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Phytophthora palmivora: a serious threat to papaya production in South Africa

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Abstract *Phytophthora palmivora* is an Oomycete pathogen widespread in tropical and subtropical regions, causing severe diseases such as fruit rot, bud rot, blight, cankers, and root rot. Papaya is grown in South Africa by smallholder and commercial farmers in the Limpopo and Mpumalanga provinces. In 2019, widespread symptoms of crown and root rot were observed in South African papaya orchards, leading to significant plant collapse. This study aimed to identify and characterize the pathogen causing papaya tree decline in South Africa, investigate their distribution, and evaluate their virulence. Samples were collected from six commercial orchards. Diseased stems and soil samples were analysed, resulting in isolation of *Phytophthora palmivora*. Molecular identification using rDNA-ITS, the translation elongation factor-1α (tef-1α), β-tubulin, *Cox I* and *Cox II* sequencing confirmed the pathogen, and pathogenicity tests revealed its aggressiveness on papaya fruits. This is the first disease report of *P. palmivora* in South Africa, where it is a regulated pathogen. Given its destructive potential, *P. palmivora* poses a serious threat to the papaya industry and possibly other crops such as macadamia, citrus, and avocado. Understanding its distribution and potential introduction routes is critical for implementing effective management strategies to protect South African agriculture from further damage.

Keywords Carica papaya · Root Rot · Oomycete

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Phytophthora palmivora, an Oomycete pathogen, was first identified on palmyra palm (*Borassus flabellifer*) and coconut (*Cocos nucifera*) as *Pythium palmivorum* (Butler, 1907) in India, however, later changed to *Phytophthora palmivora* (Butler, 1919). This species is now widespread in tropical and subtropical regions, reported from 72 countries globally by causing severe diseases in over 280 plant species (https://fungi.ars.usda.gov). This species affects various plant tissues, and resulting fruit rot, bud rot, blight, cankers on branches and trunks, as well as root and crown rot. *Phytophthora palmivora* causes substantial damage on crops, including durian, rubber, coconut, oil palm, black pepper, citrus, papaya, and pineapple. *Phytophthora palmivora* impacts every part of the cocoa tree at all growth stages. It causes 20–30% of pod losses through black pod rot and results in the death of up to 10% of trees annually due to stem cankers (Guest, 2007). It is also prevalent in papaya orchards, reported in 23 countries (Lamour, 2013), and has caused a 35% reduction in the papaya crop annually in Hawaii (Alvarez & Nelson, 1982).

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Papaya (*Carica papaya*) is a fruit crop that is native to South America. It is grown worldwide in tropical and subtropical areas (Jiménez et al., 2014). In South Africa, papaya production involves both smallholder and commercial farming. The main production regions are in the Limpopo province near Tzaneen and in the Mpumalanga province (Connolly, 2008). However, the number of commercial papaya producers in South Africa has declined drastically from 15 to just six, largely due to disease pressures. There are very little studies regarding papaya disease in South Africa. Only few pathogens have been reported, such as *Colletotrichum siamense* (Jayawardena et al., 2016; Rampersad, 2011), *Asperisporium caricae, Erysiphe cruciferarum, Phyllosticta* spp., *Pythium myriotylum* and *P. vexan* (Crous et al., 2000) from papaya in the country. In 2019 extensive symptoms of crown and root rot were observed in papaya trees causing significant plants collapses in South African orchards. Samples analysed by the Agricultural Research Council (ARC) identified *Phytophthora* species as the cause. Despite this, there has been no further research on *Phytophthora* species affecting papaya in South Africa. Therefore, the aims of this project were to identify *Phytophthora* species on papaya in South Africa and examine the aggressiveness of all obtaining *Phytophthora* species.

During August to December 2023, six commercial papaya orchards in Mpumalanga and Limpopo provinces in South Africa, were visited (Fig. 1A-B). Samples were collected from 48 trees, aged 1–3 years old, showing symptoms such as yellowing and wilting of the leaf canopy which was soon followed by leaf drop. Interestingly, the fruits remained on the plants without exhibiting any disease symptoms. At the same time, stem rot emerged at the soil surface

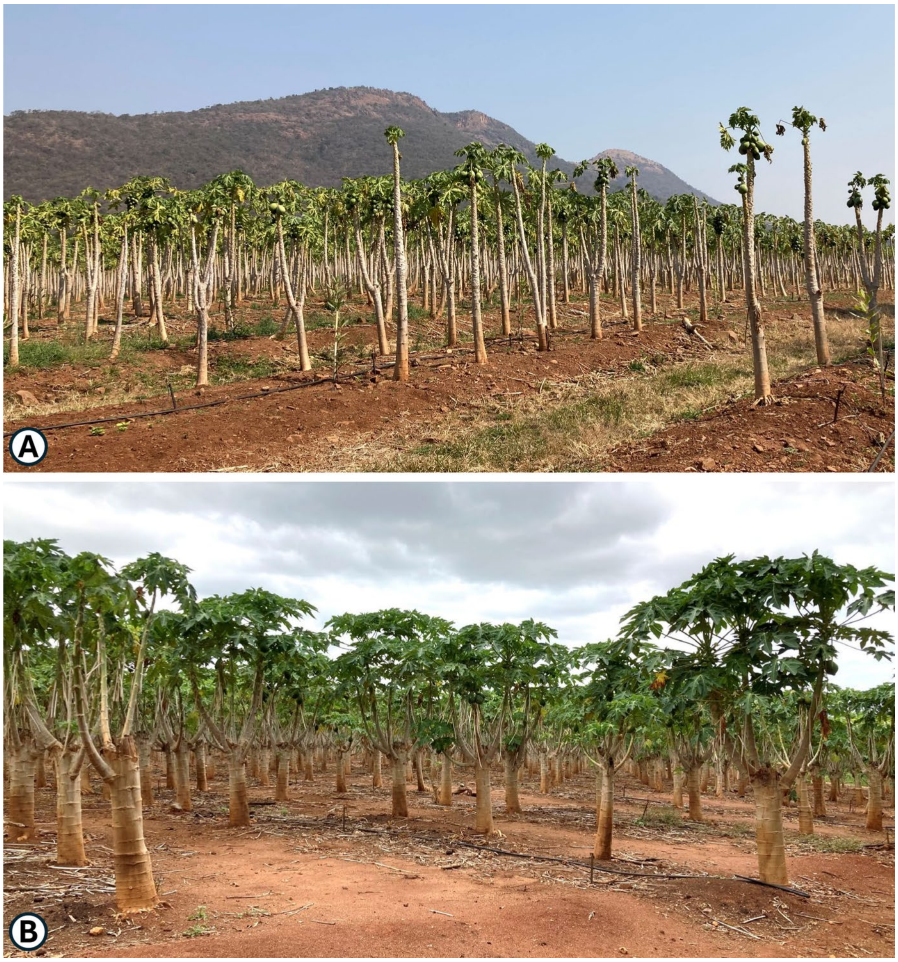

Fig. 1 **A.** Highly infected papaya orchard with *Phytophthora palmivora*. **B.** Healthy papaya orchard

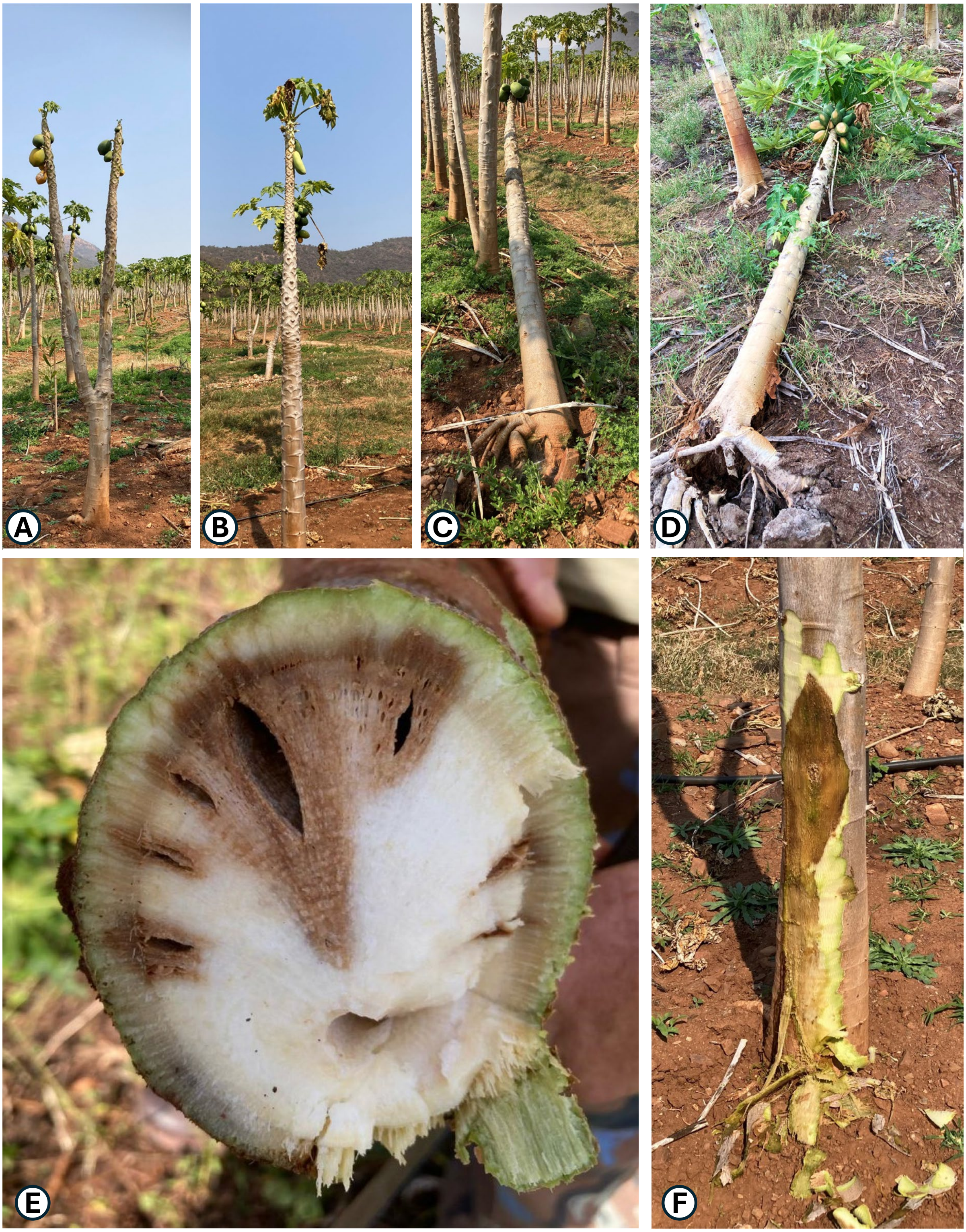

Fig. 2 Symptoms of disease caused by *Phytophthora palmivora* on papaya trees **A-B.** Yellowing and loosing leaves, small fruits. **C-D.** Collapsed trees in the orchards due to rot roots. **E–F.** Extensive rot and discolouration of main stem

Table 1 Representative *Phytophthora palmivora* isolates of this study were identified

Isolate	Collection Date	Substrate	Region	ITS	TUB	TEF	Cox I	Cox II
PPRI35346	Aug-23	Plant	Mpumalanga, South Africa	PQ932531	PV166313	PV166314	PX872557	PX872561
PPRI36545	Nov-23	Soil	"	PQ932532	-	-	-	-
PPRI35347	Nov-23	Plant	"	PQ932533	-	-	-	-
PPRI35348	Nov-23	Plant	"	PQ932534	-	-	-	-
PPRI35349	Dec-23	Soil	Limpopo, South Africa	PQ932536	PV166312	PV166315	PX872558	PX872562
PPRI35350	Dec-23	Plant	"	PQ932537	PV166311	PV166316	PX872559	PX872563
PPRI36546	Dec-23	Plant	"	PQ932538	-	-	-	-
PPRI35351	Dec-23	Plant	"	PQ932539	-	-	-	-
PPRI35352	Dec-23	Soil	"	PQ932540	-	-	-	-
PPRI35353	Dec-23	Plant	"	PQ932541	-	-	-	-
PPRI35354	Dec-23	Plant	"	PQ932542	-	-	-	-
PPRI35355	Dec-23	Soil	"	PQ932543	-	-	-	-
PPRI35356	Dec-23	Soil	"	PQ932535	-	-	-	-
PPRI35357	Dec-23	Plant	"	PQ932544	-	-	-	-
PPRI35361	Dec-23	Plant	"	PQ932545	-	-	-	-
PPRI35362	Dec-23	Soil	"	PQ932546	PV166310	PV166317	PX872560	PX872564

and gradually progressed to soft rot of the main trunk and root destruction. As the disease advanced, the decay spread internally throughout the entire stem, ultimately weakening it, and causing the tree to collapse (Fig. 2A-F). The samples included stems with discolorations and the soil around the roots. The samples were transported to the laboratory for further analyses.

Bark was removed from plant materials, and the pieces were taken from the border zone between healthy and discoloured wood and placed onto an Oomycete-selective medium, PARPH (Potato Dextrose Agar contains pimarcin, Pimaricin 20 mg/L, Ampicillin 150 mg/L, Rifamicin 10 mg/L, Pentachloronitrobenzene 25 mg/L, Hymexazol 50 mg/L) following a modified method of Jeffers and Martin (1986). The plates were incubated at 25°C for 5 days. The Oomycete-like mycelial growth from each wood sample were transferred from the primary isolations to new Potato Dextrose Agar (PDA) plates. After 4–5 days, all those isolates showing typical white hyphae, were transferred to 15% WA (water agar) to make single hyphal tip sub-cultures. The roots and soil were baited using citrus and papaya leaf discs. After 2–5 days, the baits that showed brownish lesions were plated onto PARPH medium. The typical *Peronosporales* colonies were transferred onto water agar to purify the isolates by single hyphal tipping. All purred isolates were kept in half-strength PDA and maintained in the National Collection of Fungi (NCF) under PPRI accession numbers (Table 1), Biosystematics, Plant Health and Protection, Agricultural Research Council, South Africa.

DNA was extracted from mycelium taken from 4-day-old pure cultures using a Zymo Quick-DNA Fungal/Bacterial Miniprep (Zymo Research). DNA sequences were generated for the internal transcribed spacer region of the ribosomal RNA (rRNA) operon amplified with primers ITS-1 (Gardes & Bruns, 1993) and ITS-4 (White et al., 1990), the translation elongation factor-1α (tef-1α) using primers EF1-1018F and EF1-1620R (Stielow et al., 2015), β-tubulin using primers TUBUF2 and TUBUR1 (Kroon, 2010), cytochrome oxidase subunit I (CoxI) using primers OomCoxILevup and Fm85mod (Ginetti et al., 2014) and cytochrome c oxidase subunit II (CoxII) using primers FM82 and FM78 (Martin and Tooley 2003). Polymerase Chain Reaction (PCR) amplifications were performed on thermal cycler MyCycler (Bio-Rad Laboratories, Inc). The PCR mixtures consisted of 1 µl genomic DNA (50 ng), 0.5 µl of 10 nM each primer, 12.5 µl of *OneTaq* Quick-Load 2X Master Mix and 10.5 µl Nuclease-free water in a total volume of 25 µl. To amplify the ITS, the PCR protocol was used; initial denaturation at 94 °C, 5 min; 35 amplification cycles of denaturation at 94 °C, 30 s; annealing

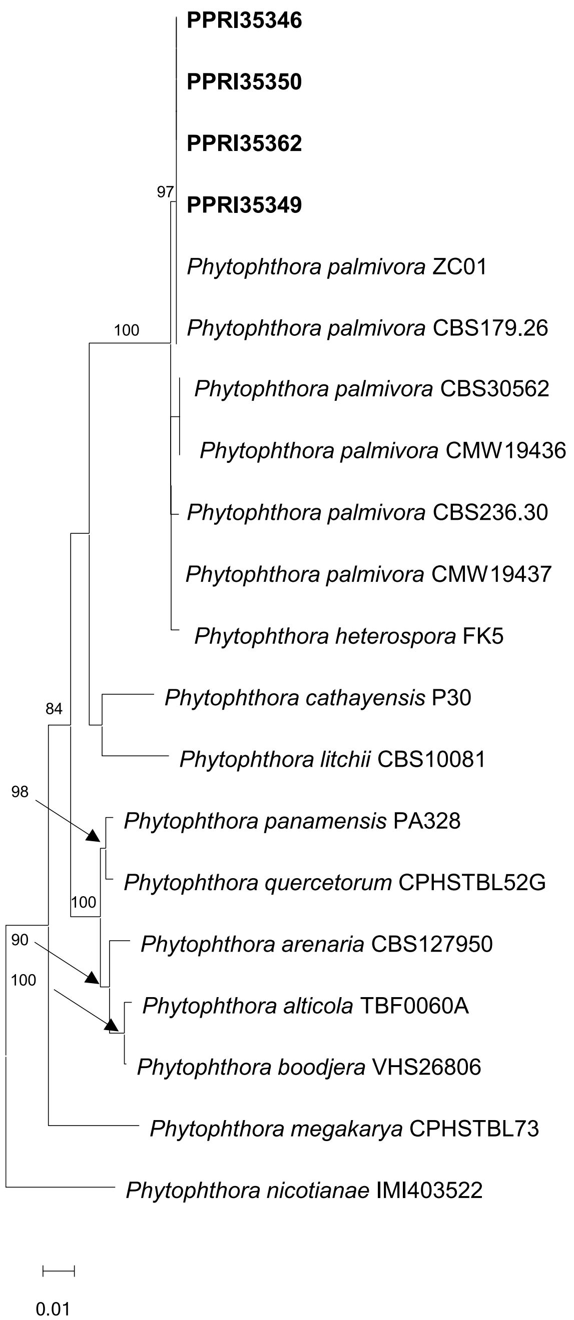

Fig. 3 Maximum Likelihood (ML) tree of the set of ITS, *β-tubulin, TEF1-α, Cox I* and *Cox II* loci sequences. The tree is rooted to *Phytophthora nicotianae*. Bootstrap values above 75% are given at the nodes. Representative of isolates of this study are indicated in bold

at 53 °C, 30 s; extension at 68 °C, 1 min and a final extension cycle at 68 °C, 5 min for all primer sets.

The sequencings reactions were performed using ABI 3500XL Genetic Analyzer at Inqaba Biotec (Pretoria, South Africa). Sequences of the isolates were edited using CLC-Bio Workbench V9.0 (Qiagen, Hilden, Germany). DNA sequences for relevant *Phytophthora* species previously published were retrieved from GenBank (http://www.ncbi.nlm.gov). The resulting data matrices was rooted to *Phytophthora nicotianae* and were aligned online using MAFFT (http://align.bmr.kyushuu.ac.jp/mafft/ online/server/) version 6 (Katoh et al., 2019) and checked manually for alignment errors. Phylogenetic analyses for all the datasets were performed using Maximum Likelihood (ML) using PhyML 3.0 online (http://www.atgc-montpellier.fr/phyml/; Guindon et al., 2010). The confidence levels for ML were determined with 1000 bootstrap replications.

A total of 32 samples were positive for the presence of *Phytophthora,* and 17 isolates were purified and grouped into one based on morphological characters. The sequence dataset for all isolates based on ITS gene region that contained 706 characters, were analysed. All isolates were identified as *Phytophthora palmivora* (Fig. 3). All the sequences emerging from this study were deposited in GenBank (Table 1).

Phytophthora palmivora is characterized by distinct morphological features, including sporangia with short pedicels and sympodial sporangiophores. The morphology of chlamydospores and hyphal swellings are also valuable for identification when combined with other aspects of the asexual phase. *Culture* colonies on potato dextrose agar exhibit a slight radiate chrysanthemum pattern with minimal aerial mycelium. *Asexual phase*, chlamydospores are numerous, (sub-)globose, terminal or intercalary, with an average diameter of 36 µm. Hyphal swellings can be globose, sub-globose, elongate, and irregular. Sporangia are formed on solid media and can be globose, ovoid, obpyriform, ellipsoid, and irregularly shaped. They are caducous with short pedicels and papillate. Sporangia are produced on simple sympodia. *Sexual phase*, *P. palmivora* is heterothallic. Oogonia are terminal and smooth-walled. Oospores are plerotic to slightly aplerotic with a thick wall (Fig. 4).

Pathogenicity trials were conducted first on the fruit for the initial screening of aggressiveness of isolates. Fourteen isolates were selected (Table 1). Discs (5 mm in diameter) of agar were cut from the actively growing margins of the cultures and placed into

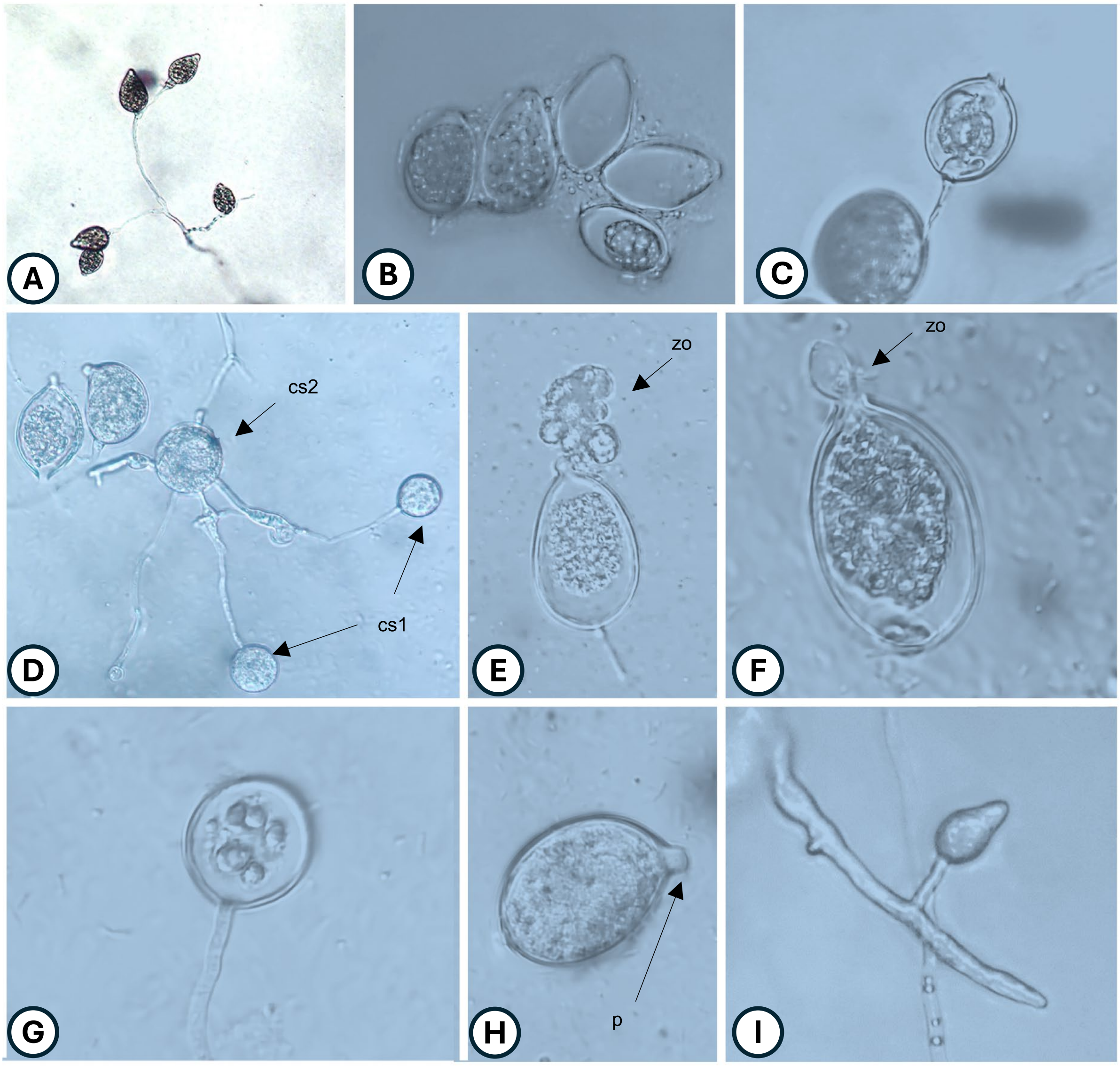

Fig. 4 Morphological characteristic of *Phytophthora palmivora*. **A-C.** Sporangia, **D.** terminal spherical chlamydospore (cs1) and intercalary spherical chlamydospores (cs2), **E–F.** sporangium releasing zoospores (zo), **G.** spherical oogonium, **H.** papillate (p) on ovoid sporangium, I. pear-shape sporangium

wounds of the same size on the papaya fruits, which were surface disinfested. In the case of the controls, inoculations were made with sterile PDA discs. The inoculated sections were sealed with masking tape to reduce desiccation and the chance of contamination. These fruits were maintained at 25 °C and observed for the appearance of symptoms daily. All fourteen isolates induced decay on the inoculated sections with white mycelia on tissues. The size of decay caused by all isolates was significant, as there were no decay symptoms on controls (Fig. 5). Re-isolation of all 14 isolates of *P. palmivora* from the inoculated fruits was consistent based on their morphology.

Two isolates were selected to inoculate two-month-old seedlings from three different cultivars (RL, SS, T1) to test the pathogenicity of the isolates on the plants. Prior to inoculation, two samples were randomly taken from each cultivar and tested for the

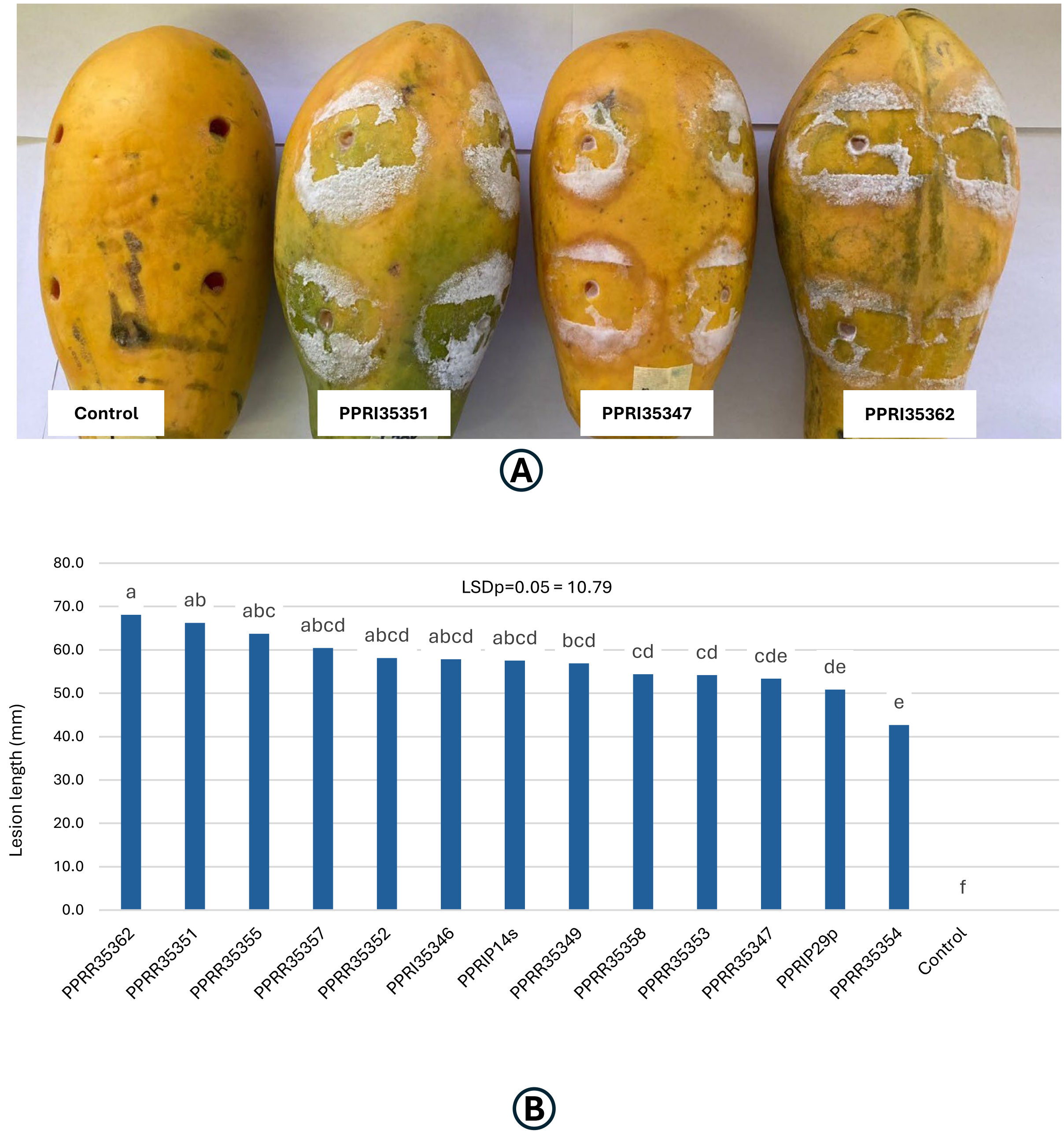

Fig. 5 Pathogenicity test of *Phytophthora palmivora* isolates on papaya fruits: **A.** Rot and mycelial growth on the inoculation sections after four days of inoculation. **B.** Length of lesion/rot cause by each isolate

presence of any pathogens, all tested negative. Discs (5 mm in diameter) of the *P. palmivora* isolate were inoculated onto the collar of the seedlings. For the controls, sterile PDA discs were used for inoculation. The inoculated sections were sealed with parafilm to prevent desiccation and reduce the risk of contamination. Symptoms were observed on the seedlings three weeks after inoculation (Fig. 6A–B). There were no differences in disease severity among the three cultivars; all exhibited the same symptoms at the same time. Therefore, no tolerance differences were observed among the tested cultivars.

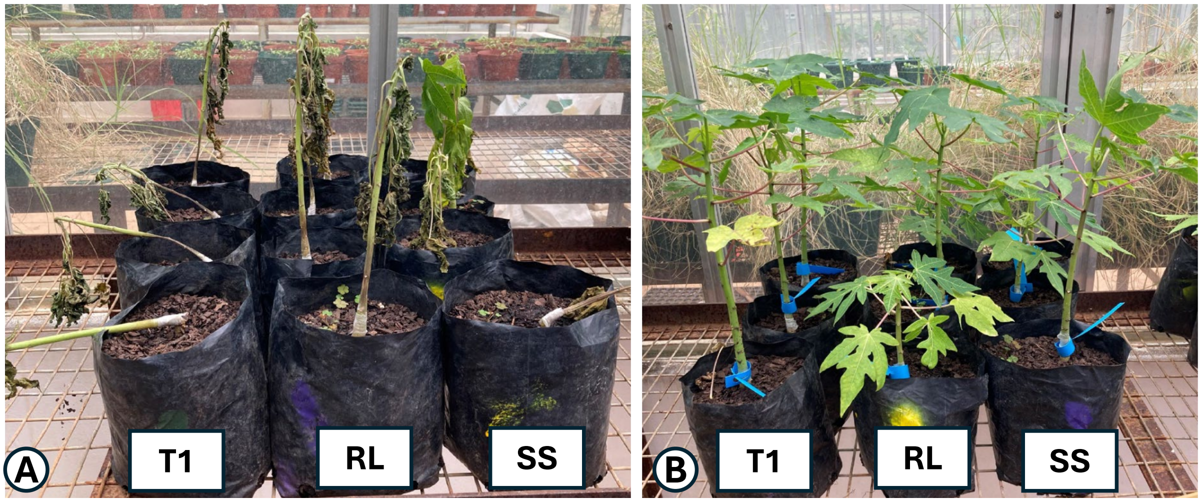

Fig. 6 Pathogenicity test of *Phytophthora palmivora* isolates on papaya seedlings of three cultivars: **A.** Wilting and root rot on the inoculated seedlings. **B.** Seedlings with no symptoms (control)

The results of this study showed that all isolates were highly pathogenic in artificial inoculation on papaya. This is not surprising as other studies have shown high p

athogenicity on other crops such as cocoa pods, leaves of young durian and rubber (Latifah et al., 2018) as well as citrus fruits (Tashiro et al., 2012). This is the first official disease report of *P. palmivora* in South Africa, where it is a regulated pathogen and the stem rot completely devastated papaya plantations. *Phytophthora palmivora* was first reported from papaya in Hawaii (Parris, 1942), where it caused 35% reduction in papaya production (Alvarez & Nelson, 1982). Since then, it has been reported from all papaya growing areas, including Indonesia, Japan (Masanto et al., 2019), Philippine, Malaysia (Drenth & Guest, 2004), Australia (Vawdrey, 2001), Brazil (Kader, 2002) and USA (Erwin & Ribeiro, 1996). These widespread reports demonstrate the global significance of *P. palmivora* as a major constraint to papaya production.

South Africa is the largest producer of macadamia nuts globally and ranks among the top exporters of citrus and avocados. Given the importance of these crops, *P. palmivora* poses significant threats, having been identified as the cause of various plant diseases such as citrus root rot in Egypt (Ahmed et al., 2014), blight on macadamia (Aragaki & Uchida, 1980), avocado root rot in Spain and Cuba (Machado et al., 2013; Rodriguez-Padron et al., 2018), and crown and root rot of mango in Philippine nurseries (Tsao et al., 1994). These reports emphasize the pathogen's broad host range and its potential risk to South Africa's key horticultural industries.

However, the pathway by which *P. palmivora* entered South Africa remains unknown. As this pathogen is widely distributed, possible routes include the importation of infected plant material, contaminated soil, or through water movement. Additionally, human activities such as agricultural trade, movement of infected nursery stock or orchards, or contaminated agricultural equipment might have facilitated its spread. Understanding the specific introduction pathway will be investigated for implementing effective quarantine and management strategies to prevent further dissemination and protect South African agriculture.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations The authors have no relevant financial or non-financial interests to disclose.

Ethical approval The authors confirm that there are no ethical issues in the publication of this research, it does not involve human participants or animals.

Conflict of interest The authors declare that they have no conflict of interest.

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