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Modes of action and inhibitory activity of *Trichoderma* species on potato and tomato pathogenic *Phytophthora infestans*: A review

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ABSTRACT

Late blight, caused by the oomycete *Phytophthora infestans*, is one of the most devastating diseases of potatoes and tomatoes, resulting in low yields and economic losses for farmers. *Trichoderma* spp. are known for their antagonistic abilities against a wide range of pathogens, including *P. infestans*. This review provides an overview of the current knowledge on *Trichoderma* spp., by (1) classifying the diversity of modes of action of *Trichoderma* species and (2) assessing the antagonistic ability of several species and strains of *Trichoderma* spp. against *P. infestans* in dual culture, through a meta-analysis. We found that many species of *Trichoderma* spp. have a double action against *P. infestans*, both (1) direct on the plant pathogen by emitting enzymes and volatile organic compounds and (2) plant-mediated by enhancing the host plant's defence potential. The meta-analysis showed that direct *Trichoderma* antagonistic ability against *P. infestans* is species and strain dependant. Among the most effective species, *T. asperellum* stands out with a mycelial inhibition potential of up to 90% for some strains. These findings were used to build a decision-making system, that accounts for *Trichoderma*-plant-*Phytophthora* interactions, pedoclimate, and strategies of *Trichoderma* spp. application on crops. The paper provides new insights into the management of *P. infestans* on potato and tomato crops and highlights promising biocontrol or fungicide mixtures, including several *Trichoderma* spp. and little-known species with promising regulatory effects on *P. infestans*.

1. Introduction

Late blight of tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) is one of the most devastating diseases for these crops, leading to yield decreases and economic shortfalls reaching more than 50% under hot and wet conditions (Kerroum et al., 2015; Lal et al., 2018; Yao et al., 2015). It caused the Great Irish Potato Famine in the 1840s, which led to the death of approximately 1 million people and to mass emigration from Ireland (Yoshida et al., 2013). The causal agent is *Phytophthora infestans*, a hemibiotrophic oomycete that colonises host cells by forming haustoria (Leesutthiphonchai et al., 2018). Among the management levers available (chemical solutions, resistant varieties, biocontrol), many farmers in conventional agriculture use phytochemicals, which can be efficient in removing sporangia, zoospores and mycelia. However, such products can also trigger pathogen resistance and cause environmental damage due to their high persistence. This is

especially true for systemic products, i.e which are absorbed and distributed throughout the entire plant, providing overall protection rather than targeting only one part (Majeed et al., 2017). To address these issues and respond to growing agroecological concerns, new biocontrol solutions using rhizobacteria or fungi, including *Trichoderma* species, are currently being tested (Hashemi et al., 2022; Lourenço Júnior et al., 2006; Stephan et al., 2005). *Trichoderma* (teleomorph *Hypocrea*) is a soil-borne genus of fungi belonging to the order *Hypocreales*, within the division *Ascomycota*. *Trichoderma* species are already known to promote plant growth and reduce the pathogenicity and virulence of a wide diversity of parasites, including several *Phytophthora* species (Contreras-Cornejo et al., 2016; Elsherbiny et al., 2020; Ladi et al., 2020). They help maintain satisfactory yields and acceptable margins for farmers (Kilonzi et al., 2020a; Manjunath et al., 2017).

Published works often report results following the testing of individual isolates of *Trichoderma* spp. or address only one aspect of late

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blight management (direct effects on the plant pathogen or plant-mediated effects), but they more rarely focus on understanding the global *Trichoderma*-plant-pathogen system. To our knowledge, some articles review the existing biocontrol agents against *P. infestans* but with very few references mentioning *Trichoderma* (Hashemi et al., 2022; Wang and Long, 2023), while others review the use of *Trichoderma* against various plant pathogens (Saldaña-Mendoza et al., 2023; Vinale et al., 2008) without focusing on *P. infestans*.

As *Trichoderma* species are among the most efficient microbial species to control late blight in the field, this review aims to describe, compare and evaluate how species and strains of *Trichoderma* spp. can improve plant protection against *P. infestans*. It first presents the ways *Trichoderma* species are involved in the regulation of *P. infestans*. Then, a comparative approach based on published collected data is proposed to assess the antagonistic ability of different *Trichoderma* species and strains. Finally, a discussion is led to understand how to set up a biocontrol strategy involving *Trichoderma* spp. and that accounts for the dose, the frequency of treatments and abiotic factors. The efficacy of *Trichoderma* spp. is compared with other biocontrol solutions and to synthetic molecules to evaluate the interest of using these fungi to protect crops against *P. infestans*.

2. Bibliographic search strategies

The bibliographic search was carried out using Google Scholar, based on three strategies to target articles dealing with the modes of action or the efficacy of *Trichoderma* spp. against late blight. A “global keyword strategy” was primarily used, consisting of entering two or three keywords into the search engine. This process was repeated twenty-eight times for different combinations of words, and 108 articles were selected in this way (Supplementary Material, Table S1).

Then, a more detailed approach consisted of entering specific keywords about precise topics (e.g., technical sections of the present review) required to understand biological phenomena. For example, references dealing with interactions between specific reactive oxygen species (ROS) and *Trichoderma* spp. on potato or tomato were found by entering the following combination: “[Name of ROS species] AND *Trichoderma* AND [Crop studied]”.

The roles of offensive molecules against *P. infestans* – pathogenesis-related (PR) proteins, cell wall degrading enzymes (CWDE) and volatile organic compounds (VOC) – were found by entering the following combination: “[Name of a PR/CWDE/VOC] AND *infestans* AND *Trichoderma* AND [Crop studied]”. Thirty-three new articles were added to the list in this way.

Seventeen articles were selected by checking the references cited in the articles already consulted and completed the list. They were often old and described precise phenomena or experimental protocols, such as the dual culture method mentioned in the second section of this review (Dennis and Webster, 1971). Some of them were not directly related to *Trichoderma*-plant or *Trichoderma*-*P. infestans* interactions, so they were not covered by the keyword strategies (e.g., the pathogenic potential of *Trichoderma longibrachiatum* for humans).

3. Modes of action

Trichoderma spp. mitigate the severity and/or incidence of tomato and potato late blight. Their antifungal potential has been known and studied since the 1970s (Brasier, 1971). This section describes the main processes and pathways that contribute to the inhibition of plant mycelial infection by *P. infestans*, i.e. i) direct antibiotic interactions of *Trichoderma* spp. against *P. infestans* that disrupt its functional integrity and ii) plant-mediated actions that enhance the defence potential of tomato and potato against a wide range of plant pathogens, including *P. infestans*.

3.1. Direct effects of *Trichoderma* spp. against *Phytophthora infestans*: enzymes, peptides and contact molecules

Direct actions of *Trichoderma* species cause major damage and disrupt *P. infestans* integrity at different levels, releasing antifungal molecules (antibiosis) or even engaging in hyphal interactions and feeding on *P. infestans* for some species (mycoparasitism), such as *T. harzianum* (Alfiky et al., 2023; Bailey et al., 2008; Yao et al., 2015) or *T. longibrachiatum* (Priya et al., 2022).

P. infestans is particularly sensitive to CWDE, including cellulases, pectinases and proteases produced by many *Trichoderma* species such as *T. viride*, *T. asperellum*, *T. atroviride* or *T. koningiopsis* (El-Naggar et al., 2016; La Spada et al., 2020; Purwantisari et al., 2018a; You et al., 2016). Unfortunately, too few studies have addressed the ability of *Trichoderma* spp. to produce polygalacturonases, proteases or cellulases, and further research is needed to better understand the roles played by CWDE in the *Trichoderma*-plant pathogen interactions.

Other molecules and secondary metabolites interfere directly with the plant pathogen. This is the case of Koniginin D, gliotoxin, and koningic acid, three antifungal metabolites released by *T. virens*, and affecting *P. infestans* (Lalaymia et al., 2022). Bisvertinolone, an oxo-sorbicillinol derivative produced by *T. longibrachiatum*, inhibits β -1-6-glucan biosynthesis and induces morphological malformations in *P. infestans*, resulting in up to 100% tomato late blight control at 500 μ g/mL concentration in greenhouse (Ngo et al., 2021). The rare sugar D-tagatose produced by some *Trichoderma* species including *T. harzianum* contributes to severe metabolic disturbances in *P. infestans* by interfering with mitochondria and leading to ROS accumulation (Chahed et al., 2021). Cellular respiration of *P. infestans* is impaired by amino acids produced by *T. harzianum* mold (Kai et al., 2018; Purwantisari et al., 2021). Viridifungin A produced by *T. harzianum* inhibits pathogenic reproduction at high concentrations by preventing sporangia from germinating and developing properly (El-Hasan et al., 2009, 2022).

T. harzianum appears to be the most studied species for direct interactions. Similar studies on other species would be of interest. In addition, Lalaymia et al. (2022) highlight that many other unidentified compounds are produced by *Trichoderma* spp. against *P. infestans*, with potential antifungal activities: further research is expected to enrich the non-exhaustive list of metabolites provided in this review.

3.2. Direct and plant-mediated effects of *Trichoderma* spp. against *Phytophthora infestans*: remote effects - volatile organic compounds

Trichoderma species emit volatile organic compounds (VOC) which quickly reach the target organism and have various effects, including antifungal activity and plant growth promotion.

3.2.1. Inhibition of *Phytophthora infestans* growth

The ability of *Trichoderma* VOC to inhibit *P. infestans* is low documented. Elsherbiny et al. (2020) found 39 VOC released by *T. atroviride*, but only four of them, 6-pentyl-(2H)-pyran-2-one, acetoin, 2-methyl-1-propanol and 3-methyl-1-butanol, are mainly emitted. These four compounds completely inhibited *P. infestans* mycelial growth at low concentrations. Other studies focused on the effects of *Trichoderma* VOC on the growth of other pathogenic oomycetes. For example, Lazazzara et al. (2021) identified 31 VOC from *T. harzianum*, *T. atroviride* and *T. asperellum*, including 6-pentyl-(2H)-pyran-2-one and 2-pentylfuran with antifungal activity against *Plasmopara viticola*, which also induced hypersensitive response (HR) and decreased the severity of downy mildew in grapevine.

Trichoderma VOC also regulate the expression of genes involved in potato response to its pathogens. To our knowledge, no studies have been carried out on *P. infestans*, but Martínez-Medina et al. (2017b) showed that VOC emitted by *T. harzianum* and *T. asperellum* up- or down-regulate the expression of genes involved in potato resistance to *Botrytis cinerea*.

3.2.2. Tomato and potato growth promotion

VOC including acetoin and 6-pentyl-(2H)-pyran-2-one are produced by selected strains of *T. atroviride*, *T. harzianum*, *T. viride*, *T. longibrachiatum*, *T. pseudokoningii* and *T. aggressivum* and enhance (1) root and stem growth and (2) root development in *Arabidopsis thaliana* (Garnica-Vergara et al., 2016; Lee et al., 2015, 2016; Vinale et al., 2008). 6-pentyl-(2H)-pyran-2-one also enhances tomato stem and root growth and influences the direction of root growth (Rao et al., 2022; Vinale et al., 2008). 6-pentyl-(2H)-pyran-2-one has dual activity: it has both antifungal activity and promotes plant growth (Rao et al., 2022). *T. harzianum* and *T. asperellum* VOC also increase the expression of genes involved in iron uptake and solubilization on potato (Martínez-Medina et al., 2017b). VOC from *T. viride* promote other biological functions such as increasing the chlorophyll content or the shoot and root weight in *A. thaliana* (Lee et al., 2016).

3.3. Plant-mediated effects of *Trichoderma* spp.: improvement of plant agronomic performance

It has been shown that the ability of tomato and potato host plants to defend themselves against *P. infestans* is highly dependent on their growth dynamics and morphology. Indeed, larger plants with a high growth potential have a greater ability to resist *P. infestans* attack, through enhanced genetic expression (Brouwer et al., 2004; Nowicki et al., 2012). *Trichoderma* species (1) increase the growth (i.e. size and/or volume of organs) of both potato and tomato and (2) stimulate their development (i.e. appearance of new organs): both processes condition the agronomic performance of the plant.

Trichoderma species, and in particular *T. harzianum* and *T. longibrachiatum*, increase the plant's defence potential by stimulating growth through increased nutrient uptake and strong solubilizing activity of phosphate and micronutrients (Fe, Zn, Cu, Mn) (Table 1). For example, iron solubilization in *T. harzianum*/host plant associations is facilitated by the production of harzianic acid, a secondary metabolite (Alfiky et al., 2023; Vinale et al., 2009).

Several tomato and potato growth variables are improved by *Trichoderma* species (Table 1). *T. harzianum*, but also other *Trichoderma* species such as *T. asperellum*, *T. longibrachiatum* or *T. atroviride*, increase both size-related variables such as leaf area and height of different compartments (roots, shoots, whole plant) and biomass-related variables (root, shoot, fruit/tuber weight).

Several developmental variables, such as seed vigour and emergence or number of organs per plant (leaves, branches, fruit/tubers) are enhanced by *Trichoderma* species (Table 1). Moreover, *T. harzianum* enhances potato and tomato development by regulating genes that enable the following phenological stages to be reached (e.g. MYB13 for tomato leaf development, MADS for tomato flowering and NAC for tomato fruit ripening, Aamir et al. (2023)). Some *Trichoderma* species, such as *T. harzianum* and *T. longibrachiatum*, also improve tomato physiology by increasing stomatal conductance and leaf water potential (Khoshmanzar et al., 2020). Finally, Molla et al. (2012), Nzanza et al. (2012) and Sani et al. (2020) showed that *T. harzianum* improves tomato fruit quality by increasing protein, vitamin C, total sugar and antioxidant content.

3.4. Plant-mediated effects of *Trichoderma* spp. against *Phytophthora infestans*: increased production of phytohormones and other signalling molecules

Phytohormones are chemical molecules involved in plant growth and development and in biological processes, including plant protection against biotic and abiotic stresses (Gravel et al., 2007; Martínez-Medina et al., 2017a; Ruiz-Cisneros et al., 2018; Saubeau et al., 2016; You et al., 2016). For example, indole acetic acid (IAA) and gibberellin (GA₃) are involved in cell elongation and plant morphology, growth, and yield performance (Gravel et al., 2007; Shohat et al., 2021; Vessey, 2003).

Table 1
Trichoderma-enhanced growth and developmental variables on potato and tomato.

Category	Measured variable	Species	<i>Trichoderma</i> species involved and references
Nutrient uptake/content	Increase N/P/K	Tomato	<ul style="list-style-type: none"> • <i>T. virens</i> (Jogaiah et al., 2018) • <i>T. harzianum</i> (Cai et al., 2015; Khoshmanzar et al., 2020; Li et al., 2015; Molla et al., 2012; Sani et al., 2020) • <i>T. longibrachiatum</i> (Khoshmanzar et al., 2020) • <i>T. atroviride</i> (Gravel et al., 2007)
	Increase microelements (Fe, Zn, Cu, Mn)	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Khoshmanzar et al., 2020; Li et al., 2015; Molla et al., 2012) • <i>T. longibrachiatum</i> (Khoshmanzar et al., 2020; Priya et al., 2022)
	Enhance mineral solubilization and uptake	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Bader et al., 2020; Khoshmanzar et al., 2020; Li et al., 2015; Mastouri et al., 2012) • <i>T. longibrachiatum</i> (Khoshmanzar et al., 2020)
Growth/morphology	Increase chlorophyll content	Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Martínez-Medina et al., 2017b) • <i>T. asperellum</i> (Martínez-Medina et al., 2017b)
		Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Al-Askar et al., 2016; Mastouri et al., 2012; Ruiz-Cisneros et al., 2018) • <i>T. asperellum</i> (Ruiz-Cisneros et al., 2018; Singh et al., 2016) • <i>T. longibrachiatum</i> (Ruiz-Cisneros et al., 2018) • <i>T. atroviride</i> (Lee et al., 2015)
	Leaf area	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Bader et al., 2020; Chowdappa et al., 2013; Kumar et al., 2015a, 2015b)
Plant/shoot height	Plant/shoot height	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Bader et al., 2020; Bahramisharif and Rose, 2019; Chowdappa et al., 2013; Ghazanfar et al., 2019; Kumar et al., 2015a, 2015b; Molla et al., 2012; Naffaa et al., 2022; Ruiz-Cisneros et al., 2018; Sain and Pandey, 2016) • <i>T. longibrachiatum</i> (Ruiz-Cisneros et al., 2018)
		Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Rakibuzzaman et al., 2021)
	Root length	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Bahramisharif and Rose, 2019; Chowdappa et al., 2013; Kumar et al., 2015a, 2015b; Li et al., 2015; Ruiz-Cisneros et al., 2018) • <i>T. asperellum</i> (Ruiz-Cisneros et al., 2018) • <i>T. asperelloides</i> (Heflish et al., 2021) • <i>T. longibrachiatum</i> (Ruiz-Cisneros et al., 2018) • <i>T. atroviride</i> (Gravel et al., 2007)
Plant weight	Plant weight	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Kariuki et al., 2020)

(continued on next page)

Table 1 (continued)

Category	Measured variable	Species	<i>Trichoderma</i> species involved and references
	Shoot weight	Tomato	<ul style="list-style-type: none"> • <i>T. asperellum</i> (Herrera-Téllez et al., 2019; Kariuki et al., 2020) • <i>T. virens</i> (Jogaiah et al., 2018) • <i>T. harzianum</i> (Bader et al., 2020; Bahramisharif and Rose, 2019; Chowdappa et al., 2013; Ghazanfar et al., 2019; Khoshmanzar et al., 2020; Kumar et al., 2015a, 2015b; Mastouri et al., 2012; Molla et al., 2012; Nanza et al., 2012) • <i>T. asperellum</i> (Singh et al., 2016) • <i>T. asperelloides</i> (Heflish et al., 2021) • <i>T. longibrachiatum</i> (Khoshmanzar et al., 2020) • <i>T. atroviride</i> (Gravel et al., 2007; Rao et al., 2022)
			Root weight
Tuber weight	Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Al-Askar et al., 2016) 	
Development	Fruit weight	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Molla et al., 2012; Sani et al., 2020)
	Seed vigour and emergence	Tomato	<ul style="list-style-type: none"> • <i>T. koningiopsis</i> (Moreno et al., 2009) • <i>T. harzianum</i> (Aamir et al., 2023; Chowdappa et al., 2013; Kumar et al., 2015a, 2015b; Mastouri et al., 2012; Naffaa et al., 2022; Sandri et al., 2023)
	Number of leaves	Tomato	<ul style="list-style-type: none"> • <i>T. virens</i> (Jogaiah et al., 2018) • <i>T. harzianum</i> (Ghazanfar et al., 2019; Molla et al., 2012)
		Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Rakibuzzaman et al., 2021)
	Number of branches	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Molla et al., 2012)
	Number of tubers	Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Al-Askar et al., 2016) • <i>T. viride</i> (Purwantisari et al., 2018b)
	Fruit per plant	Tomato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Molla et al., 2012; Ruiz-Cisneros et al., 2018; Sani et al., 2020) • <i>T. asperellum</i> (Ruiz-Cisneros et al., 2018)

Table 1 (continued)

Category	Measured variable	Species	<i>Trichoderma</i> species involved and references
	Total fruit/tuber yield	Tomato	<ul style="list-style-type: none"> • <i>T. longibrachiatum</i> (Ruiz-Cisneros et al., 2018) • <i>T. harzianum</i> (Molla et al., 2012; Nanza et al., 2012; Ruiz-Cisneros et al., 2018; Sain and Pandey, 2016; Sani et al., 2020) • <i>T. asperellum</i> (Ruiz-Cisneros et al., 2018) • <i>T. longibrachiatum</i> (Ruiz-Cisneros et al., 2018) • <i>T. atroviride</i> (Gravel et al., 2007)
		Potato	<ul style="list-style-type: none"> • <i>T. harzianum</i> (Gopi et al., 2020) • <i>T. asperellum</i> (Gopi et al., 2020)

They enhance the plant's ability to take up soil nutrients and water and constitute raw sap, an essential input for further photosynthesis (Vessey, 2003). Several *Trichoderma* species – *T. harzianum*, *T. koningiopsis*, *T. atroviride* – increase IAA and GA₃ production by tomato and potato (Table 2).

Similarly, *Trichoderma* spp. enhance many different defence mechanisms in the host plant (Table 2), including systemic acquired resistance (SAR) and systemic induced resistance (SIR). On the one hand, SAR is activated by an increase in salicylic acid (SA) content after a local pathogenic attack and contributes to the inhibition of pathogenic infection through various chain reactions, including the production of reactive oxygen species (ROS). On the other hand, SIR is activated by external molecular stimuli and is induced by jasmonic acid (JA), and contributes to increasing signal transduction and physicochemical barriers between the host plant and its pathogen (Arévalo-Marín et al., 2021; Chowdappa et al., 2013; Cohen et al., 1993; Martínez-Medina et al., 2013; Purwantisari et al., 2018a; Yang et al., 2022).

3.4.1. Induction of potato and tomato defence mechanisms against *P. infestans* by *Trichoderma*-enhanced phytohormones

3.4.1.1. Induction of systemic acquired resistance.

The amount of SA increases rapidly after inoculation of potato leaves with *P. infestans*, and contributes to the induction of early defence responses in potato, leading to mycelial growth inhibition (Halim et al., 2007). SA, along with ROS species, is one of the major signalling molecules involved in the response of potato to *P. infestans* (Ren et al., 2012). It enhances SAR in tomato and potato by increasing the activity of the WRKY1 transcription factor (TF) (Aamir et al., 2019; Cui et al., 2019; Martínez-Medina et al., 2017a; Saubeau et al., 2016; Zehra et al., 2017). WRKY1 is a TF of the *lncRNA33732* gene, which is itself a TF of *RBOH* genes involved in the production respiratory burst oxidase homolog (RBOH) proteins (Cui et al., 2019). RBOH enzymes induce the ROS pathway by reducing O₂ to O₂⁻ (Chapman et al., 2019). *T. harzianum* and *T. erinaceum* increase WRKY gene expression in tomato: they induce ROS production and prepare the cell to trigger the hypersensitive response (Aamir et al., 2019; De Palma et al., 2019).

3.4.1.2. Progression of systemic acquired resistance: ROS and PAL pathways.

Trichoderma species facilitate the up-regulation of genes involved in the systemic acquired response against *P. infestans*. For example, *T. harzianum* enhanced DNA methylation in tomato root cells 72 h after inoculation (De Palma et al., 2019). This modulates the expression of genes that trigger the production of enzymes involved in the ROS pathway and that regulate phytohormone or VOC production (Moreno et al., 2009).

Table 2

Phytohormone regulation by several *Trichoderma* spp. and roles in *Phytophthora infestans* management.

Enhanced phytohormone	<i>Trichoderma</i> species involved	Role for the plant	Comparative importance against <i>P. infestans</i>
IAA	<i>T. harzianum</i> (Aamir et al., 2023; Bader et al., 2020; Chowdappa et al., 2013; You et al., 2016) <i>T. koningiopsis</i> (You et al., 2016) <i>T. atroviride</i> (Gravel et al., 2007) <i>T. asperellum</i> (Singh et al., 2022) <i>T. longibrachiatum</i> (Priya et al., 2022)	Plant shoot and root growth stimulation, plant morphology (Gravel et al., 2007) Improved nutrient access in the soil (Vessey, 2003)	++ Enhance defence potential
GA ₃	<i>T. harzianum</i> (Aamir et al., 2023; Al-Askar et al., 2016; Chowdappa et al., 2013; You et al., 2016) <i>T. koningiopsis</i> (You et al., 2016)	Increased growth (stem elongation, leaf and shoot growth) and enhanced yield and development (seed germination, flowering, number of fruit) (Shohat et al., 2021)	++ Similar to IAA
SA	<i>T. harzianum</i> (Martínez-Medina et al., 2017a) <i>T. virens</i> (Jogaiah et al., 2018)	ROS enzyme production (Zehra et al., 2017) PR1, PR2 and PR5 induction (Ali et al., 2018)	+++ Most involved pathway, triggers systemic reaction
JA	<i>T. harzianum</i> (Martínez-Medina et al., 2013, 2017a)	Enhancement of antioxidant production (Yang et al., 2022; Zehra et al., 2017) PR and other defence genes induction (Ali et al., 2018; Martínez-Medina et al., 2013; Yang et al., 2022)	++ Involved in SIR, less so than SA
Et	<i>T. harzianum</i> (Aamir et al., 2023; Ruiz-Cisneros et al., 2018)	Phytoalexin production in <i>N. benthamiana</i> (Ohtsu et al., 2014) Induction of plant maturity genes (Cara and Giovannoni, 2008) General stress reaction (Saubeau et al., 2016)	+Secondary pathway induced

“+”, “++” and “+++” in the last column describe the relative degree of involvement of each *Trichoderma*-enhanced phytohormone in *P. infestans* management, based on the literature reporting (and sometimes comparing) i) the diversity of the growth, defence and offense mechanisms induced in tomato and potato by each phytohormone, and ii) the relative contribution of each enhanced mechanism to *P. infestans* control.

Table 3

Trichoderma spp. enhance the production of proteins and antioxidant molecules involved in decreasing potato and tomato oxidativestress.

Molecules and antioxidant species in ROS and phenylpropanoid pathways	<i>Trichoderma</i> involved in production enhancement	References
Respiratory burst oxidase homolog (RBOH) proteins	<i>T. harzianum</i> <i>T. erinaceum</i>	De Palma et al. (2019) Aamir et al. (2019)
Superoxide dismutase (SOD)	<i>T. harzianum</i> <i>T. koningii</i> <i>T. erinaceum</i>	Chen et al. (2019); Chowdappa et al. (2013); Mastouri et al. (2012); Zehra et al. (2017) Tripathi et al., 2021 Aamir et al. (2019)
Peroxidase (PO)	<i>T. harzianum</i> <i>T. koningii</i> <i>T. asperellum</i>	Aamir et al. (2023); Al-Askar et al. (2016); Kumar et al. (2015b) Tripathi et al. (2021) Patel and Saraf (2017); Singh et al. (2016)
Catalase (CAT)	<i>T. harzianum</i>	Chen et al. (2019); Mastouri et al. (2012); Zehra et al. (2017)
Glutathione peroxidase (GPX)	<i>T. harzianum</i>	Aamir et al. (2023); Zehra et al. (2017)
Ascorbate peroxidase (APX)	<i>T. harzianum</i>	Chen et al. (2019); Mastouri et al. (2012); Zehra et al. (2017)
Polyphenol oxidase (PPO)	<i>T. harzianum</i> <i>T. koningii</i> <i>T. asperellum</i>	Al-Askar et al. (2016); Kumar et al. (2015b) Tripathi et al. (2021) Patel and Saraf (2017); Singh et al. (2016)
Phenylalanine ammonia-lyase (PAL)	<i>T. koningii</i> <i>T. viride</i> <i>T. harzianum</i> <i>T. asperellum</i>	Tripathi et al. (2021) Purwantisari et al. (2020) Gallou et al. (2009); Kumar et al. (2015b) Patel and Saraf (2017); Singh et al. (2016)
Anthocyanins	<i>T. harzianum</i>	Bahramisharif and Rose (2019)

Many *Trichoderma* species enhance the production of defence molecules and antioxidants by tomato and potato (Table 3); their effects are summarised in Fig. 1. *T. harzianum* and *T. asperellum* are particularly efficacious, leading to a marked decrease in the contents of ROS species and phenylalanine ammonia-lyase (PAL) enzymes (Table 3, Fig. 1). *T. longibrachiatum* also produces bisorbicillinol, an antioxidant that can control tomato late blight up to 80% in greenhouse at a concentration of 500 µg/mL (Ngo et al., 2021).

Underproduction of antioxidants such as superoxide dismutase (SOD) leads to the release of toxic free radicals through Fenton’s reaction ($O_2^- \rightarrow \cdot OH$) and triggers lipid oxidation (Glasauer and Chandel, 2013). However, appropriate levels of antioxidants provide benefits. SOD prevents Fenton’s reaction and produces H_2O_2 (Fig. 1), which triggers hypersensitive response and inhibits the growth of the

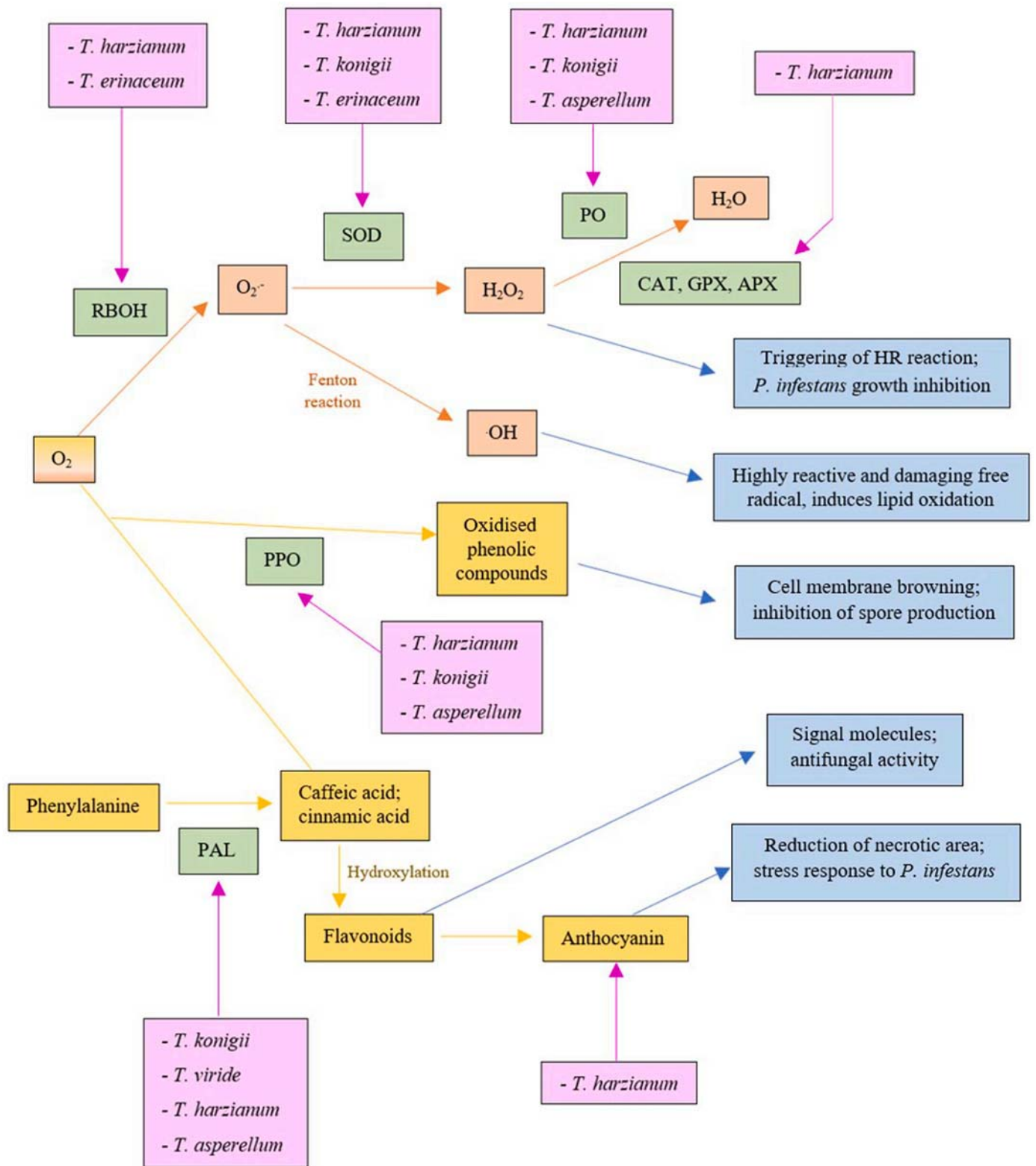


Fig. 1. Involvement of *Trichoderma* species in the ROS and phenylpropanoid pathways before pathogenic infection, and roles in the induction of *S. tuberosum* and *S. lycopersicum* defence against *P. infestans*. Adapted from Kimura et al. (2005), Samanta et al. (2011), Sharma et al. (2012b). Each colour refers to a part of the *Trichoderma*-induced plant defence system. Rose-coloured boxes and arrows, positive regulation of molecules or antioxidant production by several *Trichoderma* spp.; green boxes, antioxidants and proteins involved in the ROS (orange reaction chain) and phenylpropanoid (yellow reaction chain) pathways; blue boxes, functions of the final molecules. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pathogenic mycelium (Cui et al., 2019; Wu et al., 1995). Polyphenol oxidase (PPO) oxidises the phenolic compounds involved in cell membrane browning and inhibits *P. infestans* sporulation (Busch, 1999; Sakuma and Tomiyama, 1967). In addition, the phenylpropanoid pathway leads to the production of flavonoids and anthocyanins. Flavonoids are signalling molecules with antifungal activity, while anthocyanins trigger plant stress responses to *P. infestans* and reduce the total necrotic area caused by late blight infection (Aamir et al., 2023; De Vries et al., 2018; Samanta et al., 2011) (Fig. 1). Phenolic compounds and peroxidase (PO) production induced by *Trichoderma* spp. lead to cell wall lignification in tomato and potato plants, providing an additional barrier that hinders the progress of *P. infestans* (Purwantisari et al., 2020; Singh et al., 2016).

3.4.1.3. Systemic induced resistance. JA is a lipid derivative synthesised from linolenic acid that is also involved in the response of tomato and potato to pathogen attack (Saubeau et al., 2016). By increasing the physical and chemical barriers against the plant pathogen, increased JA production by potato and tomato plants enhances SIR (Cohen et al., 1993; Martínez-Medina et al., 2013). JA activates both local and systemic resistance against *P. infestans* in tomato and potato, with lower leaf area blighted and inhibition of sporangia germination (Cohen et al., 1993; Yang et al., 2022). Stomatal conductance is reduced and the infection process of *P. infestans* is delayed (Arévalo-Marín et al., 2021).

3.4.1.4. Other defence pathways. Ethylene (Et) is another hormone involved in tomato SIR (Martínez-Medina et al., 2013). In *P. infestans*-infected parts of the tomato leaves, the amount of 1-aminocyclopropane-1-carboxylate (ACC) synthase and ethylene forming enzyme (EFE) – which leads to ethylene production – increased rapidly just before the onset of symptoms (Spanu and Boller, 1989). Although Et has been identified as a phytoalexin inducer against *P. infestans* in *Nicotiana benthamiana*, its role in tomato and potato late blight management is limited. Its accumulation in infected tomato plants does not increase the production of PR proteins, and it has a minimal effect on strengthening plant defences (Cara and Giovannoni, 2008; Ohtsu et al., 2014). Increased Et production is a common stress response also observed in susceptible potato cultivars (Cohen et al., 1994; Ohtsu et al., 2014; Saubeau et al., 2016).

Similar observations have been made regarding the roles of the oxidative pentose phosphate (OPP) pathway and the glutathione-ascorbate (AsA-GSH) cycle in the biocontrol activity. These two pathways play a role in plant integrity (carbon fixation, NADPH production)

Table 4

Role of PR proteins in *P. infestans* management and enhancement potential of *Trichoderma*. Adapted from Sels et al. (2008).

PR protein	Function	<i>Trichoderma</i> influenced expression	References
PR-1	Antifungal	<i>T. harzianum</i> <i>T. asperellum</i> <i>T. asperelloides</i> <i>T. atroviride</i>	Leonetti et al. (2017) La Spada et al. (2020) Heflish et al. (2021) La Spada et al. (2020)
PR-2	β -1,3-glucanase	<i>T. harzianum</i> <i>T. asperellum</i> <i>T. asperelloides</i> <i>T. atroviride</i>	Aamir et al. (2023) La Spada et al. (2020) Heflish et al. (2021) La Spada et al. (2020)
PR-3/ PR-4	Chitinase	<i>T. harzianum</i> <i>T. asperelloides</i>	Aamir et al. (2023) Heflish et al. (2021)
PR-5	Thaumatococcal-like	<i>T. harzianum</i>	Aamir et al. (2023); Leonetti et al. (2017)

and defence against a wide variety of plant pathogens (Hu et al., 2019). *T. harzianum* can stimulate the activity of key enzymes in cucumber plants to keep the OPP pathway functional despite the pathogenic activity of *Fusarium oxysporum*. Moreover, *T. harzianum* enhances ascorbate and glutathione activities in tomato (Aamir et al., 2023; Mastouri et al., 2012) and preserves the activity of the AsA-GSH cycle when the plant is infected with *F. oxysporum* (Chen et al., 2019). One can assume that the same process also occurs in potato and tomato challenged with *P. infestans*, but further research is required for potential validation.

3.4.2. Activation of PR proteins by *Trichoderma*-enhanced phytohormones

The SA signalling pathway regulates the expression of offense genes such as the PR genes (*PR1*, *PR2* and *PR5*) (La Spada et al., 2020; Leonetti et al., 2017). PR peptides are involved in plant protection against various biotic and abiotic infections, and the most studied ones (PR-1 to PR-6) are mainly lytic enzymes that alter the metabolic functioning of the plant pathogen (Sels et al., 2008).

The high ability of *T. harzianum* to enhance the production of β -1,3-glucanase and chitinase (PR-2, PR-3 and PR-4 families, Table 4) and to induce plant defence responses makes it a very efficacious species for improving plant protection against *P. infestans* (Aamir et al., 2023; El-Naggar et al., 2016; Sain and Pandey, 2016; Singh et al., 2020; You et al., 2016). *Trichoderma* enhances the production of PR-1 and PR-5 proteins (Table 4), also mostly involved in the management of *P. infestans*. PR-1 has antifungal activity, even against oomycetes such as *P. infestans*. It both inhibits zoospore germination and reduces the leaf area infected by the plant pathogen (Niderman et al., 1995). The role of PR-5 against *P. infestans* has also been proved using transgenic plants overexpressing the PR-5 gene. *In vitro* results showed a higher resistance of transgenic tomato plants compared to the control plants (Korneeva et al., 2011).

As discussed in section 3.4.1.3, the JA pathway is induced by some *Trichoderma* species, e.g. *T. harzianum*. It is also involved in PR gene regulation in tomato (Martínez-Medina et al., 2017a) and potato (Yang et al., 2022) plants. This molecule induces the production of PR-3 and PR-4 chitinases, which are involved in *P. infestans* cell wall disruption (Ali et al., 2018; Arévalo-Marín et al., 2021).

However, up-regulation of PR-7 to PR-17 genes in relation to *Trichoderma* spp. activity has not been described. Additional knowledge on these relationships is expected to explain the influence of *Trichoderma* spp. on PR gene expression.

3.4.3. Comparison of phytohormone involvement in plant defence against *P. infestans*

As *P. infestans* is a hemibiotrophic plant pathogen, it can be assumed that the SA pathway is mainly involved in late blight management, although the JA pathway also plays a role in plant defence activation through SIR (Arévalo-Marín et al., 2021; Tucci et al., 2011). This trend is confirmed by the higher number of research articles reporting an influence of the SA pathway in late blight control and the important roles of PR1, PR2 and PR5 (SA pathway) compared to PR3 and PR4 (JA pathway) in plant defence activation (Halim et al., 2007; Jogaiah et al., 2018; Martínez-Medina et al., 2017a; Ren et al., 2012). For example, *T. virens* significantly increased the SA content compared to the JA content in different tomato cultivars prior to plant pathogen inoculation (Jogaiah et al., 2018). The ethylene pathway remains least activated by *Trichoderma* (Table 2).

4. Antagonistic ability in dual culture experiments

This section is devoted to comparisons of dual culture experiment results found in different articles and involving several *Trichoderma* spp. to control *P. infestans in vitro*. An introductory subsection explains to what extent the ability of *Trichoderma* to inhibit *P. infestans* growth is modified depending on the pathogenic strain to be controlled.

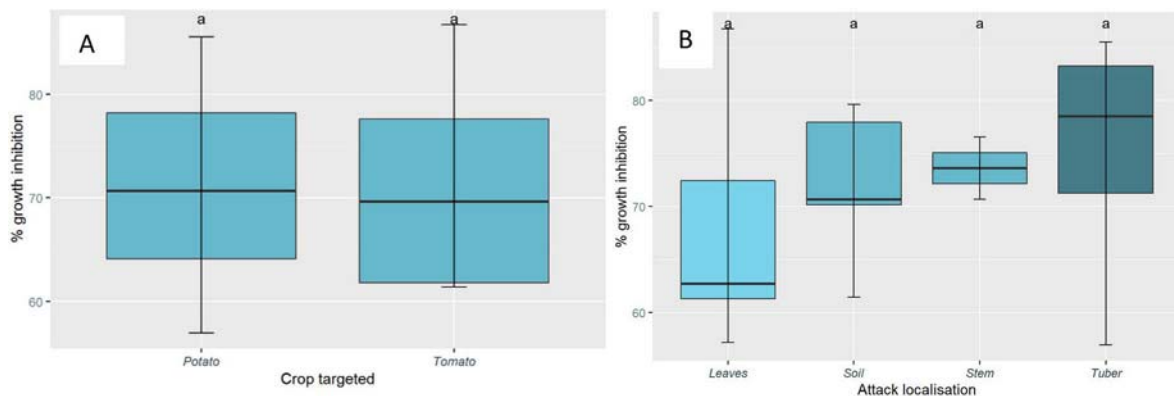


Fig. 2. Ability of *T. harzianum* to inhibit *P. infestans* mycelial growth depending on *P. infestans* pathogenic strain and its specific characteristics. (A) Variations in mycelial growth inhibition of *P. infestans* strains according to the host crop. (B) Variations in mycelial growth inhibition of *P. infestans* strains according to the localisation of the attack (from Kerroum et al., 2015).

4.1. Ability of *Trichoderma* to control *P. infestans* according to pathogenic strain

4.1.1. Statistical analyses

The ability of *T. harzianum* to inhibit the growth of *P. infestans* was tested *in vitro* in dual cultures using one strain of *T. harzianum* against 44 strains of *P. infestans* obtained from soil, stems, tubers or leaves of infected plants (Kerroum et al., 2015). Results were reported for 26 strains of *P. infestans* specifically targeting tomato or potato. Six strains of *P. infestans* infected tomato, and the other 20 strains infected potato. The virulence of *P. infestans* strains was compared according to i) the target crop and ii) the part of the plant from which they were isolated (likely location of attack) in order to identify potential plant vulnerabilities. After normality validation using a Shapiro test on the database, ANOVA and Tukey HSD parametric means comparison tests were performed, and two boxplot charts were generated using R software and the “ggplot2” package (v3.3.3; Wickham, 2016).

4.1.2. *Trichoderma* antagonistic ability is independent of *P. infestans* strain

Inhibition of *P. infestans* mycelial growth by *T. harzianum* did not depend on *P. infestans* host crop (Kerroum et al., 2015). No significant difference was found between host crops, with comparable median values in each group (approximately 70% of *P. infestans* growth inhibition on both tomato and potato) and similar interquartile ranges (Fig. 2A).

Similarly, inhibition of *P. infestans* mycelial growth was not organ-dependent. No significant difference was observed (p -value > 0.05, one Tukey group), despite a boxplot chart that distinguished strains targeting tubers and leaves. *T. harzianum* management of *P. infestans* strains targeting potato tubers was relatively easier than management of strains attacking tomato and potato leaves (mean comparison p -value = 0.22) (Fig. 2B).

4.2. Evaluation of the *in vitro* growth inhibitory potential of different *Trichoderma* spp., in dual culture with *Phytophthora infestans*: a meta-analysis

4.2.1. Data selection and statistical analyses

The ability of *Trichoderma* strains to inhibit the growth of *P. infestans* can be measured *in vivo* or *in vitro* to assess the antagonistic activity of the late blight biocontrol agent. *In vitro* antagonistic tests usually involve dual culture experiments, whereas *in planta* assessments consist of (1) manual spraying of *P. infestans* and of selected *Trichoderma* spp. (usually on leaves), and (2) subsequent growth measurements on control and infected plants (Dennis and Webster, 1971; El-Naggar et al., 2016; García-Núñez et al., 2017). In the following comparison, articles using dual culture assessments were selected because *in vitro* conditions can be

easily determined and standardised.

All the selected experiments followed the same protocol. An explant (usual diameter of 4–6 mm) taken from the growth zone of a 6.8 ± 2.8 day old culture of *P. infestans* was placed on potato dextrose agar (PDA) medium (based on values given in 7 selected articles), 1 cm away from the edge of a Petri plate, and an explant taken from the growth zone of a 6.2 ± 2.2 day old culture of *Trichoderma* spp. (based on values given in 8 selected articles) was placed on the opposite side of the Petri plate. The inoculated plates were incubated for 7 ± 1 days at 18–30 °C, depending on the article. The ratio of the radial growth of *P. infestans* colonies alone to the radial growth of *P. infestans* colonies confronted with *Trichoderma* strains quantified the inhibitory activity of *Trichoderma*.

The growth inhibitory potential of a single strain of *T. harzianum* against 26 different strains of *P. infestans* was tested (Kerroum et al., 2015). The mean value of all these results was considered. The results obtained with different strains or species of *Trichoderma* used in this type of confrontation on agar medium were also considered in our analysis (e.

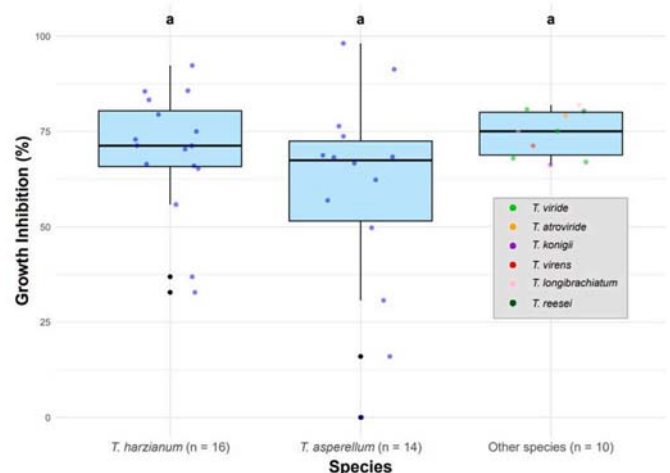


Fig. 3. Growth inhibition of *P. infestans* by several *Trichoderma* spp. in dual culture.

The boxplots represent the diversity of potential growth inhibition of *P. infestans* by *Trichoderma* species in dual culture, whose experiments shared comparable protocols (as defined in section 4.2.1.): *T. harzianum* (n = 16, individuals in blue), *T. asperellum* (n = 14, blue) and other species (n = 10), including *T. viride* (n = 4, pale green), *T. virens* (n = 1, red), *T. atroviride* (n = 1, orange), *T. longibrachiatum* (n = 2, pink), *T. koningii* (n = 1, purple), *T. reesei* (n = 1, dark green). Letters above the boxplots refer to the Tukey groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

g. García-Núñez et al., 2017). Other studies have tested several strains of *Trichoderma* but only identified some of them, along with morphological or molecular characterisation; therefore, insufficiently determined strains were omitted from the analysis (i.e. some strains used in Singh et al. (2022)). For further statistical comparison, all species for which less than five different strains per species were tested were grouped in a boxplot “other species”. The results of 14 different strains of *T. harzianum*, 16 strains of *T. asperellum* and 10 strains of other *Trichoderma* species (Supplementary Material, Table S2) were compared with Tukey HSD means comparison test, and the results were represented with boxplots, using the “ggplot2” package (Wickham, 2016).

It is important to emphasize that (1) the concentration of *Trichoderma* spp. was not reported in all the publications and that (2) few studies specified whether the Petri dishes were sealed or not. Unsealed plates do not take into account the role of VOC emitted by *Trichoderma* in inhibiting *P. infestans* growth: this could introduce an unquantifiable experimental bias. The choice of the dual culture protocol may also influence the final results (Ghazanfar et al., 2019). However, despite differences in the size of the Petri dishes, most articles followed a method close to that described by Dennis and Webster (1971). The experimental parameters of each publication are summarised in Supplementary Material Table S2.

4.2.2. Comparison of species and strain antagonistic ability against *P. infestans*

Dual culture results showed that the currently most used (and tested) species *T. harzianum* ($n = 14$) and *T. asperellum* ($n = 16$) both strongly inhibited *P. infestans* growth, with mean inhibition values of 69.4% and 59.1% respectively (Fig. 3). We found no significant variation in *P. infestans* growth inhibition between the *Trichoderma* species tested, but the work of Lalaymia et al. (2022) reported that the antagonistic activity of *Trichoderma* against *P. infestans* was species-dependant. In a differently designed dual culture experiment (which cannot be used in the meta-analysis), they showed that *T. pseudokoningii* led to 0% growth inhibition of *P. infestans*, vs more than 80% for other *Trichoderma* species, including *T. virens*.

Besides the effect of species on growth inhibition potential, we sought to understand if the ability of *T. harzianum* and *T. asperellum* to inhibit *P. infestans* growth was strain-dependant. An F-test showed that the variance in growth inhibition for *T. harzianum* was 36% of that observed for *T. asperellum*, with the difference in variances approaching statistical significance (p -value = 0.06). Growth inhibition potential tended to be more strain-dependent for *T. asperellum* than for *T. harzianum*. Therefore, strain selection is crucial for an optimal biocontrol strategy. Our analysis showed that only strains of *T. asperellum* result in excellent *P. infestans* inhibition (almost 100% *in vitro*), but time and priority must be given to identifying the right strains to use (some strains of *T. asperellum* do not inhibit the growth of *P. infestans*, Joeniarti et al. (2014)). Less selection effort is required for *T. harzianum*, where the growth inhibition potential of *P. infestans* is less strain-dependant.

Finally, the group with all other species (*T. viride*, *T. virens*, *T. atroviride*, *T. koningii*, *T. reesei* and *T. longibrachiatum*) showed very promising results, with 74.5% mean inhibition of *P. infestans* growth (Fig. 3): further research is needed to test more strains of these species, in order to understand whether they constitute an interesting alternative to the main species.

4.3. In planta comparisons

Some of the best-known species have been compared in *in planta* experiments. For example, *T. asperellum* strains reduced disease severity on tomato seedlings by 10%–40% more than *T. harzianum* strains, depending on soil type (Kariuki et al., 2020). *T. harzianum* also increased mycelial growth inhibition by 8% compared to *T. viride* on clay soils (El-Naggar et al., 2016). However, these results must be interpreted with

caution in as far as a strong strain effect remained according to dual culture experiments. Moreover, it was almost impossible to compare the results between publications because the type of soil and climate, the crop and cultivar, the mode of treatment (seedling treatment, powder or spray on leaves), or the *Trichoderma* spp. concentration varied too much. Statistical analysis requires more experiments sharing the same experimental conditions to detect species and strain effects: further research is needed to enable such comparisons.

5. Choice of a biocontrol strategy

Diversified modes of action and convenient direct antagonistic ability in decreasing late blight incidence make *Trichoderma* spp. a robust candidate for building an integrated biocontrol strategy against *P. infestans*. Nevertheless, defining an adapted strategy is definitely a no simple task. The key is to determine the right technique (HOW) to spread the right treatment (WHAT) under appropriate environmental conditions (WHEN). The following discussion is structured so as to deal with this tricky issue: courses of action are proposed for most stakeholders such as farmers and technical institutes (operating method), and researchers and firms (possible biocontrol combinations). In the first section, different aspects of the operational method implemented by farmers in the field are discussed. Then, the survival ability of *Trichoderma* spp. and *P. infestans* under various pedoclimatic conditions is considered to determine which conditions require more support against late blight of tomato and potato crops. Most of the results of our statistical analysis are included and are discussed in the third section to suggest possible biocontrol systems for late blight involving the crop, the plant pathogen and adapted *Trichoderma*-based treatments (Fig. 4).

5.1. Operating method

The real efficacy of a *Trichoderma*-based formulation can only be assessed in the field and it differs according to the way it is spread on the targeted crop. Beyond agronomic practices, the techniques used by farmers contribute to the success of the treatment work. How many propagules to spread, how often to apply the treatment and where to apply the biocontrol mixture are key practical issues considered in this section.

5.1.1. Dose applied

Both *in vitro* and field studies have investigated the effects of differently concentrated *Trichoderma* formulations on mycelial growth of *P. infestans*, disease severity and resulting yield.

The efficacy of the treatment varied with the concentration of the biocontrol agent. *In vitro* experiments with *T. asperellum* versus *P. infestans* on Petri dishes showed that, for the same volume applied, high-concentration suspensions of *Trichoderma* (3×10^5 propagules/mL) were 40% better than low-concentration suspensions (30 propagules/mL) at inhibiting *P. infestans* mycelial growth (Al-Mughrabi, 2008). However, a threshold effect may occur if the treatment is too concentrated. The radial growth inhibition of *P. infestans* by *T. asperellum* suspensions remains the same despite increasing the propagule concentration beyond 7×10^6 propagules/mL (Kilonzi et al., 2020b).

Below the threshold of inhibitory activity observed at high propagule concentrations, the area under the late blight disease progression curve (AUDPC) was found to be strongly negatively correlated with the *T. asperellum* concentration on both potato leaflets and seed tubers (Kilonzi et al., 2020b; Mutuku et al., 2021). However, the lower concentrations used in these two studies were not high enough to inhibit lesions and *P. infestans* growth. This resulted in poor potato yields, close to those of the untreated plants (Kilonzi et al., 2020b; Mutuku et al., 2021).

The dose of *T. asperellum* used for tomato seed priming determines its ability to modulate plant growth. Low-dose priming increases both tomato radicle length and seed germination. However, doses greater than

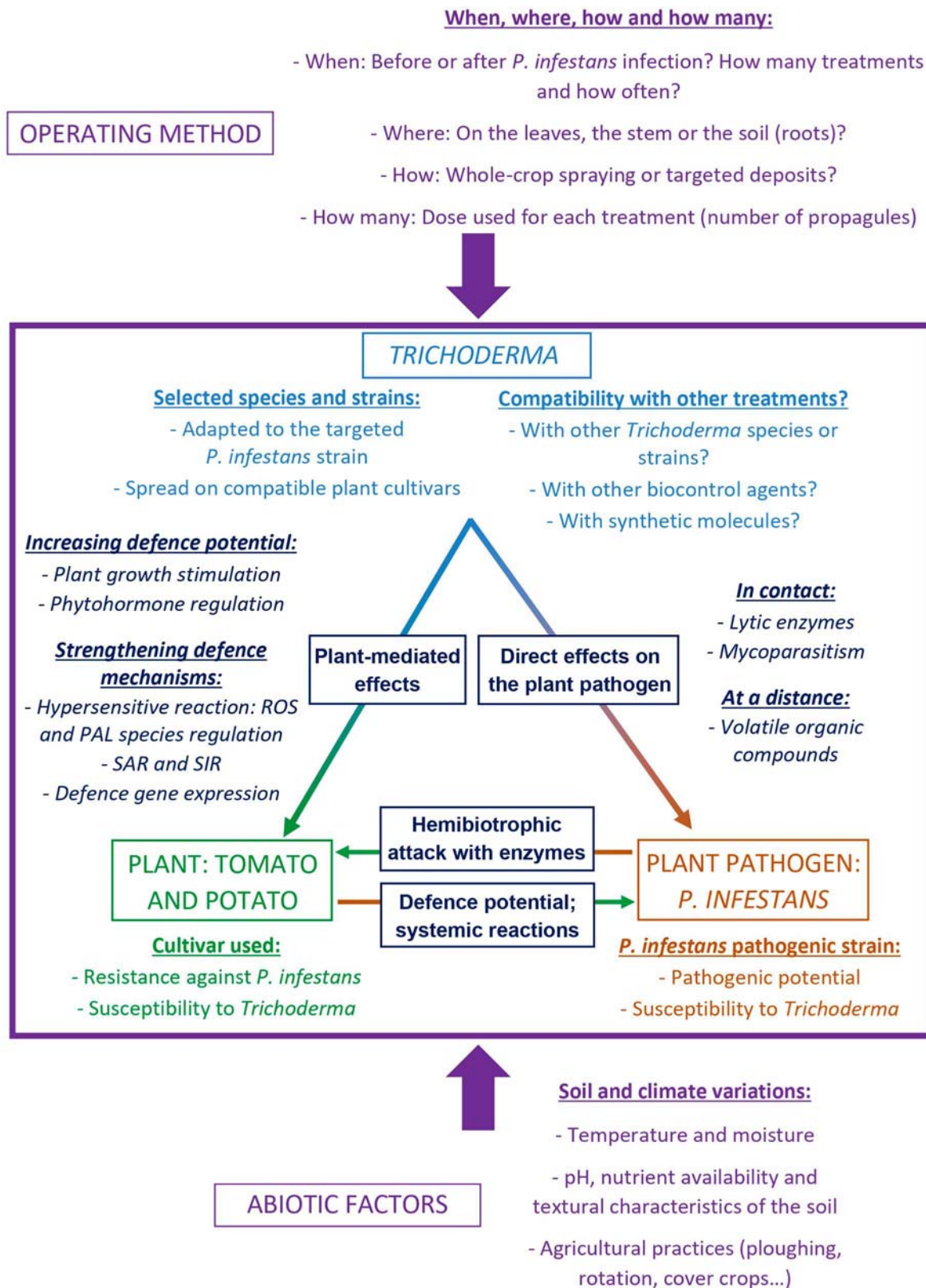


Fig. 4. Tomato and potato - *P. infestans* - *Trichoderma* interactions, and possible explanatory factors of variation. External factors and variables likely to impact the biocontrol system are represented in purple. Internal factors are represented in three colours: green, host plant; orange, *P. infestans*; light blue, *Trichoderma*. Control mechanisms are described in dark blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

10^4 spores/mL decreased radicle length and doses exceeding 10^6 spores/mL even significantly decreased seed germination (Singh et al., 2016).

Thus, the dose of *Trichoderma* spp. in biocontrol products is an important parameter to consider. Further field trials are needed to define this critical point for practical applications of the most commonly used *Trichoderma* spp.

5.1.2. Frequency of treatments

The frequency of treatments is also an important factor to be determined. The time range must be adapted to the persistence of the biocontrol species. For example, a combined treatment of *T. harzianum* and *Bacillus subtilis* on tomato seedlings remained efficacious up to 11 days after the greenhouse treatment (Kumar et al., 2015b). In another experiment in the field, potato tuber treatments with *T. asperellum* provided optimal biocontrol of late blight when applied every two weeks. Weekly applications resulted in equivalent yield and AUDPC results, but reducing the frequency to one application every three weeks allowed the plant pathogen to develop and significantly affected the final yield (up to 50% decrease) (Mutuku et al., 2021). As an answer to the question “HOW OFTEN”, these greenhouse and field studies on tomatoes and potatoes converge on the idea that the treatment should be renewed every 11–14 days, depending on the species in the formulation. However, these results are too few to be generalised and more studies are needed for each host plant, especially in the field and for a greater variety of pedoclimatic conditions.

5.1.3. Treated organs and adaptation according to the physiological stage

The location of the treatment also influences its efficiency: the works carried out on this topic led to different conclusions. A first option is to use *Trichoderma* spp. as soil inoculants: this strategy may be relevant since *T. harzianum* is an active competitor for resources in the soil (Hýsek et al., 2002), able to efficiently reduce the growth potential and pathogenicity of *P. infestans* zoospores located in the soil surrounding potato plants (Alfiky et al., 2023). Another option is to treat the seeds: this strategy decreased seed piece decay caused by *P. infestans* (Wharton et al., 2012), and enabled both a reduction in pre-emergence disease incidence and an increase in *P. infestans* control efficacy in tomatoes (Naffaa et al., 2022). Using both *T. harzianum* and *B. subtilis* as seed treatment agents to prevent *P. infestans* development and produce disease-free plants enhanced growth and systemic resistance in tomato seedlings (Kumar et al., 2015b). Soil and seed treatments are both beneficial techniques, but they enhance different mechanisms in tomato: *T. harzianum* seed treatment increases seed vigour and both radicle and hypocotyl length whereas soil treatment increases stem diameter and root weight (Sandri et al., 2023). The choice of treatment location should also be adapted to the location of *P. infestans* zoospores: soil inoculation with *T. harzianum* was efficient in controlling soil-borne *P. infestans*, but not foliar *P. infestans* (Alfiky et al., 2023).

The answer to “WHERE” is not yet fully clear and raises new concerns. Two commonly used seed treatment techniques, dipping and peridermal injections, were compared (Kilonzi et al., 2020a). Although dipping provided better control of late blight, it resulted in lower yields than peridermal injections, probably because plant enhancement mechanisms were less induced.

The use of *Trichoderma* spp. from the earliest physiological stages is an interesting option, in as far as the ascomycete accompanies plant growth and prevents infection when plant defences are less developed (Kilonzi et al., 2020a). At later physiological stages, another study suggested that spraying *T. harzianum* against late blight was more efficacious than watering: spraying resulted in a lower infection rate, with less damage to potato leaves (Purwantisari et al., 2021). Further research in this direction is needed to complete current knowledge.

5.2. Environmental and pedoclimatic conditions

The design of a biocontrol strategy against late blight must take into

account the environmental factors that may interfere with its proper functioning under field conditions. Environmental variables and abiotic factors must be taken into account to determine which pedoclimatic conditions influence the development and growth of *P. infestans* and *Trichoderma* spp. and which period of the year may be critical for the crop. This information is essential for optimising crop treatments and for spreading the biocontrol agent at the appropriate time.

5.2.1. Soil characteristics

The soil richness, its structure and texture influence the pathogenicity of *P. infestans* and plant responses. *P. infestans* developed better and had a higher incidence in sterilised sandy soils and low biodiversity potting soils than in silty loamy soils (Lacey, 1965; Porter et al., 2005). Agronomic practices should also be adapted to reduce disease severity. Higher organic fertilisation enhanced the growth of tomato plants and increased their defence potential, while reduced tillage decreased the AUDPC of potato leaves (Finckh et al., 2015; Sharma et al., 2012a).

The growth and development of *Trichoderma* spp. is dependent on the soil characteristics, and not all species are equally active under the same soil conditions. For example, using *T. asperellum* instead of *T. harzianum* on vitric andosols was more efficacious in reducing disease severity in tomato. On rhodic nitrisols (low pH, low P availability), it was preferable to use a biocontrol solution such as *T. asperellum* instead of a chemical fungicide (RidomilR) (Kariuki et al., 2020). In addition to better disease reduction, *T. asperellum* improved plant growth and resistance to *P. infestans* (Kariuki et al., 2020). *Trichoderma* spp. can easily grow in slightly acidic conditions (pH 5–7) and even at very acidic pH values down to pH 3 (Gueye et al., 2016; Moreno-Mateos et al., 2007), which are unsuitable for other biocontrol agents such as *B. subtilis* (Gauvry et al., 2021). Moreover, knowing the ability of a strain to develop depending on the soil conditions is a useful tool for effective use of *Trichoderma*-based biocontrol (Hussain et al., 2014).

5.2.2. Temperature and moisture

Local climatic conditions contributes to determining the activity patterns of *P. infestans* and *Trichoderma* spp. This subsection compares the weather tolerance of the two organisms in terms of temperature and moisture to understand under which conditions the crops are susceptible to late blight and could benefit from efficacious treatments with *Trichoderma*.

P. infestans produces oospores in potato leaves between 5 and 25 °C, and is particularly sensitive to higher temperatures (Drenth et al., 1995; Mutuku et al., 2021). *P. infestans* was more active in Africa during the long rainy season, with cooler temperatures (20 °C), higher relative humidity (77%) and longer wet days. During this period, disease severity on tomatoes was two times higher than during short wet days (Mutuku et al., 2021). A field study conducted in Indonesia on potatoes showed similar results, with an increase in the quantity of oospores at temperatures around 20 °C and high humidity levels (>90%) (Purwantisari et al., 2018b). Cool nights, warm days and prolonged high moisture levels are ideal conditions for plant pathogen development in potato and tomato crops (Guchi, 2015; Shrestha and Ashley, 2007).

T. harzianum, *T. viride* and *T. virens* are tolerant to a wide range of temperatures and fully develop between 20 and 30 °C (Hajieghrari et al., 2008; Hussain et al., 2014). This is correlated with CWDE chitinase and glucanase activity, which increases at lower water potentials and higher temperatures (25 and 37 °C) (Kredics et al., 2000). Not all *Trichoderma* species develop and grow within exactly the same temperature ranges. *T. harzianum* reaches the highest dry biomass and a maximum development at 25 °C, whereas *T. asperellum* and *T. longibrachiatum* grow better when incubated at 30 °C (Priya et al., 2022; Singh et al., 2014). In addition, spore germination increases under moisture conditions above 60%, suggesting that moisture is a key parameter to consider for *Trichoderma* spp. multiplication (Cavalcante et al., 2007).

These results show that the activities of *Trichoderma* spp. and *P. infestans* are dependent on similar temperature and moisture

conditions. High humidity levels favour their growth and development, and both are tolerant to the same temperature ranges, although *P. infestans* also develops well at temperatures below 20 °C. Therefore, in temperate areas such as Europe, increased vigilance is required in early spring when temperatures between 15 and 20 °C favour the spread of *P. infestans*, while *Trichoderma* spp. cannot reach their maximum growth potential. In the case of early intensive *P. infestans* sporulation, it may be necessary to combine conventional fungicides with biocontrol agents to optimise the antifungal strategy.

5.3. Biocontrol system

Besides the specific outdoor context of the field, the efficacy of a treatment strategy is determined by the interaction of the plant pathogen/plant/biocontrol agent ternary system. Since it is not possible to select the intrinsic characteristics of the plant pathogen, two remaining levers can be activated: i) selecting less sensitive potato and tomato cultivars, and ii) choosing the adapted *Trichoderma*-based formulation. As shown previously, *Trichoderma* species and strains must be selected according to their antifungal and plant stimulating activities (direct and plant-mediated effects). They can be used alone or integrated into biocontrol mixtures to achieve efficacious and sustainable management of late blight.

5.3.1. Selection of potato and tomato cultivars

The choice of cultivar has a major impact on *Trichoderma*-plant-*P. infestans* interactions.

- (1) The ability of *Trichoderma* spp. to reduce late blight harmfulness depends on the cultivar chosen. For example, the widely used cultivar Spunta is more susceptible to late blight than other less common cultivars such as Kondor (Kerroum et al., 2015). Also, the most susceptible cultivars show less disease reduction at the same dose of *Trichoderma* spp. The highly susceptible potato cultivar Kufri Bahar and the moderately resistant cultivar Kufri Mohan inoculated with the same concentrations of *T. viride* and *P. infestans* were not equally supported. Disease severity decreased from 95% to 66.7% on Kufri Bahar tubers, versus from 81.2% to 46.2% on Kufri Mohan tubers. The effect of treatment was greater on the moderately resistant variety, probably because *T. viride* better enhanced the plant's defence potential (Lal et al., 2021). Similar results were obtained when evaluating the late blight inhibition potential of *T. harzianum* on two potato cultivars: the moderately resistant Diamant and the susceptible native Challisha. While a solution of synthetic Mancozeb® showed identical inhibition of *P. infestans* on both potato cultivars, *T. harzianum* totally inhibited late blight on Diamant, but not on Challisha (Monjil et al., 2021). On Diamant, the use of a biocontrol product based on *T. harzianum* (Lycamax) was more effective in the field against *P. infestans* than a fungicide such as Mancozeb® (4-fold reduction in leaf infection) (Mollah and Hassan, 2023).
- (2) The profitability of plant-*Trichoderma* interactions also depends on the cultivar. *T. harzianum* increased the concentration of microelements (especially Mn and Fe) and total flavonoids in the *P. infestans* tolerant tomato cultivar Gružanski zlatni better than in the *P. infestans* susceptible tomato cultivar Narvik. Conversely, *T. harzianum* decreased both nitrogen and chlorophyll contents in Gružanski zlatni, whereas they remained unchanged in Narvik cultivar (Vukelić et al., 2021).

Species interaction preferences are a key parameter to consider when selecting a cultivar to be treated with biocontrol agents such as *Trichoderma* spp. Plant genetics also explain the ability of potatoes to host *Trichoderma* spp. and must be known as accurately as possible (Hashemi et al., 2022).

5.3.2. Combined treatments

A possible way to improve the efficacy of *Trichoderma* spp. in *P. infestans* control is to use them in mixed culture with other biocontrol agents or in combination with synthetic molecules, following compatibility testing.

Combining *T. harzianum* and *B. subtilis* improve late blight management (Djaya et al., 2021; Kumar et al., 2015a). The combination not only contributed to improved aerial and basal development of tomato seedlings, with higher leaf area and longer roots and shoots, but also increased the production of phytohormones and antioxidant species (IAA, GA3, PO, PPO, SOD). The level of late blight infection on the leaves of tomato seedlings was more than five times lower than that of control tomato plants (Kumar et al., 2015a). Combinations of different strains of *Trichoderma* spp. were more efficacious than single strains in other pathosystems (Chebil et al., 2022). Combining *T. harzianum*, *B. subtilis* and *Pseudomonas putida* was highly efficient in reducing the incidence of late blight, and as efficacious as a synthetic fungicide treatment with Mancozeb® and Fenamidone® (Kumar et al., 2015b). This combination could be an interesting eco-friendly alternative to commonly used fungicides.

Despite compatibility, mixed cultures are not always more efficacious than each agent alone. A biocontrol solution using *T. viride* and *P. fluorescens* against *P. infestans* on potato had less effect on disease severity than each biocontrol agent applied independently (Zegeye et al., 2011). Combining *Rhizophagus irregularis* and *T. virens* to control late blight on potato cultivar Annabelle did not significantly reduce the area under the disease progression curve compared to a single *R. irregularis* treatment (Lalaymia et al., 2022). Using *T. asperellum* and *T. harzianum* together was also less efficient than choosing one of them to control late blight in tomato, probably due to competition for resources and nutrients (Kariuki et al., 2020).

Enrichment of compost or biochar with *Trichoderma* spp. is also a promising solution to control late blight and reduce chemical inputs. *T. viride* combined with farmyard manure (FYM) or vermicompost mixtures resulted in lower incidence and intensity of leaf blight than a single *T. viride* treatment on a potato crop (Peerzada and Bhat, 2020). Furthermore, Cai et al. (2015) showed that replacing 25% of chemical fertiliser with a combination of compost and *T. harzianum* increased the growth and yield of tomato plants to the same level as using 100% chemical fertiliser. Combining biochar and *T. harzianum* increased both tomato fruit yield and quality compared to either *T. harzianum* or biochar alone (Sani et al., 2020).

Both natural and synthetic molecules have also been used in combination with *Trichoderma* spp. As *T. asperellum* is tolerant to high copper concentrations, a dual treatment combining *T. asperellum* and copper hydroxide improved the mitigation of potato late blight severity compared to the single use of either of these two solutions (Andrade et al., 2017; Ladi et al., 2020; Shukla et al., 2021). Similarly, RidomilR® and Mistress72® did not inhibit the growth and development of *T. asperellum* (Kilonzi et al., 2020b). Combined treatments of fungicides and biocontrol species such as *Trichoderma* spp. were more efficacious for yield preservation and late blight management than synthetic molecules used alone at higher doses (Manjunath et al., 2017). However, a mixed culture of Mistress72® or RidomilR® with *T. asperellum* did not result in better efficacy against *P. infestans* (Kilonzi et al., 2020b). Field trials are still needed to confirm that the mixtures result in an effective yield increase.

Combining a biocontrol agent such as *Trichoderma* spp. with other biocontrol agents and/or with synthetic molecules may be a useful approach for the future, based on functional complementarity. Combined treatments such as *Trichoderma* spp. and *B. subtilis* allow a higher temporal coverage. They combine a 'preventive' agent (*B. subtilis*) to improve plant growth and a 'curative' agent (*T. harzianum*) to control *P. infestans*, even if both microorganisms have direct and plant-mediated effects (Bahramisharif and Rose, 2019; Chowdappa et al., 2013; Wharton et al., 2012). Other treatments, such as copper-chitosan-*Trichoderma*

mixtures, can be designed to combine both direct (copper and *Trichoderma*) and plant-mediated (chitosan and *Trichoderma*) modes of action to control *P. infestans* (Rautela et al., 2018; Shukla et al., 2021).

5.3.3. New *Trichoderma* species to be considered?

Commercialised fungicides based on *Trichoderma* spp. include mainly *T. harzianum*, *T. atroviride* and *T. asperellum*. Trianium-P® and Trianium-G® (Koppert), Rootshield® WP (BioWorks) and Cères® (Biovitis) are composed of *T. harzianum*; Tri-Soil® WP and Esquive® WP (Agrauxine) or Vintec® (Belchim Crop Protection) contain *T. atroviride*, and ASPERELLO®, T34 Biocontrol® (Biobest), Xedavir Patriot Dry® (Aedes Protecta) and Tusal® (Certis Europe) are composed of *T. asperellum*. All of these products can be applied to tomato or potato plants to control late blight. Some of them are also used against other plant pathogens such as *Fusarium oxysporum*, *Rhizoctonia solani*, *Sclerotium rolfsii* or *Pythium aphanidermatum* (French Ministry of Agriculture and Food Sovereignty, 2022). The ability of the most commonly used species to maintain high levels of operational performance against a wide range of plant pathogens, and the fact that they benefit from a wider market with optimised industrial processes, encourage companies to keep developing biocontrol products based on these three species (Kumar et al., 2015c).

Our dual culture analysis highlighted that other *Trichoderma* species show promising inhibition results against *P. infestans*, but specific efficacy evaluations in the field and under different pedoclimatic conditions are required to consider potential practical applications (Colombo et al., 2019). Strains of *T. viride* (Bouziiane et al., 2016; El-Naggar et al., 2016; Kumar et al., 2015c; Myrchiang et al., 2014) and *T. longibrachiatum* (Kumar et al., 2015c; Priya et al., 2022) have shown high antagonistic ability against *P. infestans*, with more than 65% and 75% mycelial growth inhibition in dual culture, respectively (Supplementary Material, Table S2), sometimes performing better than *T. harzianum* and *T. asperellum*. Given the ability of *T. longibrachiatum* to infect humans (Kuhls et al., 1999), it would be necessary to identify and extract the corresponding active metabolites for potential use in the field. *T. hamatum* may also be an alternative for late blight management: tested strains were 34% more efficacious than *T. harzianum* in inhibiting mycelial growth after 3 days in dual culture, according to a study (Salem et al., 2014). Another promising low studied species is *T. lignorum* (biocontrol formulation Trichodermin), which inhibited *P. infestans* spore germination by 42% and reduced tomato late blight severity by 29% in greenhouse (Borzykh et al., 2022). Further research is expected on these little known but very promising species in order to develop new biocontrol treatments specifically targeting late blight.

5.3.4. Could *Trichoderma* spp. be used to control potato and tomato early blight in addition to late blight?

In addition to *P. infestans*, *Trichoderma* spp. can also be used against other plant pathogens, including *Alternaria solani*, which is responsible for tomato and potato early blight. Some studies are even looking at both plant pathogens together and the effectiveness of *Trichoderma* species in controlling them (Borzykh et al., 2022; Chowdappa et al., 2013; Mollah and Hassan, 2023). The mechanisms involved are similar to those involved in *P. infestans* management.

- (1) Direct action against *A. solani*: *Trichoderma* spp. have high antagonistic ability and produce CWDE against *A. solani* (Haque et al., 2024). Numerous studies have shown the high ability of *T. harzianum* (Chowdappa et al., 2013; Haque et al., 2024; Metz and Hausladen, 2022; Mollah and Hassan, 2023), *T. virens* (Haque et al., 2024), *T. atroviride* (Metz and Hausladen, 2022), *T. asperellum* (Haque et al., 2024; Metz and Hausladen, 2022), *T. hamatum* (Metz and Hausladen, 2022) and *T. lignorum* (Borzykh et al., 2022) to control *A. solani* on potato (Metz and Hausladen, 2022; Mollah and Hassan, 2023) and tomato

(Borzykh et al., 2022; Chowdappa et al., 2013; Haque et al., 2024), *in vitro* and in the field.

- (2) Plant-mediated effects: *Trichoderma* species improve the growth and development of tomato plants and increase the defence potential against *A. solani* (Chowdappa et al., 2013; Haque et al., 2024). Little work has been done on the ability of *Trichoderma* spp. to induce systemic response of tomato and potato plants against *A. solani*, but Bassant et al. (2024) reported that *T. afroharzianum* can increase defence-related enzymes and antioxidant production (CAT, SOD, PPO) in tomato plants confronted with another *Alternaria* species, *Alternaria alternata*.

6. Conclusion

Trichoderma species are among the best multifunctional microorganisms for controlling *P. infestans* in potato and tomato crops. Both direct and plant-mediated modes of action diversify the ways late blight can be managed. On the one hand, *Trichoderma* spp. inhibit mycelial growth and development through their antifungal activity, by contact and remotely, resulting in reduced disease severity in all organs of the target plant. On the other hand, they enhance the growth, development and defence potential of plants by inducing higher production of phytohormones and antioxidant species. However, not all species have the same efficacy, and only three of them – *T. harzianum*, *T. asperellum* and *T. atroviride* – are currently widely marketed. Although *T. harzianum* and *T. asperellum* are very efficacious in decreasing *P. infestans* mycelial growth, spending time choosing the ideal strain is even more important because standard deviations can reach high levels, especially among *T. asperellum* strains. In addition, other species such as *T. viride* and *T. longibrachiatum* showed promising inhibitory activity of *P. infestans* in dual plate assays, but further field experiments with different pedoclimatic conditions are expected to refine these results and consider practical applications.

Selecting the best possible species and strain is essential to build a successful biocontrol strategy, but the *Trichoderma*-plant-pathogen system must be adapted to outdoor factors and conditions. Abiotic factors, such as climate and soil variables, help in decision making. *Trichoderma* species do not all have the same ability to develop and to grow within the same temperature and moisture range, and some species such as *T. asperellum* easily adapt to changes in soil conditions (poor nutrient availability, soil texture). At the same time, the operating method must be adapted to find the best possible balance between reducing financial costs (with minimal use of biocontrol products and only when necessary) and reaching a correct final yield to make a profit (using enough *Trichoderma* spp. to manage late blight). Three levers must therefore be considered: the dose of the product, the frequency of applications, and the localisation of the product. Treatments must target precise parts of the crop and adapt to its physiological stage, from soil and seed treatment in early stages to spray treatments in later stages. However, the ideal concentration of *Trichoderma* inoculum and the interval between treatments should be determined more precisely in the field, depending on the host plant and the pedoclimatic conditions.

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Ethical guidelines

Ethics approval was not required for this research.

CRediT authorship contribution statement

Quentin Courmault: Conceptualization, Investigation, Data analysis, Writing – original draft. Stéphanie Gibot-Leclerc: Supervision, Methodology, Resources. Noadya Monnier: Supervision, Funding acquisition, Resources. Christian Steinberg: Resources, Funding acquisition, Final Reviewing.

Declaration of competing interest

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

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Appendix A. Supplementary data

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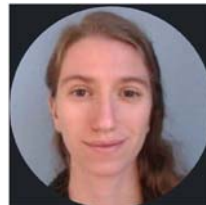
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PhD student and recently graduated from a French agronomy school (Institut Agro Dijon), Quentin Courmault specialises in plant pathology. His research areas focus on sustainable regulation of phytopathogens (especially pests and weeds) in the context of climate change, through alternative levers to pesticides, including biological control. This review reflects some of his work and highlights the potential of biotic regulation as an effective agroecological solution. Quentin Courmault's work will contribute to extending scientific literature and propose new solutions that can be reused by farmers and technical agricultural institutes in fields.



S. Gibot-Leclerc is a lecturer at the Institut Agro Dijon. As a plant ecophysiological, she seeks to decipher the mechanisms of interaction between parasitic plants and their host plants in the soil, integrating genetic, evolutionary and adaptive aspects. Molecular signalling between these plants in the rhizosphere is fundamental for the success of the interaction. Therefore, S. Gibot-Leclerc looks for the role of the microbiota in the definition of the parasitic holobiont and more specifically, in the role that fungi could play in regulating the interaction. The objective is to characterize mycoherbicides for protective biocontrol of host plants.



Noadya Monnier is deputy director of the Research and Development team of Elephant Vert group (EV). After a PhD in plant protection and a short career in academics, she joined the Research and Development team of EV in 2019. Her academic work focused on the use of bacterial metabolites for biocontrol of fungal pests, which is still one of her main research topics. She progressively enlarged her research area to other biocontrol microbial active substances, particularly fungi, and to microbe based biostimulants.



Research director in the unit Agroecology, within the National Institute for Research on Agriculture, Food and Environment (INRAE), C. Steinberg is a soil microbial ecologist with a particular focus on fungal communities. He is interested in the interactions between pathogenic and non-pathogenic fungi with a view to regulating the former by the latter for the biological protection of crops. He is also interested in the interactions between pathogenic fungi and weeds with a view to proposing mycoherbicides, just as he is interested in entomopathogenic fungi to control plant pests without resorting to synthetic insecticides that are harmful to the environment.