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Phytophthora spp. diversity in commercial nursery stocks shown through examination of plant health practices for growers and traders of ornamental plants

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Summary. Management of *Phytophthora* in commercial plant nurseries is important for biosecurity of traded plants, and monitoring of incidence of this important plant pathogen is a prerequisite to prevent its spread. Potted plants showing *Phytophthora* spp. symptoms, and nursery irrigation and runoff water, were sampled from a commercial and a non-commercial nursery in Tuscany, Italy. The samples were processed to detect *Phytophthora* spp., using baiting, and molecular identification of obtained isolates. High *Phytophthora* incidence was shown in the commercial nursery. Twelve *Phytophthora* spp. were isolated from potted plants or nursery runoff water. Individual symptomatic potted plants were infected with up to four pathogenic *Phytophthora* spp. The water sampled from nursery drainage canals had the greatest *Phytophthora* species diversity, with less diversity in 'flow-through' water samples (irrigation water percolated through potted plants) and samples from water puddles inside the nurseries. This study showed high incidence of *Phytophthora* in the commercial nursery, and associated risk of spread of these pathogens within and outside nursery operations. Lack of appropriate disease management probably increases occurrence of these pathogens.

Keywords. Oomycetes spread, biological hazard, potted plants health, stakeholder involvement, risks warning.

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INTRODUCTION

Phytophthora spp. are plant-damaging oomycetes (*Peronosporales*) that can cause significant economic losses in many different crops. From approx. 500 estimated species (Yang *et al.*, 2017). More than 200 *Phytophthora* type species have been described (Abad *et al.*, 2023). Most of these taxa are poten-

tially invasive and lethal pathogens of woody plants (Brasier, 1999), that have been directly responsible for ecological, economic and social impacts on a continental scale during the past 150 years (Brasier *et al.*, 2022).

Phytophthora is strictly linked to soil for dispersal, is well-adapted to living in water, and spreads from plant to plant via motile zoospores (Erwin and Ribeiro, 1996). Many species can survive in soil as chlamydospores, under unfavourable conditions and for long periods (Hwang, 1978; Fichtner *et al.*, 2007; Shishkoff, 2007). Persistent high humidity, close proximity to potential host species, movement of plant growth media and irrigation water, general lack of sterilization steps in plant propagation, and use of external or imported plant propagation material, make commercial nurseries the sites of introduction, survival and spread of many *Phytophthora* spp. (Themann *et al.*, 2002; Moralejo *et al.*, 2009; Migliorini *et al.*, 2015; Jung *et al.*, 2016). Such conditions explain the many destructive outbreaks of these pathogens that have occurred in nurseries during the last decades (Brasier *et al.*, 2022, and other publications cited in the present paper). Nurseries that produce plants in pots are therefore responsible for spreading of *Phytophthora* spp. due to the significant presence of *Phytophthora* inoculum in soil and roots of the final products, which are sold as asymptomatic plants (Migliorini *et al.*, 2015).

For these reasons and during the last decade, large scale investigations have aimed to characterize *Phytophthora* diversity in plant nurseries, and have been implemented at national level, with the scope to identify the greatest phytosanitary risks in individual nurseries and in the production links between nurseries. Examples are the outcomes obtained in Oregon, United States of America, by Parke *et al.* (2014), and by Schiffer-Forsyth *et al.* (2023) in the United Kingdom as part of the PHYTO-THREATS project (Green *et al.*, 2020, 2021). Through results of extensive diagnostic services based on molecular techniques, both of these studies provided foundations for implementing systems approaches in nursery production, by providing information on *Phytophthora* spp. presence and abundance at critical control points, and outlining best disease management practices.

The present research has been part of the EUPHRESCO project 'ID-PHYT' ("EUPHRESCO 'ID-PHYT-Early detection of *Phytophthora* in EU and third country nurseries and traded plants').

The objective of this study was to characterize *Phytophthora* spp. in a commercially active retail nursery which had robust production and frequent exchanges of potted woody plants, and in a non-commercial nursery with minimal entry and exit of potted plants. These two nurseries were situated in the same geographic area. The results of this study have been shared with the project partner, and have been used within this study to enhance *Phytophthora* sampling for refinement of best management practices in productive ornamental nurseries.

MATERIALS AND METHODS

Sample collection

The two potted-plant nurseries selected for this study were in Northern Tuscany, Italy, within the peri-urban areas of Florence (nursery 1) and Pistoia (nursery 2). Nursery 1 (N1) was a non-commercial, research nursery, while nursery 2 (N2) was a commercial retail nursery associated with international trading of potted plants.

Following the 'ID-PHYT' protocol, selection of sample types aimed to maximize taxonomic characterization of *Phytophthora* spp. Care was taken to extend detection to all potential inoculum sources within the two nurseries. Samples analysed in consisted of: i) potted plants, ii) potted plant 'flow-through water' (see below), and iii) water from the irrigation systems. Sample types slightly differed between N1 and N2. Plant samples selected in N1 and N2 were of different species. Water samples from N1 were collected from the irrigation pipe system and the irrigation pond. Water samples from N2 were collected from irrigation pipes, nursery runoff water and puddled water (Puddles) (Table 1). Sampling occurred in May 2021, according to criteria outlined below.

Potted plants

Two plants per species, showing dieback symptoms (leaf discolouration, and/or leaf spotting, poor foliage development) were selected, and then processed for the 'flow-through" procedure (Flow-through water, see below). They were then brought to a laboratory where the associated potting soil (Potting soil), consisting of soil and roots, was processed using baiting for isolation of oomycetes.

Flow-through water

Potted plants when still in the nursery were placed in sterile trays, and were irrigated with local irrigation water to reach the 10–20% of pot water holding capacity for 20 min, to stimulate release of Potting soil Oomycete inoculum into the trays. Water from the trays was then

Table 1. Sources of the samples collected form two nurseries. The samples consisted of potted plants, potted plant 'flow-through water' and water from the irrigation systems. Plant samples from the two nurseries of different species. Water samples from N1 were collected from the irrigation pipe and the irrigation pond, and samples from N2 were from the irrigation pipe, runoff nursery water, and puddled water present in the nursery.

Sample source	Nursery		Potting Soil	Water	
	1	2		Irrigation system	Flow-through
Irrigation pond	/			/	
Irrigation pipe	/			/	
Cupressus sempervirens	/		/		/
Fagus sylvatica	/		/		/
Ilex aquifolium	/		/		/
Myrtus communis	/		/		/
Pinus nigra	/		/		/
Ulmus minor	/		/		/
Viburnum tinus	/		/		/
Irrigation pipe		/		/	
Runoff water		/		/	
Puddles		/		/	
Magnolia grandiflora		/	/		/
Choisya ternata		/	/		/
Choisya ternata 'Aztec Pearl'		/	/		/
Ceanothus concha		/	/		/
Elaeagnus angustifolia		/	/		/

collected in sterile tanks and processed in the laboratory for oomycetes isolations.

Water

Water from the nursery irrigation systems, including an irrigation pond (N1), water from irrigation pipes (N1 and N2), water from small puddles on the dirt roads of N2, and runoff water of N2, was collected in previously sterilized water tanks and processed for oomycetes isolations.

Sample processing

Baiting

All samples, including Potting soil, Flow-through and Puddles water, and water from irrigation pipes and pond, were immediately processed for isolation of oomycetes in the laboratory, using the baiting technique outlined in Figure 1. The analysis was conducted according to 'Baiting Method 1' described by Burgess

Figure 1. Baiting of water and potted plant samples. Containers were 280 × 190 × 140 mm deep, and each contained 3 L of distilled water. Baits used were young leaves of *Hedera* sp. and *Quercus ilex*, and rose petals.

et al., 2021, with the following exceptions: each sample was analysed in duplicate (two containers each); containers were 280 × 190 × 140 mm deep, filled with a final volume of 3 L of distilled water. Baits used were young leaves of *Hedera* sp. or young leaves and rose petals of *Quercus ilex* (Figure 1); all isolation culture plates were incubated at 20°C in the dark, and checked daily for growth of oomycetes.

DNA sequencing

Cultures were transferred onto '½ PDA' medium plates (19.5 g L^{-1} of Potato dextrose agar, 7.5 g L^{-1} of Agar, 1 L of deionized water). Aerial hyphae (ca. 80 mg) were scraped from the surface of each culture, and then ground in a 2 mL capacity microfuge tube with two tungsten beads (3 mm) (Qiagen) and 400 µL of Buffer P1 (EZNA Plant DNA Kit, Omega Bio-tek), using a Mixer Mill 300 (Qiagen) set for 2 min at 20 Hz. DNA was extracted from all samples using the EZNA Plant DNA Kit (Omega Bio-tek), following the manufacturer's instructions. The DNA concentrations were measured using a Nanodrop ND1000 spectrophotometer (NanoDrop Technologies). For phylogenetic analyses, the internal transcribed spacer ITS regions (including spacers ITS1 and ITS2 and the 5.8S gene of the rDNA) were amplified using the primers ITS6 and ITS4 (White *et al.*, 1990; Cooke *et al.*, 2000), following the protocol by Migliorini *et al.* (2020). PCR amplicons were purified with a miPCR Purification Kit (Metabion International), and were sequenced in one direction by Macrogen (Seoul,

South Korea). The qualities of amplified nucleotide sequences were checked with the Geneious ver. R10 software package (Biomatters; https://www.geneious.com/).

Phylogenetic analyses

BLAST searches of the generated sequences were carried out using the NCBI GenBank database (https://blast.ncbi.nlm.nih.gov/Blast.cgi), to identify the most closely related sequences. Isolate sequences of *Pythiaceae* were compared to those of known *Pythium* and *Phytopythium* spp. obtained from GenBank. The ITS sequences of *Phytopythium* and *Pythium* were from *Pythium kashmirense* (HQ643671), *Phytopythium vexans* (HQ643400) (Robideau *et al*., 2011) or *Phytopythium paucipapillatum (*KX372749, Crous *et al*., 2020). BLAST searches of the generated ITS gene sequences of *Phytophthora* were carried out using a custom database to identify the most closely related sequences. The *Phytopthtora* database sequences were from the type isolates found on IDPhy (Abad *et al*., 2023). The BLAST search of *Phytophthora* and the subsequent phylogenetic analysis, and the analyses of *Pythium* and *Phytopythium*, were conducted at Geneious. Sequences were aligned using the MAFFT alignment within Geneious, using the default parameters. Phylogenetic trees were constructed in Geneious Tree Builder using the Neighbour-Joining Method (Genetic Distance Model: HKY). Bootstrap was selected as Resampling method (2000 Number of Replicates). Gaps were treated as missing data.

RESULTS

Thirty-eight isolates were obtained in this study, of which four were from N1 (Florence) and 34 were from N2 (Pistoia). Twenty-seven of the isolates were from water samples, including 12 from Run-off, 13 from Flow-through, two from Puddles, and one from the irrigation pond. Ten isolates were obtained from Potting soil. The ITS sequences were sufficient to identify each isolate. The 15 detected species were: *Phytophthora acerina, Phytophthora cactorum, Phytophthora cambivora, Phytophthora chlamydospora, Phytophthora cinnamomi, Phytophthora gonapodyides, Phytophthora hydropatica, Phytophthora lacustris, Phytophthora multivora, Phytophthora nicotianae, Phytophthora plurivora, Phytophthora pseudocryptogea* (Figure S1), *Pythium kashmirense, Phytopythium paucipapillatum, Phytopythium vexans* (Figure S2). Three isolates of *Pythium* and *Phytopythium,* and one of *Phytophthora gonapodydes* were obtained from N1. All the other *Phytophthora* species, including *P. gonapodyides,* were isolated from N2 (Table S1). Sequences were deposited in the GenBank (Table S1).

Phytophthora *taxa*

Twelve *Phytophthora* spp. were isolated from N2, and one isolate of *P. gonapodydes* was obtained from N1 (Table 2). Seven different *Phytophthora* spp. were detected in Run-off water samples, four each in Flow-through and Potting soil samples, and one was detected in Puddles samples, while none were detected in the irrigation pond (Table 2, Figure 2). Several *Phytophthora* species were detected from N2, from different matrices and/or plant species: *P. cinnamomi* from Flow-through of *Magnolia grandiflora* and *Ceanothus concha*, and from Potting soil of *C. concha* and *Elaeagnus angustifolia*; *P. gonapodyides* from Run-off water and Puddles; *P. nicotianae* from Potting soil of *Choisya ternata* 'Aztec Pearl', and Flow-through of *C. ternata* and *C. concha; P. plurivora* from Flow-through of *M. grandiflora* and *C. ternata* 'Aztec Pearl', and from Run-off water (Table 2). *Ceanothus concha* was the plant species from which the largest number of *Phytophthora* species were isolated (*P. cinnamomi* and *P. nicotianae* from Flow-through and *P. cactorum*, *P. cinnamomi* and *P. multivora* from Potting

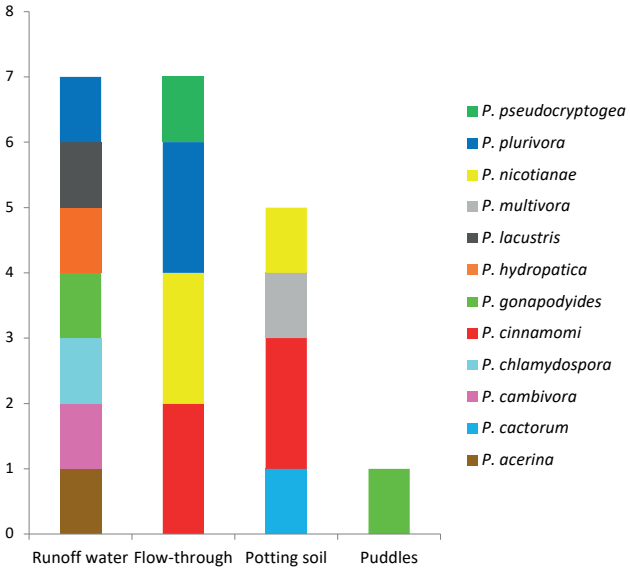

Figure 2. Distributions of the twelve *Phytophthora* spp. isolated in this study, across the four isolation matrices (Runoff water, Flow-through, Potting soil or Puddles). Each rectangular unit represents one detection of each pathogen per matrix per plant species. The double rectangular units for *P. cinnamomi*, *P. nicotianae* and *P. plurivora* indicate that these organisms were detected from the same isolation matrix in two different plant species (see Table 2 for taxonomic details).

Table 2. List of *Phytophthora* species obtained in this study. The table indicates the nursery of provenance, if the pathogen was isolated from one of the sampling categories, including Runoff water, Flow-through, Puddles, irrigation pond or from Potting soil. Plant species from which Flow-through and Potting soil isolates were obtained are also indicated. Numbers of total species and total species from each isolation matrix in each plant species per each matrix are also summarized.

Phytophthora species	Nursery		Plant species	Isolation matrix				
				Water				Potting soil
	1	2		Runoff water	Flow-through	Puddles	Irrigation pond	
P. acerina		/		/				
P. cactorum		/	*Ceanothus concha*					/
P. cambivora		/		/				
P. chlamydospora		/		/				
P. cinnamomi		/	*Magnolia grandiflora*		/			
		/	*Ceanothus concha*					/
		/	*Ceanothus concha*		/			
		/	*Elaeagnus angustifolia*					/
P. gonapodyides		/		/				
		/				/		
P. hydropatica		/		/				
P. lacustris		/		/				
P. multivora		/	*Ceanothus concha*					/
P. nicotianae	/		*Cupressus sempervirens*					/
		/	*Choisya ternata* 'Aztec Pearl'					/
		/	*Choisya ternata*		/			
		/	*Ceanothus concha*		/			
P. plurivora		/	*Magnolia grandiflora*		/			
		/		/				
		/	*Choisya ternata* 'Aztec Pearl'		/			
P. pseudocryptogea		/	*Choisya ternata* 'Aztec Pearl'		/			
Species per isolation matrix per plant species				7	7	1	0	6
Total species	1	12		7	4	1	0	4

soil), followed by *C. ternata* 'Aztec Pearl' (*P. plurivora* and *P. pseudocryptogea* from Flow-through and *P. nicotianae* from Potting soil), *M. grandiflora* (P. *cinnamomi* and *P. plurivora* from Flow-through), *E. angustifolia* (*P. cinnamomi* from Potting soil) and *C. ternata* (*P. nicotianae* from Flow-through) (Figure 3).

DISCUSSION

Several cases of spread of different *Phytophthora* species have been reported from non-commercial plant restoration nurseries into wild areas, where these oomycetes had not been previously detected (Rooney-Latham *et al.*, 2015, 2019). In the present study, however, in the non-commercial nursery (N1) only one *Phytophthora* sp. was detected, as a single isolate. In contrast, several *Phytophthora* spp. known as pathogens of different host plant species, and from different isolation matrixes, were found in the commercial nursery (N2), including 12 species from six *Phytophthora* clades.

Several important pathogens, including *P. cactorum*, *P cinnamomi*, *P. pseudocryptogea*, *P. nicotianae* and *P. plurivora*, were isolated from one location. All of these *Phytophthora* spp. are classified as polyphagous species, which are well-adapted to nurseries, forestry, and agricultural environments (Jung *et al.*, 2018). Within this group, *P. cinnamomi* is particularly important. This organism is one of the most devastating plant pathogens, in terms of geographic distribution and host range. It has been listed as one of the 100 worst invasive species (Burgess *et al.*, 2017), and is well-known as the cause of large-scale dieback of *Eucalyptus* (jarrah dieback) in Australian forests (Dell and Malajczuk, 1989) and as a cause of oak decline in the Iberian Peninsula (Brasier *et al.*, 1993).

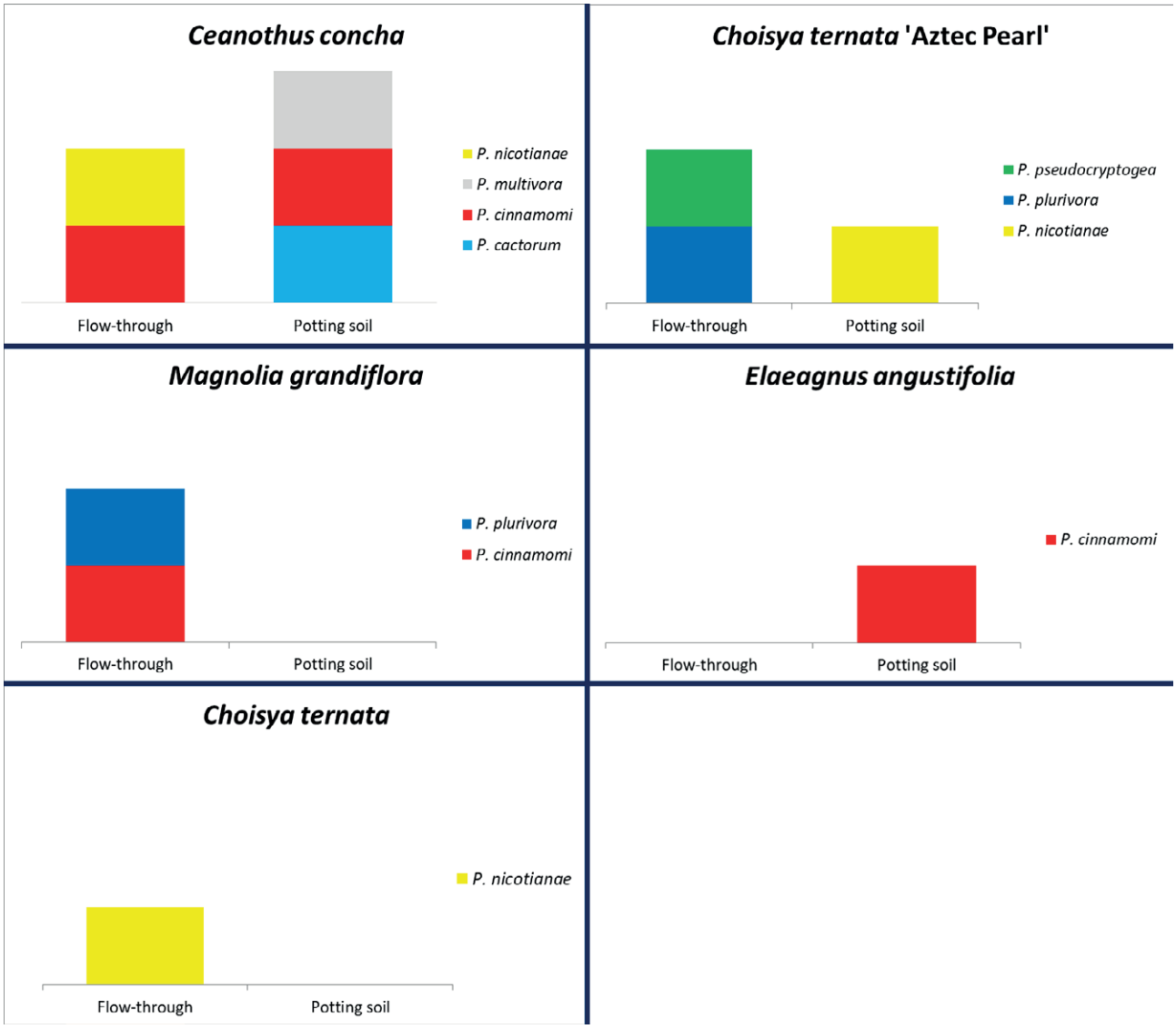

Figure 3. *Phytophthora* spp. isolated in this study from five plant hosts. The two columns in each histogram indicate the isolate sources (Flow-through or Potting soil; see text).

During the present study, *P. cinnamomi* was detected from three plant species, and from potting soil and flow-through water, underlining the potential spread of viable inoculum across a nursery. *Phytophthora nicotianae* was similar, being found on three host species and in the same isolation matrices. Like *P. cinnamomi*, *P. nicotianae* is a severe disease agent of many plant taxa, but apart from ornamentals and citrus trees, it is not responsible for dieback diseases of woody plants in the wild (Brasier *et al.*, 2022). *Phytophthora cactorum*, *P. pseudocryptogea*, and *P. plurivora* are notorious root and collar rot disease agents on many hosts, but while *P. cactorum and P. pseudocryptogea* have broad host ranges including herbaceous and crop species (Hudler, 2013; Delshad *et al.*, 2020), *P. plurivora* is mainly a woody host pathogen, both in woodland and on ornamentals (Jung and Burgess, 2009).

Phytophthora acerina, *P. cambivora* and *P. multivora* are aggressive woody plant pathogens that were found during the present survey. *Phytophthora acerina* was first reported on *Acer pseudoplatanus* and olive trees in northern Italy, and recently on *Metasequoia glyptostroboides* in China (Liu *et al.*, 2022) and walnut trees in California (Forbes *et al.*, 2019). *Phytophthora cambivora* has been frequently reported as the cause of ink disease of chestnut trees in southern and eastern Europe

(Vettraino *et al.*, 2005; Černý *et al.*, 2008), but this is also a species with broad international distribution and associated with declining trees. *Phytophthora multivora* is known as a dieback and bleeding canker agent in forest (Scott *et al.*, 2009, 2012) and urban trees of Western Australia (Barber *et al.*, 2013), where it has been demonstrated to be highly pathogenic on multiple native plants (Migliorini *et al.*, 2019). This species is now considered a significant pathogen with a wide host range and broad international distribution in nurseries, urban environments and natural ecosystems, and has been widely detected, mainly in nurseries of woody plants (Migliorini *et al.*, 2019; other reports cited elsewhere in this paper).

The other *Phytophthora* spp. detected in this survey included aquatic species that are common in nurseries but have not been associated with severe pathogenicity traits. These included *P. gonapodyides*, *P. lacustris*, *P. chlamydospora* from clade 6, and *P. hydropatica* from clade 9.

Other species of *Pythiaceae* were also detected in the present study. These belong to genera known for their pathogenicity on woody plants. However, these organisms are secondary concerns in mature potted plants cultivated in ornamental nurseries, as they are primarily damping-off agents affecting young hosts during the seedling stages. *Pythium kashmiriense* and *Phytopythium paucipapillatum* are rare soilborne species, which have been detected only once, respectively, in Europe (Benavent-Celma *et al.*, 2021) and South Africa (Crous *et al.*, 2020). *Phytopythium vexans* has aggressiveness and dissemination capabilities that are similar to some of the most pathogenic *Phytophthora* spp. isolated in the present study, although this pathogen does not exhibit the same levels of invasiveness in forests and natural environments (Panth *et al.*, 2021). Notably, *P. vexans* was the only relevant pathogen obtained in the non-commercial nursery.

The outcomes of this research indicate that the different plant production procedures used in two potted-plant nurseries may have determined their levels of biosecurity, emphasising that the implementation of effective management practices should be a priority in commercial nurseries. Both N1 and N2, the first with little presence of *Phytophthora*, the second with abundant *Phytophthora* spp. associated with all the different analysed sample types, did not utilize any biosecurity practises, such as filtering of irrigation water prior to use, cultivation of potted plants on benches, and use of pre-sterilized potting soil. It is probable that the difference in production procedures led to the difference in pathogen abundance between the two nurseries, both in pathogen taxa and their spatial distributions. The production techniques in N2, which did not differ from those of most of the retail nurseries located in the same area, were characterised by the constant input of propagation material from other producers. This practice is known to be linked to high biological risks, due to the potential abundance of pathogens (Ghelardini *et al.*, 2016; Eschen *et al.*, 2017). The non-application of simple, effective safety practices encourages spread and persistence of all newly introduced *Phytophthora* species within nurseries and results in losses to customers and to final recipients of plants, causing financial damage. The lack of biosecurity measures will lead to further ecological impacts where plants will be finally planted, both on large scales, through international trade in pot plants contaminated with pathogens, and locally, with spread of *Phytophthora* in areas neighbouring nurseries through contaminated irrigation water. This last aspect was documented in the present study, which detected up to seven species in N2 runoff water.

In conclusion, the results of this research demonstrate that non-adoption of internal prevention protocols aimed at systemic control of *Phytophthora* spp. in commercial nurseries can lead to severe economic losses. In this specific case, the N2 growers and traders were briefed on the necessary actions to be taken to implement a progressive process limiting infected propagation material and, consequently, producing and selling potted material that is not contaminated with *Phytophthora* spp.

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LITERATURE CITED

Abad Z.G., Burgess T.I., Redford A.J., Bienapfl J.C., Srivastava S., Mathew, R. and Jennings K., 2023. IDphy: An International Online Resource for Molecular and Morphological Identification of *Phytophthora*. *Plant Disease* 107: 987–998. https://doi.org/10.1094/PDIS-02-22-0448-FE

Barber P.A., Paap T., Burgess T.I., Dunstan W., Hardy G.E.S.J., 2013. A diverse range of *Phytophthora* species are associated with dying urban trees. *Urban Forestry and Urban Greening*, Elsevier GmbH. 12: 569–575. https://doi.org/10.1016/j.ufug.2013.07.009

Benavent-Celma C., Puertolas A., McLaggan D., van West P., Woodward S., 2021. Pathogenicity and host range

of Pythium kashmirense—a soil-borne oomycete recently discovered in the uk. *Journal of Fungi* 7 https://doi.org/10.3390/jof7060479

Brasier C.M., 1999. Phytophthora pathogens of trees: their rising profile in Europe. Information Note 30, 1–5. Available at: www.gov.uk/government/organisations/forestry-commission. Accessed November 1, 2023.

Brasier C.M., Robredo F., Ferraz J.F.P., 1993. Evidence for *Phytophthora cinnamomi* involvement in Iberian oak decline. *Plant Pathology* 42: 140–145. https://doi.org/10.1111/j.1365-3059.1993.tb01482.x

Brasier C., Scanu B., Cooke D., Jung T., 2022. *Phytophthora*: an ancient, historic, biologically and structurally cohesive and evolutionarily successful generic concept in need of preservation. *IMA Fungus* 13 https://doi.org/10.1186/s43008-022-00097-z

Burgess T.I., Scott J.K., McDougall K.L., Stukely M.J.C., Crane C., … Hardy G.E.S.J., 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. Global Change Biology. *Global Change Biology* 23: 1661–1674. https://doi.org/10.1111/gcb.13492

Burgess T.I., López-Villamor A., Paap T., Williams B., Belhaj R., … Hardy G.E.S.J., 2021. Towards a best practice methodology for the detection of *Phytophthora* species in soils. *Plant Pathology* 70: 604–614. https://doi.org/10.1111/ppa.13312

Černý K., Gregorová B., Strnadová V., Tomšovský M., Holub V., Gabrielová Š., 2008. *Phytophthora cambivora* causing ink disease of sweet chestnut recorded in the Czech Republic. *Czech Mycology* 60: 267–276.

Cooke D.E.L., Drenth A., Duncan J.M., Wagels G., Brasier C.M., 2000. A molecular phylogeny of *Phytophthora* and related oomycetes. *Fungal Genetics and Biology* 30: 17–32. https://doi.org/10.1006/fgbi.2000.1202

Crous P., Cowan D., Yilmaz N., Larsson E., Angelini C., … Leonard P., 2020. Fungal Planet description sheets. *Persoonia* 45: 251–409. https://doi.org/10.3767/persoonia.2020.45.10

Dell B., Malajczuk N., 1989. Jarrah dieback – A disease caused by *Phytophthora cinnamomi*. In: *The Jarrah Forest* (Springer, ed.), Dordrecht, The Netherlands, 67–87.

Delshad D., Mostowfizadeh-Ghalamfarsa R., Safaiefarahani B., 2020. Potential host range and the effect of temperature on the pathogenicity of *Phytophthora pseudocryptogea* and its close relatives. *Journal of Plant Pathology* 102: 753–763. https://doi.org/10.1007/s42161-020-00501-w

Erwin D.C., Ribeiro O.K., 1996. *Phytophthora: Diseases Worldwide*. St. Paul, Minnesota, USA, APS Press, 408–422 pp.

Eschen R., Douma J.C., Grégoire J.-C., Mayer F., Rigaux L., Potting R.P.J., 2017. A risk categorisation and analysis of the geographic and temporal dynamics of the European import of plants for planting. *Forest Invasions* 19: 3243–3257. https://doi.org/10.1007/s10530-017-1465-6

EUPHRESCO 'ID-PHYT-Early detection of Phytophthora in EU and third country nurseries and traded plants,' (n.d.). Available at: https://drop.euphresco.net/data/d6902388-be48-4b72-ad6e-709ea37f18ea. Accessed October 25, 2023.

Fichtner E.J., Lynch S.C., Rizzo D.M., 2007. Detection, distribution, sporulation, and survival of *Phytophthora ramorum* in a California redwood-tanoak forest soil. *Phytopathology* 97: 1366–1375. https://doi.org/10.1094/PHYTO-97-10-1366

Forbes H.K., Rizzo D.M., Browne G.T., 2019. Reexamination of *Phytophthora* populations affecting almond and walnut trees in California. University of California. Available at: https://www.proquest.com/openview/385fe9f7d9b5b5b292c2e8f366b7b1fa/1?pq-origsite=gscholar&cbl=18750&diss=y

Ghelardini L., Pepori A.L., Luchi N., Capretti P., Santini A., 2016. Drivers of emerging fungal diseases of forest trees. *Forest Ecology and Management* 381: 235–246. https://doi.org/10.1016/j.foreco.2016.09.032

Green S., Cooke D.E.L., Dunn M., Barwell L., Purse B., … Marzano M., 2021. Phyto-threats: Addressing threats to OK forests and woodlands from *Phytophthora*; identifying risks of spread in trade and methods for mitigation. *Forests* 12: 1617. https://doi.org/10.3390/f12121617

Green S., Marzano M., Frederickson-matika D., Valatin G., Pérez-sierra A., … Thorpe P., 2020. Thapbi final report form 1., 1–28. Available at: https://www.forestresearch.gov.uk/research/global-threats-from-phytophthora-spp-phyto-threats/#:~:text=The multidisciplinary "Phyto-threats",pathogens in the wider UK.

Hudler G.W., 2013. *Phytophthora cactorum*. *Forest Phytophthoras* 3. https://doi.org/10.5399/osu/fp.3.1.3396

Hwang S.C., 1978. Biology of Chlamydospores, Sporangia, and Zoospores of *Phytophthora cinnamomi* in Soil. *Phytopathology* 68: 726–731. https://doi.org/10.1094/phyto-68-726.

Jung T., Burgess T.I., 2009. Re-evaluation of Phytophthora citricola isolates from multiple woody hosts in Europe and North America reveals a new species, *Phytophthora plurivora* sp. nov. *Persoonia: Molecular Phylogeny and Evolution of Fungi* 22: 95–110. https://doi.org/10.3767/003158509X442612

Jung T., Orlikowski L., Henricot B., Abad-Campos P., Aday A.G., … Peréz-Sierra A., 2016. Widespread *Phytophthora* infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of Phytophthora diseases. *Forest Pathology* 46: 134–163. https://doi.org/10.1111/efp.12239

Jung T., Pérez-Sierra A., Durán A., Jung M.H., Balci Y., Scanu B., 2018. Canker and decline diseases caused by soil- and airborne *Phytophthora* species in forests and woodlands. *Persoonia: Molecular Phylogeny and Evolution of Fungi* 40: 182–220. https://doi.org/10.3767/persoonia.2018.40.08

Liu D.C., Zhao W.X., Xia J.P., Cai S.S., Huai W., … Li B., 2022. First Report of Root Rot Caused by *Phytophthora acerina* on *Metasequoia glyptostroboides* in China. *Plant Disease* 106: 2270. https://doi.org/10.1094/PDIS-12-21-2722-PDN

Migliorini D., Ghelardini L., Tondini E., Luchi N., Santini A., 2015. The potential of symptomless potted plants for carrying invasive soilborne plant pathogens. *Diversity and Distributions* 21: 1218–1229. https://doi.org/10.1111/ddi.12347

Migliorini D., Khdiar M.Y., Padrón C.R., Vivas M., Barber P.A., … Burgess T.I., 2019. Extending the host range of *Phytophthora multivora*, a pathogen of woody plants in horticulture, nurseries, urban environments and natural ecosystems. *Urban Forestry and Urban Greening* 46. https://doi.org/10.1016/j.ufug.2019.126460

Migliorini D., Luchi N., Pepori A.L., Pecori F., Aglietti C., … Santini A., 2020. *Caliciopsis moriondi*, a new species for a fungus long confused with the pine pathogen C. pinea. *MycoKeys* 73: 87–108. https://doi.org/10.3897/MYCOKEYS.73.53028

Moralejo E., Pérez-Sierra A.M., Álvarez L.A., Belbahri L., Lefort F., Descals E., 2009. Multiple alien *Phytophthora* taxa discovered on diseased ornamental plants in Spain. *Plant Pathology* 58: 100–110. https://doi.org/10.1111/j.1365-3059.2008.01930.x

Panth M., Baysal-Gurel F., Avin F.A., Simmons T., 2021. Identification and chemical and biological management of *Phytopythium vexans*, the causal agent of *Phytopythium* root and crown rot of woody ornamentals. *Plant Disease* 105: 1091–1100. https://doi.org/10.1094/PDIS-05-20-0987-RE

Parke J.L., Knaus B.J., Fieland V.J., Lewis C., Grünwald N.J., 2014. *Phytophthora* community structure analyses in Oregon nurseries inform systems approaches to disease management. *Phytopathology* 104: 1052–1062. https://doi.org/10.1094/PHYTO-01-14-0014-R

Robideau G.P., De Cock A.W., Coffey M.D., Voglmayr H., Brouwer H., … Lévesque C.A. DNA barcoding of oomycetes with cytochrome c oxidase subunit I and internal transcribed spacer. *Molecular Ecology Resources* 11(6):1002-1011. https://doi.org/10.1111/j.1755-0998.2011.03041

Rooney-Latham S., Blomquist C.L., Swiecki T., Bernhardt E., Frankel S.J., 2015. First detection in the USA: new plant pathogen, *Phytophthora tentaculata*, in native plant nurseries and restoration sites in California. *Native Plants Journal* 16: 23-27. https://doi.org/10.3368/npj.16.1.23

Rooney-Latham S, Blomquist C.L., Kosta K.L., Gou Y.Y., Woods P.W., 2019 .*Phytophthora* species are common on nursery stock grown for restoration and revegetation purposes in California. *Plant Disease* 2019 103:448-455. https://doi.org/10.1094/PDIS-01-18-0167-RE. Epub 2019 Jan 10. PMID: 30632470

Schiffer-Forsyth K., Frederickson Matika D., Hedley P.E., Cock P.J.A., Green S., 2023. *Phytophthora* in Horticultural Nursery Green Waste—A Risk to Plant Health. *Horticulturae* 9: 1–12. https://doi.org/10.3390/horticulturae9060616

Scott P.M., Burgess T.I., Barber P.A., Shearer B.L., Stukely M.J.C., … Jung T., 2009. *Phytophthora multivora* sp. nov., a new species recovered from declining *Eucalyptus*, *Banksia*, *Agonis* and other plant species in Western Australia. *Persoonia: Molecular Phylogeny and Evolution of Fungi* 22: 1–13. https://doi.org/10.3767/003158509X415450

Scott P.M., Jung T., Shearer B.L., Barber P.A., Calver M., Hardy G.E.S.J., 2012. Pathogenicity of *Phytophthora multivora* to *Eucalyptus gomphocephala* and *Eucalyptus marginata*. *Forest Pathology* 42: 289–298. https://doi.org/10.1111/j.1439-0329.2011.00753.x

Shishkoff N., 2007. Persistence of *Phytophthora ramorum* in soil mix and roots of nursery ornamentals. *Plant Disease* 91: 1245–1249. https://doi.org/10.1094/PDIS-91-10-1245

Themann K., Werres S., Lüttmann R., Diener H.A., 2002. Observations of *Phytophthora* spp. in water recirculation systems in commercial hardy ornamental nursery stock. *European Journal of Plant Pathology* 108: 337–343. https://doi.org/10.1023/A:1015614625414

Vettraino A.M., Morel O., Perlerou C., Robin C., Diamandis S., Vannini A., 2005. Occurrence and distribution of *Phytophthora* species in European chestnut stands, and their association with Ink Disease and crown decline. *European Journal of Plant Pathology* 111: 169–180. https://doi.org/10.1007/s10658-004-1882-0

White T.J., Bruns T., Lee S., Taylor J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A Guide to Methods and Applications* (Innis M.A., Gelfland D.H., Sninsky J.J., White T.J., ed.), San Diego, CA,USA, Academic Press, 315–322.

Yang X., Tyler B.M., Hong C., 2017. An expanded phylogeny for the genus *Phytophthora*. *IMA Fungus* 8: 355–384. https://doi.org/10.5598/imafungus.2017.08.02.09