause disease in plantations of exotic timber in Vietnam include *P. acaciivora*, *P. cinnamomi* and *P. parvispora* on *Acacia* (Burgess et al., 2020; Thu, 2016), and an unidentified species on *Casuarina* (Hoang et al., 2017). As well as having the broadest range of woody host species in Vietnam, *P. cinnamomi* also has by far the broadest geographical range, being reported from many regions including Tuyen Quang, Lao Cai, Yen Bai, Thanh Hoa, Ba Ria Vung Tau, Dong Nai, Dac Nong and Quang Tri (Jung et al., 2020; Quynh et al., 2017; Thanh et al., 2004; Thu et al., 2013). It is also a problem in some nurseries providing seedlings for plantations, for example, in a nursery in Tuyen Quang producing *Acacia mangium*, in *Acacia* hybrid nurseries in Quang Nam and *C. cassia* nurseries in Lao Cai (Dinh et al., 2017; Quynh, Thu, Quang, & Binh, 2021; Thu et al., 2013). The geographical spread of *Phytophthora* in areas in Vietnam is not known. A wide range of pathogens has been identified from cinnamon plantations in Vietnam, and apart from *P. cinnamomi*, *Fusarium oxysporum*, *Botryodiplodia theobromae*, *Phellinus noxius* and *Phytophthora helicoides* have been identified as causing root rot in cinnamon (Cen et al., 1994; Cen & Deng, 1994; Dao, 2003; Thu et al., 2016). Thus, for effective control treatments, more information on the *Phytophthora* species present is required.

Phytophthora species are also detrimental to native trees and shrubs in natural ecosystems in Vietnam, such as *Castanopsis acuminatissima* and *Neolitsea poilanei* (Jung et al., 2020; Quynh et al., 2017; Thu et al., 2014). A high diversity of *Phytophthora* species is present in Vietnamese natural forests and aquatic ecosystems, seemingly without causing disease. Jung et al. (2020) investigated natural and seminatural forest stands and rivers in temperate and subtropical mountainous and lowland regions and reported 13 species, five unofficial taxa and 21 previously unknown taxa of *Phytophthora* and suggested Vietnam as the centre of origin of many *Phytophthora* taxa, including the highly invasive species *P. cinnamomi* and *P. ramorum*.

Cinnamomum cassia is one of Vietnam's most important plantation species, with over 160,000 ha of plantations (Figure 1). However, across the plantations, particularly in the central region (Yen Bai), trees have declined due to a root rot initially thought to be caused solely by *P. cinnamomi* (Quynh et al., 2017; Thu, 2016). Since *P. cinnamomi* was first described on *C. burmannii* in Sumatra (Rands, 1922), it has been found on other *Cinnamomum* species such as *C. camphora*, *C. culilawan*, *C. micranthum*, *C. sintok* and *C. zeylanicum* (Spaulding, 1961). However, when *Phytophthora* species identification is based only on disease symptoms and hyphal and colony morphology, the species responsible for a disease may be misidentified. In the case of the diseased *C. cassia* trees in Vietnam, it is unclear whether *P. cinnamomi* alone is responsible for the observed damage.

Therefore, in this study, conventional and molecular methods were used to determine which *Phytophthora* species can be isolated

from *C. cassia* plantations and nurseries raising cinnamon seedlings in four regions of Vietnam. The pathogenicity and virulence of the isolated *Phytophthora* species were tested to determine which species contribute to the disease aetiology.

2 | MATERIALS AND METHODS

2.1 | Sampling and isolation

Samples were collected from *C. cassia* plants showing root rot symptoms in plantations and nurseries from four provinces of Vietnam: Yen Bai, Quang Ninh, Thanh Hoa and Quang Nam (Figure 1). Samples from healthy trees were also collected to assess whether *Phytophthora* was present without symptoms. After removing surface litter, soil samples and fine root material were collected at 2–30 cm depth under the tree canopy. Approximately 500–1000 g of soil and root material per sample was placed in sterile plastic bags and transported to the laboratory in a cool box. In the laboratory, stones were removed from the soil, and root material was cut into small pieces (Jung, 2009; Scanu et al., 2010). Approximately 300 g of soil and fine roots was placed in a plastic container (20.7 × 16 × 9 cm) and overlaid with 800 ml of nonsterile distilled water (the height of water level was 3–4 cm above the soil) and left for 1–2 h for particles to settle. Any floating litter was removed, and young, newly formed healthy leaves of susceptible species such as *Castanopsis* spp., *Castanea* spp., *Lithocarpus* spp., *A. mangium* or petals of a *Rosa* sp. were floated on the water to act as baits for *Phytophthora* and *Pythium* species. The containers were incubated at 20–25°C. After 3–4 days, the leaves were collected, blotted on a paper towel and the necrotic regions excised, cut into small (2 × 2 mm) pieces, and placed onto NARH medium (Sarker et al., 2020). The plates were incubated at 25°C in the dark for 3–7 days. Growing edges of mycelium with characteristics of *Phytophthora* were transferred to cornmeal agar (CMA; Difco) or potato dextrose agar (PDA; Becton, Dickinson and Co.) to obtain pure cultures.

In the Yen Bai, where a network of streams was present close to a *C. cassia* plantation, streams were baited following the methods of Jung et al. (2017). Briefly, nylon mesh bags containing three or four leaves of *C. cassia*, *C. camphora* and a *Litsea* sp. (i.e., 10–12 in total) were floated in relatively slow-moving water as baits (Figure 2). The leaf baits were set up on the same day as the soil samples were obtained. After 3–4 days lesions were present on the trap leaves and the bags were removed from the streams, put in separate plastic bags, and transported to the laboratory of the Forest Protection Research Center. Pieces approximately 2 mm² were cut from the margins of the brown lesions and plated onto NARH on the same day as they were collected. Colonies of suspected *Phytophthora* species growing from plated baits were transferred to V8 (V8 vegetable juice; Campbell Grocery Products Ltd) agar (V8A) or a half-strength potato dextrose agar (PDA) or carrot agar (CA) media for morphological observations, DNA extraction and storage.

FIGURE 1 Map of Vietnam showing the four locations where *Cinnamomum cassia* plantations were surveyed for this study (orange); other regions where it is cultivated are shown in green.

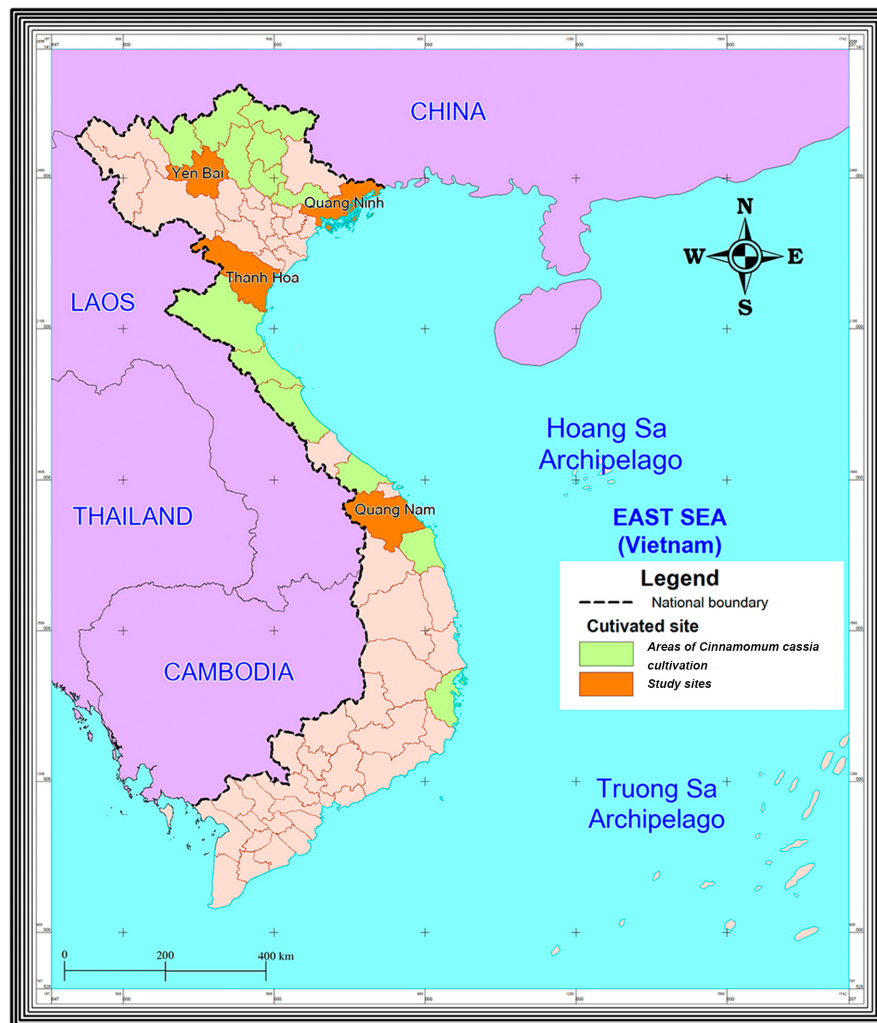


FIGURE 2 Baiting raft (red arrow) floating in a stream flowing through a *Cinnamomum cassia* plantation in Yen Bai province.

The four provinces surveyed and the number of soil and root samples and stream baits were Yen Bai (30 samples and 10 baits in different stream locations), Quang Nam (30 samples), Thanh Hoa (20 samples) and Quang Ninh (20 samples).

2.2 | DNA isolation, amplification and sequencing of ITS rDNA genetic region

From their morphology, pure cultures identified as *Phytophthora* species were grown on half-strength PDA at 20°C for 1 week. Approximately 50mg of mycelium scraped from the agar was placed in a 1.5 ml sterile Eppendorf tube and frozen in liquid nitrogen, ground to a fine powder, and genomic DNA was extracted according to Glen et al. (2002) by using a glassmilk method. The region spanning the internal transcribed spacer (ITS)1–5.8S–ITS2 region of the ribosomal DNA was amplified using the primers DC6 (5'-GAGGGACTTTTGGGTAATCA-3') (Cooke et al., 2000) and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (White et al., 1990). The PCR mixture, PCR conditions, the clean-up of products and sequencing were as described by Sakalidis et al. (2011). Sequence data were viewed in Geneious (Biomatters). Sequences were trimmed to include the full ITS1, 5.8S and ITS2 gene regions. Identity of species was confirmed by conducting distance analysis using Geneious tree builder and comparing to a curated dataset of ITS sequence data of type isolates of all described species available from IDphy online resource (<http://idtools.org/id/phytophthora/index.php>).

2.3 | Stem inoculation assay

From the 204 isolates collected (Table 1), 24 were selected for pathogenicity testing (Table 2) using both a seedling assay (see below) and under-bark inoculation of excised *C. cassia* branches following the method of Khdiar et al. (2020). Healthy branches (c.30cm long and 0.5–1 cm diameter) from *C. cassia* plants were selected, the leaves removed and the cut ends sealed with wax. They were sprayed with 70% ethanol, and when dry, a 10mm long × 5mm wide flap was cut through the outer bark in the middle of the branch using a sterile scalpel. From the margin of 7-day-old cultures on PDA, 5mm² inoculum discs were cut. One disc was placed under the flap, mycelial surface face down, and the wound was wrapped with Parafilm. Sterile PDA discs were used for control inoculations. There were 10 replicate stems for each isolate. Inoculated stems of each isolate were kept in separate zip-lock bags and incubated at 25°C in the dark. The lesions were measured after 12 days, when the lesion associated with the control inoculation was no more than approximately 2mm above and below the 10mm long wound. From the lesion lengths, pathogenicity and virulence was categorized as follows: low, lesion length <4.0 cm; medium, lesion length 4.0 to <5.5 cm; high, lesion length 5.5 to <7 cm; and very high, lesion length >7.0 cm (Figure 3). Koch's postulates were confirmed by taking necrotic material from a lesion caused by each isolate and symptomless tissue from the control branches and plating it on NARH. The R packages 'Rmisc', 'dplyr' and 'agricolae' (R Studio Team, 2019) were used to analyse the data. Differences in lesion lengths between the different *Phytophthora*

isolates were assessed using a one-way analysis of variance (ANOVA) at $\alpha = 0.05$. When ANOVAs revealed significant differences in treatment means, Duncan's multiple range comparisons were applied to test the difference among formulas and the bar graphs were drawn using Excel (Microsoft).

2.4 | Seedling inoculation assay

C. cassia seedlings were inoculated with 24 selected *Phytophthora* isolates using a modification of the method of Belhaj et al. (2018). Briefly, a 1 L Erlenmeyer flask containing 400ml of substrate (1 L vermiculite, 10 g millet [*Panicum miliaceum*] seeds and 600ml V8 broth) was autoclaved three times at 121°C for 20min over 3 days. V8 agar plugs (10 × 10mm) colonized for 7 days at 21°C by *Phytophthora* isolates were taken from one Petri dish (9 cm diameter) and inoculated into a 1 L flask. The cultures were incubated in the dark at 20°C and shaken every 3 days for the first 2 weeks. Seedlings were inoculated with 6-week-old inoculum from these flasks. Before use, the inoculum was rinsed with sterile water. The identity and viability of the inoculum were checked by plating 3 g subsamples onto NARH, and microscopically examining the inoculum mounted in water. *C. cassia* seedlings were grown in free-draining plastic pots (15 × 12 × 9 cm) containing a 70% coconut husk and 30% sand substrate. The substrate was inoculated with approximately 10 g (1% of the weight of the substrate in the pot) of inoculum when they were 4 months old. There were 10 seedlings for each isolate and 10 noninoculated plant controls. Seedlings were harvested

TABLE 1 The number of oomycete species and isolates obtained from *Cinnamomum cassia* plantations and nurseries, and forest streams in four regions of Vietnam

Species	Yen Bai				Quang Ninh				Thanh Hoa				Quang Nam				Total	
	Streams	Plantations		Nurseries		Plantations		Nurseries		Plantations		Nurseries		Plantations		Nurseries		
		D	H	D	H	D	H	D	H	D	H	D	H	D	H	D		H
<i>Phytophthora</i>																		
<i>cinnamomi</i>	–	20	11	3	–	7	3	2	–	13	6	4	1	29	10	3	–	112
<i>heveae</i>	1	2	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4
<i>virginiana</i>	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
<i>multibullata</i>	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
× <i>vanyenensis</i>	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
<i>Phytophythium</i>																		
species 1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
species 2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
species 3	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
aff. <i>vexans</i>	–	–	–	–	–	3	–	–	–	12	–	–	–	–	–	–	–	15
<i>vexans</i>	–	16	6	5	2	–	–	–	–	–	–	–	–	10	3	8	2	52
<i>helicoides</i>	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
<i>Pythium</i>																		
aff. <i>catenulatum</i>	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Total	18	68				15				36				67				204

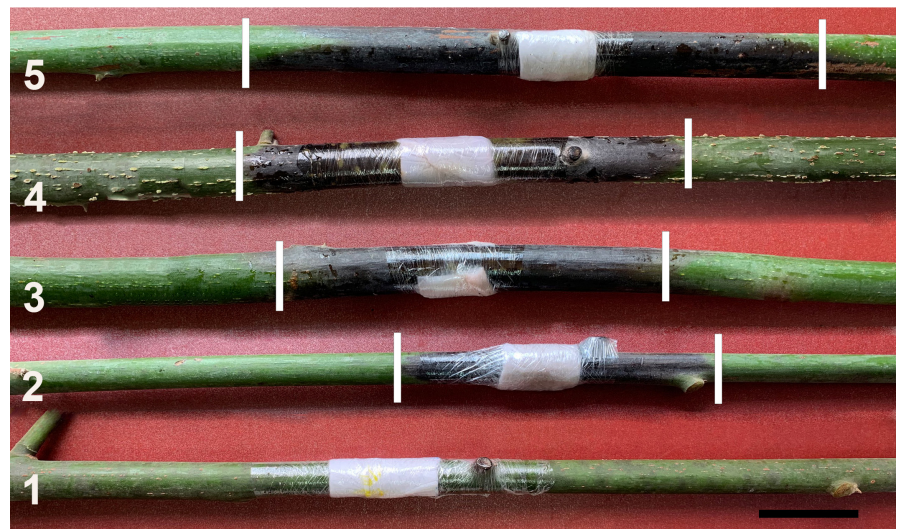
Note: Isolates originating from direct sampling either from under dead (D) or from healthy (H) trees.

TABLE 2 *Phytophthora* isolates tested for pathogenicity

<i>Phytophthora</i> species	Isolate	GenBank number	Location	GPS coordinates	Altitude (ma.s.l.)	Source of material ^a
<i>P. cinnamomi</i>	QD6	OM779076	Quang Nam	15°31.39' N, 108°18.67' E	103	DP
	QD8	OM779077	Quang Nam	15°31.40' N, 108°18.70' E	75	DP
	QD10	OM779078	Yen Bai	21°51.11' N, 104°37.00' E	107	HP
	QD18	OM779079	Quang Nam	15°20.14' N, 108°12.45' E	107	HN
	QD25	OM779080	Yen Bai	21°50.14' N, 104°36.35' E	132	DP
	QD33	OM779081	Thanh Hoa	19°50.49' N, 105°16.41' E	75	DN
	QD35	OM779082	Thanh Hoa	19°51.32' N, 105°16.45' E	142	DP
	QD37	OM779083	Quang Ninh	21°22.09' N, 107°25.45' E	80	DP
	QD40	OM779084	Quang Ninh	21°21.42' N, 107°26.46' E	80	HP
	QD41	OM779085	Quang Ninh	21°21.59' N, 107°26.46' E	90	DN
	QTH15	OM779086	Thanh Hoa	19°50.41' N, 105°16.47' E	70	DP
	QTH19.1	OM779087	Thanh Hoa	19°50.22' N, 105°16.34' E	134	HP
	QTY1.1	OM779088	Quang Ninh	21°22.12' N, 107°26.27' E	120	DP
	QTY5.2	OM779089	Quang Ninh	21°21.59' N, 107°26.46' E	90	DN
	TB5.2	OM721681	Quang Nam	15°14.41' N, 108°05.09' E	210	DP
	YB8	OM779090	Yen Bai	21°50.20' N, 104°36.06' E	137	DN
<i>P. heveae</i>	QD9	OM779091	Yen Bai	21°48.23' N, 104°36.37' E	400	DP
	QD50	OM779092	Quang Nam	15°14.46' N, 108°05.10' E	228	DP
<i>P. multibullata</i>	QD5	MT568656	Yen Bai	21°48.53' N, 104°36.28' E	342	DP
	QD27	MT568655	Yen Bai	21°51.06' N, 104°36.55' E	119	DP
<i>P. × vanyenensis</i>	QD12	MT568654	Yen Bai	21°48.22' N, 104°36.31' E	484	DP
	QD13	MT568651	Yen Bai	21°50.54' N, 104°37.06' E	103	SB
	QD30	MT568652	Yen Bai	21°51.12' N, 104°36.48' E	95	SB
	QD32	MT568653	Yen Bai	21°51.20' N, 104°37.11' E	89	SB

^aDP, dead tree in plantation; HP, healthy tree in plantation; DN, dead plant in nursery; HP, healthy plant in nursery; SB, stream baiting.

FIGURE 3 Virulence of different *Phytophthora* species assessed from lesions on *Cinnamomum cassia* branches 10 days after inoculation. (1) A control inoculation with sterile agar showing a lesion only at the initial incision; (2) medium pathogenicity inoculation with *P. heveae* (QD50); (3–4) high pathogenicity, inoculation with *P. cinnamomi* (QD6) and *P. multibullata* (QD5), respectively; (5) very high pathogenicity, inoculation with *P. cinnamomi* (TB5.2). Scale bar = 1.5 cm.



12 weeks after inoculation. The roots were carefully removed from the substrate, rinsed under running water and dried with paper towels. The degree of root disease was scored using the following scale: 1 for a healthy root system, 2 = 1%–25% brown roots, 3 = 26%–50%

dark brown roots, 4 = 51%–75% dark brown roots and 5 = 76%–100% dark brown and black roots (Figure 4). To reisolate *Phytophthora* from lesioned areas of the roots, root segments were sterilized in 70% ethanol for 1 min, washed three times in sterile water, blotted dry with



FIGURE 4 The appearance of roots ranked 1–5 for the degree of damage from *Phytophthora*. 1 = healthy roots, no damage, 2 = 1%–25% brown roots, 3 = 26%–50% dark brown roots, 4 = 51%–75% dark brown roots and 5 = 76%–100% dark brown and black roots.

sterile filter paper, cut into 1 cm segments and placed on NARH to confirm Koch's postulates. The proportion of root damage resulting from infection with each *Phytophthora* isolate was compared using the Kruskal–Wallis for chi-square test. The data analyses were conducted using the R packages 'dplyr', 'FSA' and 'lattice'. The bar graphs were drawn using Excel. A Pearson product–moment correlation coefficient was computed to estimate the relationship between the lesion lengths in the stems and the root ratings made in the glasshouse using the R packages 'ggpubr'.

3 | RESULTS

3.1 | Oomycete isolations

In total, 204 oomycete isolates were obtained, including 125 *Phytophthora* isolates and 79 isolates from other genera. Of the 125 *Phytophthora* isolates, 112 were *P. cinnamomi*, four were *P. heveae*, two were *P. virginiana* and seven were from the recently described Clade 2 species (Quynh, Thu, Arentz, et al., 2021) *P. multibullata* (three isolates) and *P. × vanyenensis* (four isolates). Six *Phytophthora* isolates were obtained from streams, and 119 isolates from *C. cassia* plantations and nurseries (Table 1).

Notably, *P. cinnamomi* was found in dead and healthy trees in the plantations in all four provinces. In contrast, *P. heveae*, *P. multibullata* and *P. × vanyenensis* were found only in roots and soil from dead trees. While *P. multibullata* was found only in plantations, *P. heveae* and *P. × vanyenensis* were found in both plantations and streams. *P. virginiana* was obtained only from streams. In nurseries, *P. cinnamomi* was recovered from dead plants in all four provinces, and only one sample from the Thanh Hoa nursery was from a healthy plant. The number of isolates relative to the number of samples was approximately the same for Quang Nam, Thanh Hoa and Yen Bai, but lower for Quang Ninh.

Yen Bai had more species diversity than the other provinces, with five species of *Phytophthora* from plantations and streams; Quang Nam had the largest number of *P. cinnamomi* isolates (42 isolates)

and one isolate of *P. heveae*. In the remaining two provinces, only *P. cinnamomi* was detected.

The other genera obtained included *Phytophthium* spp. and *Pythium* aff. *catenulatum* (Table 1). They were found in dead and healthy trees, and streams. However, for this study only the pathogenicity and virulence of *Phytophthora* species was examined, as this genus is known to include the most dangerous oomycete plant pathogens (Blair et al., 2008; Erwin & Ribeiro, 1996).

3.2 | Stem inoculation assay

The virulence of the *P. cinnamomi* isolates ranged from low to very high. An isolate from Quang Nam (TB5.2) produced the most extensive lesions, but the ones from Thanh Hoa (QTH15) and Quang Ninh (QTY5.2) were also highly pathogenic (Figure 5). Three of the four *P. cinnamomi* isolates originating from healthy plants demonstrated low virulence (QTH19.1, QD18 and QD40), while one showed moderate virulence (QD10) (Figure 5).

Both isolates of *P. heveae* tested showed moderate virulence. One isolate of *P. multibullata* (QD5) had high virulence, while the second (QD27) was moderate (Figure 5). Two isolates of *P. × vanyenensis* (QD32, QD30) had high levels of virulence, and two (QD12, QD13) were moderate.

3.3 | Seedling inoculation assay

The roots of the control seedlings were light brown and had abundant fleshy white roots. In contrast, the root systems of seedlings inoculated with *Phytophthora* were smaller, had necrotic lesions, and were mainly dark in colour with few fleshy white roots, resulting in significant differences in root ratings using the chi-square test ($p < 0.05$; Figure 6). *P. cinnamomi* showed the highest virulence (isolates TB5.2, QTY5.2 and QTH15), followed by one isolate of *P. multibullata* (QD5). There were only minor differences between the virulence of the remaining isolates, with nonsignificant differences

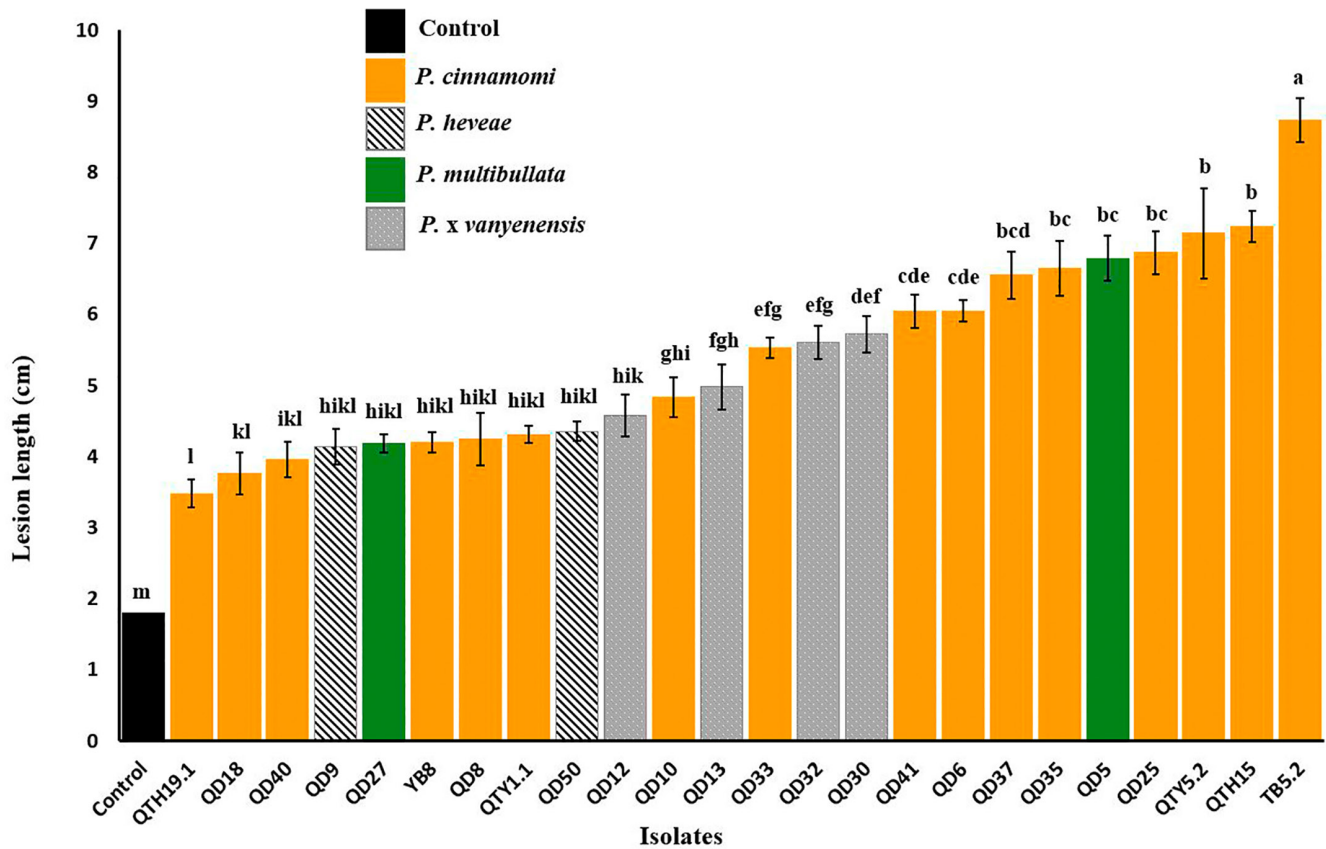


FIGURE 5 Mean lesion lengths of isolates of *Phytophthora* following under-bark inoculation of *Cinnamomum cassia* branches. Bars on columns indicate standard errors of means and those with different letters are significantly different based on the Duncan's range test.

between the isolates of *P. heveae* (QD50), *P. x vanyenensis* (QD13) and the other isolates of *P. cinnamomi*.

3.4 | Comparison of lesion length and root rating for virulence

There was a strong positive correlation ($r = 0.91$, $p < 0.001$) between the virulence assessed from lesion lengths in excised branches and the root damage in inoculated seedlings (Figure 7).

4 | DISCUSSION

Phytophthora was widespread in *C. cassia* plantations and nurseries in the Vietnamese provinces of Yen Bai, Quang Ninh, Thanh Hoa and Quang Nam, and some species were also isolated from streams in Yen Bai. The 204 isolates obtained included 125 *Phytophthora* isolates and 79 isolates of *Phytophythium* and *Pythium*. Of the 125 *Phytophthora* isolates, *P. cinnamomi* was the predominant species present; it was found from healthy and diseased trees. Low numbers of *P. heveae*, *P. virginiana*, and the two recently described species *P. multibullata* and *P. x vanyenensis* were also present. In addition to *P. cinnamomi*, *P. x vanyenensis*, *P. heveae* and *P. multibullata* also caused root rot in *C. cassia*. A good correlation between the

degree of virulence from under-bark inoculation and inoculation of seedlings suggests that the under-bark inoculation method is a reliable and quick method of testing for pathogenicity and virulence in *C. cassia*.

The abundance of *P. cinnamomi* was not unexpected. A previous study showed it to be the most frequent soilborne *Phytophthora* species in Vietnam in native forests above 700 m (Jung et al., 2020). The current survey showed it to be the most common species at lower altitudes, 70–500 m a.s.l. Previous studies have also shown it to be prevalent in *C. cassia* plantations in other countries (Anandaraj & Devasahayam, 2004; Rajapakse & Liyanage, 2007; Rands, 1922). Many of the *P. cinnamomi* isolates were highly pathogenic on *C. cassia* seedlings, and significantly, it was found in nurseries in all four provinces. The transfer of diseased plants and soil from nurseries to plantations is of great concern. There has been extensive research on the hygiene protocols necessary to prevent the transmission of *Phytophthora* to natural and agricultural ecosystems through infected planting stock from nurseries elsewhere in the world, and many of these protocols are suitable for adoption in Vietnam (Parke et al., 2014; Redekar et al., 2019, 2020; Simamora et al., 2018). Not all isolates of *P. cinnamomi* recovered in this study caused disease, particularly those isolated from healthy plants. Nonpathogenic isolates have also been noted in other studies on *P. cinnamomi* (Migliorini et al., 2019), *P. multivora* (Croeser et al., 2018) and *P. sojae* (Yang et al., 2015).

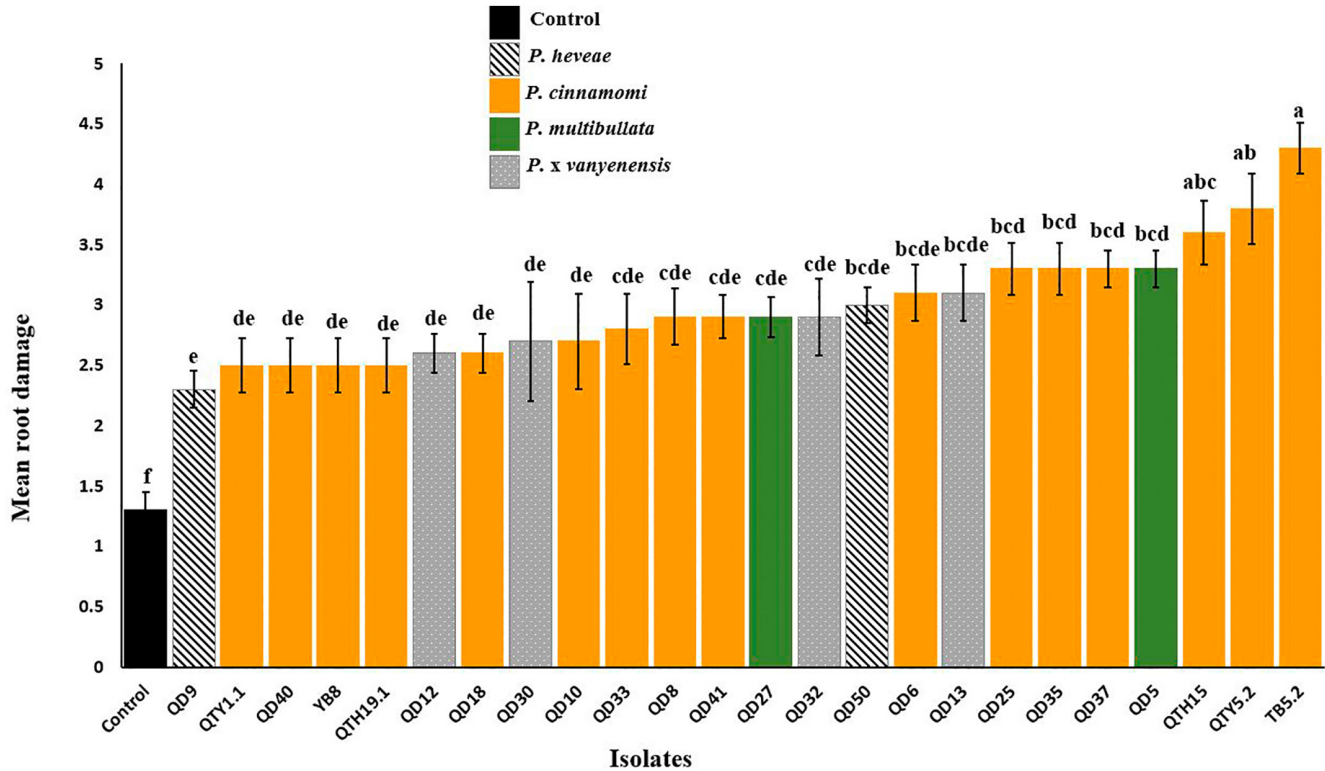


FIGURE 6 Mean root damage of seedling *Cinnamomum cassia* plants following inoculation with isolates of *Phytophthora*. Bars indicate standard errors of means, and those with different letters are significantly different based on the LSD analysis ($\alpha < 0.05$).

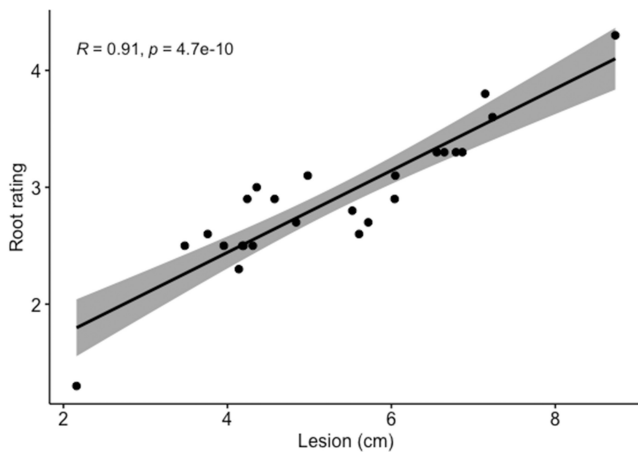


FIGURE 7 Correlation of virulence of *Phytophthora* isolates assessed from lesion lengths and root damage ratings.

Identifying additional *Phytophthora* species pathogenic on *C. cassia* demonstrates that *C. cassia* root rot can also be caused by *P. multibullata*, *P. x vanyenensis* and *P. heveae*. Notably, *P. multibullata* and *P. x vanyenensis* were first isolated from *C. cassia* plantations in Vietnam (Dang et al., 2021), but this is the first record of their pathogenicity on *C. cassia*. It is also the first record of *P. heveae* being pathogenic to *C. cassia*, but this species is a known pathogen on many ecologically or economically important trees. It results in black stripe and pod rot in rubber and cacao in Malaysia (Thompson, 1929; Turner, 1968), is associated with leaf fall in rubber

in Vietnam (Toan et al., 2017), leaf blight in Brazil nuts (*Bertholletia excelsa*; de Albuquerque et al., 1974), canker disease of avocado (Zentmyer et al., 1978), heart rot and nut fall on coconut palms (Quillec et al., 1984), the quick decline of *Macadamia integrifolia* in Hawaii (Sugiyama et al., 2020) and damping-off of *Anacardium excelsum* and *Tetragastris panamensis* seedlings in Panama (Davidson et al., 2000). Gadgil (1974) reported that *P. heveae* causes disease symptoms and death of kauri in New Zealand but it was later shown that the pathogen was not *P. heveae* but a new species, *P. agathidicida* (Weir et al., 2015).

Jung et al. (2020) concluded that as both *P. cinnamomi* and *P. heveae* were widespread in forest areas of Vietnam but resulted in no signs of disease in native plants, they may have originated in Indochina. However, it was shown in the present study that *C. cassia*, a species native to Vietnam, can be damaged by *P. cinnamomi* and *P. heveae*, so this does not fit with a hypothesis of co-evolution of the host and the pathogen. However, the soil conditions in the plantations or nurseries differ from those in the natural forest and are more conducive to the pathogen than undisturbed forest soils.

In the current study, *P. cinnamomi* was not isolated from streams, but it is of concern that *P. heveae* and *P. x vanyenensis* were present. Jung et al. (2020) did not obtain *P. cinnamomi* or *P. heveae* from streams. In Vietnam, any stream or water source close to a nursery or agricultural crop is used for irrigation. Managers of *C. cassia* nurseries need to understand that *Phytophthora* species can be introduced into irrigation water and should take appropriate steps to reduce this possibility. Recycling irrigation water for nurseries

has also been shown to increase the risk of spreading other waterborne oomycete plant pathogens such as *Pythium* and *Phytophthora* (Redekar et al., 2019).

P. virginiana, a Clade 9 species, was only found in streams and run-off from a nursery. In other studies in Vietnam and Taiwan, *P. virginiana* and *virginiana*-like species were also only detected in rivers and streams (Jung et al., 2020). This species was first recovered from run-off from ornamental plant nurseries in Virginia and is considered non-pathogenic as there no host species are recorded (Yang & Hong, 2014).

This study confirmed that *P. cinnamomi* is widespread in four *C. cassia*-growing provinces of Vietnam and is the primary cause of root rot and wilt in the field and in the nurseries. However, it was shown that other *Phytophthora* species such as *P. heveae*, *P. multibullata*, and *P. x vanyenensis* are also pathogens of *C. cassia* and are present in plantations. In the future, it seems likely that these pathogens will be detected throughout the cinnamon-growing areas of Vietnam. Control measures effective for *P. cinnamomi* should also be appropriate for the additional *Phytophthora* species. Although *P. cinnamomi* was not detected in water, *P. heveae* and *P. x vanyenensis* were isolated from streams and plantations, so water purification measures may be necessary to manage nursery water supplies when they are present. Strict hygiene is needed in nurseries to prevent the transfer of diseased planting material to clean sites in the field. In the nursery, seedlings with disease symptoms should be destroyed and not masked by the use of fungicides and the pathogen should not be introduced to the plantation (Hardy et al., 2001). For plantations with disease already present, restrictions on the movement of people, animals and equipment, although difficult to implement, will slow the spread of the pathogens. Treatment of infected trees with phosphite and possibly silica or calcium soil dressings may also improve tree health (Dann & Le, 2017; Mostowfizadeh-Ghalmfarsa et al., 2018). However, after the 10-year rotation, infested areas should not be replanted with a second rotation of cinnamon.

AUTHORS' CONTRIBUTIONS

Q.D., T.B., G.H., J.M. and T.P. were involved in conceptualization. J.M. and Q.D. were involved in the methodology. T.B., B. L. and Q.D. were involved in the formal analysis. Q.D., B.L., T. N. and X.L. were involved in the investigation. G.H., T.B. and T.P. were involved in resources. T.B., J.M. and Q.D. were involved in data curation. Q.D. was involved in writing—original draft preparation. T.B., J.M., T.P., G.H., B.L. and T.N. reviewed and edited. T.B., T.P. and G.H. were involved in supervision. Q.D., G.H., T.B., J.M., T.P. and B.L. were involved in the experimental design. Q.D., B.L., X.L. and T.N. were involved in field and laboratory work. Q.D. and T.N. were involved in data analysis and interpretation. Q.D., J.M., G.H., T.B. and T.P. were involved in manuscript preparation and review. All authors were involved in funding acquisition and have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST

There are no competing interests.

DATA AVAILABILITY STATEMENT

All sequences have been uploaded to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) with the accession numbers listed in Table 2. Other data are available from the corresponding author on reasonable request.

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