

# *Trichoderma*: a multipurpose, plant-beneficial microorganism for eco-sustainable agriculture

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## Abstract

*Trichoderma* is a cosmopolitan and opportunistic ascomycete fungal genus including species that are of interest to agriculture as direct biological control agents of phytopathogens. *Trichoderma* utilizes direct antagonism and competition, particularly in the rhizosphere, where it modulates the composition of and interactions with other microorganisms. In its colonization of plants, on the roots or as an endophyte, *Trichoderma* has evolved the capacity to communicate with the plant and produce numerous multifaceted benefits to its host. The intricacy of this plant–microorganism association has stimulated a marked interest in research on *Trichoderma*, ranging from its capacity as a plant growth promoter to its ability to prime local and systemic defence responses against biotic and abiotic stresses and to activate transcriptional memory affecting plant responses to future stresses. This Review discusses the ecophysiology and diversity of *Trichoderma* and the complexity of its relationships in the agroecosystem, highlighting its potential as a direct and indirect biological control agent, biostimulant and biofertilizer, which are useful multipurpose properties for agricultural applications. We also highlight how the present legislative framework might accommodate the demonstrated evidence of *Trichoderma* proficiency as a plant-beneficial microorganism contributing towards eco-sustainable agriculture.

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## Introduction

*Trichoderma* (teleomorph *Hypocrea*) is a genus of filamentous fungi that is capable of feeding on other fungi (mycotrophism) and is a ubiquitous colonizer in almost all environments (including agricultural, forestry, mountain, grassland and desert ecosystems, and fresh and marine waters); it prevails in any biotope and has an extensive geographical distribution worldwide<sup>1</sup>. *Trichoderma* species grow rapidly on various substrates and are prolific spore producers, easily recognized by the presence of abundant green conidia.

A review in 2004 by Harman et al.<sup>2</sup> presented *Trichoderma* species as opportunistic, avirulent plant symbiont fungi, and discussed the diverse mechanisms of action employed by the fungus that contribute to its positive impact on plants. Of particular interest were processes involved in the biological control of plant diseases, with direct action on phytopathogens and indirect mechanisms through induction of local and systemic defences in plants. Also noted was the stimulation of root development and plant growth, producing benefits to both the host plant and the invading fungus that resulted in favourable consequences for agriculture. Harman et al.<sup>2</sup> described the plant–microorganism interaction as intricate, involving multifaceted crosstalk modulated by root colonization and the plethora of compounds produced by *Trichoderma* that activate biochemical and genetic pathways determining plant defence responses to biotic and abiotic stresses.

The advancement of omics investigations<sup>3,4</sup> has resulted in increased understanding of the ecological events involved in the evolutionary progression of *Trichoderma* fungi from common soil dwellers growing on decaying organic matter (noted for their outstanding saprotrophic action on dead fungi and oomycetes), to mycoparasitism of other fungi (including those of taxonomically close species) and to interactions with plants that involve colonization of the rhizosphere and endophytism<sup>5</sup>. Omics approaches have also served to unveil the processes and regulation dynamics of the beneficial effects of *Trichoderma* to plants<sup>6,7</sup> that are of agricultural interest. The application of molecular methods for species identification and classification has resulted in the exponential expansion of *Trichoderma* taxonomy – starting 50 years ago with only 9 species aggregates described for the genus to >400 species recognized today<sup>8</sup> (Box 1).

Research interests have since expanded towards an integrated analysis of the multipurpose properties of *Trichoderma* as fungi beneficial to plants for applications and improvement of agricultural production. This variation in research objectives can be attributed to ongoing changes in agricultural policies and management over time, with an increasing focus on sustainability for the future. *Trichoderma* contributes positive effects to the agroecosystem; thus, considerations are being given to the role that this fungus has in innovative agricultural strategies as an established and accepted biotechnological tool.

In this Review, we present the latest advances in *Trichoderma* research, including ecophysiology and lifestyle changes that result in species diversification; opportunism and competition (discussing the complex relationships between plants and microbiota); use of the fungus as a direct biological control agent (BCA) in crop protection; indirect BCA effects stimulating plant immunity; and the capacity of *Trichoderma* as a plant biostimulant, both in promoting plant growth and activating defence against abiotic stress. Considerations are also presented on how to advance *Trichoderma* applications in real-world scenarios, bioformulation improvements and policy deliberations. We conclude by discussing how the use of *Trichoderma* could maximize opportunities for reducing chemical inputs, thus providing cleaner resources and healthier prospects for a more environmentally sustainable agriculture system.

## Ecophysiology and lifestyle changes

The genus *Trichoderma* demonstrates enormous morphological uniformity and nutritional diversity and has a high number of species members, greater than that found in other fungal groups with similar lifestyles<sup>1,8</sup>. These traits might be attributed to at least four major shifts over the course of evolution in nutritional habits and ecological roles that could have impacted the *Trichoderma* lifestyle, in which each transition has led to notable bursts in species diversification<sup>9,10</sup> (Fig. 1). These shifts were first, from being a parasite of plant-decomposing fungi to being a feeder on decaying plant matter (saprotroph); second, to living in the soil as a saprotroph, with mycotrophic (obtaining nutrients from live or dead fungi) and phytophagic (obtaining nutrients from plants) abilities; third, to feeding on living fungi (mycoparasite); and fourth, to establishing interactions with living plants. Genetic and comparative genomics studies<sup>5,9–11</sup> have demonstrated that *Trichoderma* are fungi that have constantly reshaped their genome to improve their ability to rapidly colonize and successfully compete in novel habitats. Mycotrophy is a very ancient trait of the *Trichoderma* genus and is a major lifestyle for many of its species, which has facilitated the evolution of its positive interactions with plants<sup>4,5</sup>.

Phylogenomic analysis has shown that the genus *Trichoderma* shares at least one common ancestor with entomoparasitic hypocrealean fungi<sup>10</sup>, and the most ancient species of the genus evolved around the time of the Cretaceous–Paleogene extinction event (66 million years ago)<sup>11</sup>. These fungi were mycoparasitic on Basidiomycota hosts, from which they acquired genes by horizontal transfer that subsequently conferred to *Trichoderma* the ability to grow on dead wood substrates, a lifestyle typical of their targeted fungal prey<sup>5,9,10</sup>. *Trichoderma* might have made a successive leap from this habitat as a participant in the strong burst of fungal populations subsequently found as feeders on the decaying biomass of plants killed by the Cretaceous–Paleogene extinction<sup>12</sup>. Most of the carbohydrate hydrolysing genes required for saprotrophic growth as mycotrophs and phytophages were probably acquired 20–30 million years ago, resulting in the diversification and establishment of noted infrageneric sections and/or clades (such as section *Trichoderma* (ST), section *Longibrachiatum*, and clades *Harzianum* and *Virens* (HV))<sup>10,11</sup>.

Many soil-living species of *Trichoderma* developed a distinctive genus characteristic for their capacity to produce a plethora of hydrolytic enzymes (exochitinase and endochitinase) that enabled them to mycoparasitize Ascomycota fungi or other phylogenetically close species (adelphoparasitism), a trait that was rare or absent in the ancestors of *Trichoderma*<sup>9,10</sup>. Approximately 40% of the vast number of hydrolytic enzymes secreted by *Trichoderma* have originated by lateral gene transfer from taxonomically close plant-associated ascomycetes<sup>10</sup>. *Trichoderma* spp. also expanded their ability to parasitize or hyperparasitize and to obtain nutrients from diverse soil-borne organisms such as *Phytophthora*, *Pythium*, *Rhizoctonia* and nematodes<sup>9</sup>. In addition, they developed mutualistic relationships with insects as demonstrated by the protection of termites from infection by entomopathogenic fungi (*Metarhizium*)<sup>13</sup>. Species diversity in *Trichoderma* was favoured by gene gains in the taxonomic groups of HV and ST and losses in section *Longibrachiatum*, coupled with a rare frequency of sexual reproduction and a high rate of conidiation (asexual reproduction) that increased the adaptive variation input by mutation<sup>9</sup>.

Subsequently, the presence of fungal prey and root-derived nutrients probably attracted the most opportunistic *Trichoderma* species to colonize the rhizosphere, whereby other species became internal plant colonizers or endophytes as the most recent major

evolutionary event of the genus<sup>5,9,11</sup> (Fig. 1). Three key features have contributed to *Trichoderma* becoming an endophyte<sup>9</sup> as a result of its progressive ‘intimacy’ in plant–microbiota interactions: as a saprotroph, it initiated the decay–degradation process after plant host death; as a mycoparasite, it was capable of parasitizing the primary fungal decomposers that colonized the vegetative tissues; and as a mutualistic non-pathogenic symbiont, it was able to interact and communicate with the living plant host, providing benefits such as growth promotion and protection against biotic and abiotic stresses. Over time, *Trichoderma* became an opportunistic plant colonizer, developing mechanisms that enabled it to overcome plant defences and not be recognized as a foe.

## Opportunism in the rhizosphere

*Trichoderma* opportunism is evidenced by the ability of this fungus to colonize a wide range of habitats, employing a combination of traits to compete for space and nutritional resources, resist environmental stresses, repair cell damage, and modify the ecological living conditions to its advantage (for example, by detoxifying noxious compounds or changing the substrate pH). The substantial increase in *Trichoderma* growth in the presence of pectin, xylan or other mucigel-released substances supports the notion that root-derived nutrients are attractors for *Trichoderma*, providing incentives for this microorganism to physically colonize roots<sup>14,15</sup>. The production of reactive oxygen species (ROS) in *Trichoderma* has been linked to antagonism against phytopathogens containing cellulose in their cell wall, such as *Pythium ultimum*<sup>16</sup>, as well as the fine-tuning of molecular crosstalk communication with plants that establishes beneficial effects<sup>17</sup>. Furthermore, tomato root exudates obtained from plants subjected to various biotic and abiotic stresses (such as pathogen attack, wounding or salt) were enriched with ROS and oxylipins, which were capable of stimulating growth and acting as selective chemo-attractants to *Trichoderma*<sup>18</sup>. *Trichoderma* can also enhance antioxidant defence in plants subjected to abiotic stresses, resulting in a decrease of ROS levels in the plant and thus limiting tissue damage<sup>19,20</sup>. Compared to other filamentous fungi, *Trichoderma* has its own robust antioxidant system with a potential role in protecting genome stability by elimination of ROS<sup>4</sup>. Evidence suggests that H<sub>2</sub>O<sub>2</sub> and oxylipins produced by *Trichoderma atroviride* might act as signal molecules in response to injury and cell damage (as in plants and animals)<sup>21</sup>.

The photoreactivation system that repairs DNA damage caused by UV radiation and is involved in the regulation of carbon and nitrogen metabolism in response to light has been studied extensively in *Trichoderma*; the ENVOY photoreceptor of *T. atroviride*, a repressor of blue light-induced genes, modulates the expression of genes involved in DNA repair, acting as a growth and conidiation checkpoint<sup>22</sup>. The high opportunistic ability of *Trichoderma* might also be a consequence of the activation of a complete range of heat shock proteins that confers tolerance to cold, heat, oxidative, osmotic or saline stresses<sup>23</sup>. *Trichoderma* genomes exhibit a high number of genes that encode for ATP-binding cassette (ABC) transporters<sup>4</sup>, which could bestow increased tolerance to toxic compounds present in the rhizosphere<sup>24</sup>. *Trichoderma* also secrete siderophores<sup>25,26</sup>, which may help them to compete in the rhizosphere and to solubilize phosphates<sup>27</sup>. The application of selected *Trichoderma* strains able to solubilize diverse phosphate sources enhanced phosphate uptake by plants, resulting in increased growth promotion<sup>28</sup>. Volatile organic compounds (VOCs), such as 6-pentyl-2H-pyran-2-one (6-PP), have known antibiotic activity, and, at low doses (similar to those expected to be released by *Trichoderma*

## Box 1

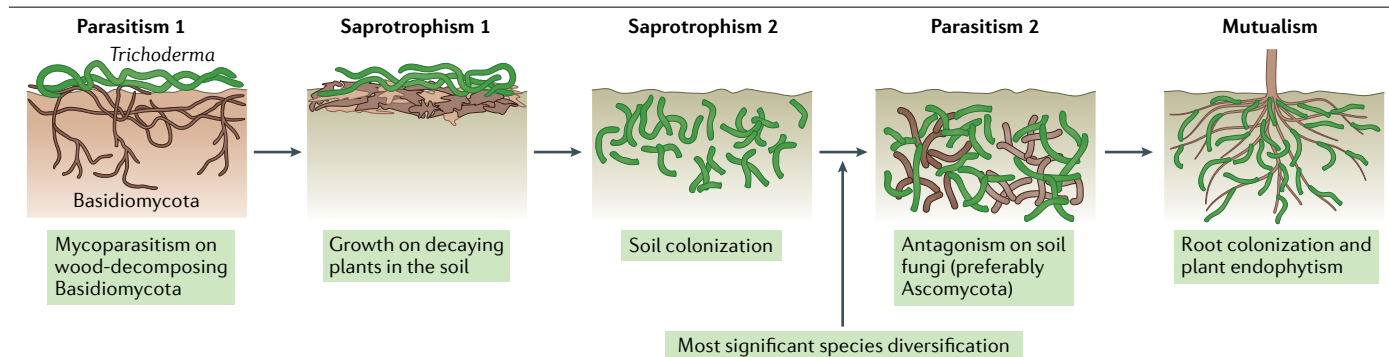
### *Trichoderma* taxonomic scenario

Persoon (1794) proposed the genus name *Trichoderma* (teleomorph *Hypocrea*) for a group of wood-decaying filamentous fungi that were producers of green asexual conidia masses at hyphal termini. These fungi are now classified as Division Ascomycota, Order Hypocreales and Family Hypocreaceae. The pleomorphism of this fungus led to the use of a dual nomenclature<sup>1</sup>; however, the sexual form (*Hypocrea*) is rarely found in nature, barely growing on plant debris and on specific basidiomycete fungi present in decaying bark, whereas the asexual form (*Trichoderma*) is abundant. Following the principle of ‘one name, one species’<sup>159</sup>, after a vote by the International Subcommittee on *Trichoderma* and *Hypocrea* taxonomy ([www.trichoderma.info](http://www.trichoderma.info)), *Trichoderma* was preferentially chosen by 54 votes to 22 over *Hypocrea* as the name to be adopted, and this genus name has been officially in use since 2013 (ref.<sup>160</sup>).

Today, the genus *Trichoderma* consists of >400 species (375 with valid nomenclature as of 2020) characterized by in vitro cultures, DNA barcoding and integration of publicly available whole-genome sequences<sup>8</sup>. DNA-based analysis has resulted in both the simplification and the complication of species classification and nomenclature for *Trichoderma*<sup>8</sup>. A species identification system has been elaborated by sequencing the ribosomal RNA locus internal transcribed spacers ITS1 and ITS2, different fragments of the *tef1* gene (encoding the translation elongation factor 1 $\alpha$ ), together with a species confirmation marker based on a fragment of the *rpb2* gene (encoding the second largest subunit of RNA polymerase II)<sup>8</sup>. In the present *Trichoderma* taxonomic framework, some species names have become obsolete, and it might be misleading to assign biological activities, such as the production of certain metabolites, to species described with an old name. For example, DNA barcoding identification of the active substances in four commercial biocontrol products determined that none were *Trichoderma harzianum* as indicated on the label<sup>63</sup>. Indeed, the worldwide marketed strain *T. harzianum* T-22 (ref.<sup>2</sup>) was renamed as *Trichoderma afroharzianum* after DNA barcoding analysis<sup>63</sup>. Therefore, the systematic reform of *Trichoderma* taxonomy might produce technical complications as some species names indicated in patents and commercial registration dossiers might need nomenclature revisions.

in nature), they may act as signalling molecules to modulate seed germination, plant growth, root architecture and immune responses in the absence of direct physical contact<sup>29,30</sup>.

*Trichoderma* genomes harbour phytohormone genes<sup>31</sup> involved in the production of auxins, gibberellins, abscisic acid, salicylic acid or cytokinins that, in a strain-dependent and/or culture medium-dependent manner, have been linked to hyphal growth, root colonization, activation of the plant antioxidant machinery and promotion of plant performance under abiotic stress<sup>20,32</sup>. The role of auxins produced by *Trichoderma* has not been established beyond doubt, but these compounds have been linked to root hair initiation and development effects



**Fig. 1 | Evolutionary shifts in *Trichoderma* ecophysiology.** Parasitism 1: evidence suggests that mycoparasitism of the wood-decomposing Basidiomycota is the most ancient trait of the genus *Trichoderma* (in green throughout). Saprotrophism 1: *Trichoderma* shifted to the development of saprotrophism and grew on plants killed during the Cretaceous–Paleogene extinction event (and acquired genes encoding a wide range of carbohydrate hydrolytic enzymes). Saprotrophism 2: many species remained as

saprophytes, colonizing the soil. Parasitism 2: species of the genus made major ecophysiological changes to parasitize taxonomically close Ascomycota as well as oomycetes, basidiomycetes and nematodes. Mutualism: the presence of potential fungal prey and plant root-derived nutrients in the rhizosphere facilitated a new leap towards a mutualistic relationship with living plants. The most recent ecophysiological change by some *Trichoderma* species is the internal colonization of plants (endophytism).

in plants<sup>33</sup>. *Trichoderma* might also stimulate plant auxin transport and signalling, resulting in plant growth promotion<sup>33</sup>. Notably, excessive accumulation of plant auxins can have the opposite effect, as rhizosphere acidification induced by *Trichoderma* can lead to inhibition of root growth through an auxin-dependent mechanism<sup>34</sup>.

Particularly interesting is the role of non-secreted molecules located in the cell wall of *Trichoderma* as well as the relative proportions of components in the cell membrane. For instance, the cysteine-rich cell wall protein QID74 of *Trichoderma harzianum* enhances the formation and elongation of root hairs, thus increasing the absorptive surface area plus translocation efficiency of nutrients into the shoots, resulting in more plant biomass<sup>35</sup>. The balance of structural squalene and ergosterol is necessary to maintain cellular membrane stability in fungi and is important for the ability of *Trichoderma* to colonize the roots as well as having a critical role in the regulation of plant defence mechanisms and biocontrol action<sup>36</sup>. The prolific endophytic colonization by some *Trichoderma* is not only a direct biocontrol mechanism that prevents pathogen colonization in the host but it can also produce plant-beneficial effects, such as increased photosynthetic capacity and growth promotion, accompanied by an increased tolerance to biotic and abiotic stresses<sup>37–39</sup>. For example, colonization of the apoplast of olive tree roots by *Trichoderma* prevents the pathogen *Verticillium dahliae* from accessing the vascular bundles, thus providing effective disease control of Verticillium wilt<sup>40</sup>. However, endophytic colonization by *Trichoderma* does not guarantee a corresponding beneficial effect for the plant<sup>20</sup>.

## Microbiomes and non-target microorganisms

The evolutionary leap to colonize the rhizosphere and plant roots, coupled with antagonism or biocontrol action, suggests that *Trichoderma* is an intrepid conqueror of ecological niches, a determined competitor and an aggressive antagonist. Therefore, it is important to investigate and evaluate the impact that *Trichoderma* strains might have on non-target organisms and plants as well as the effects in given soil and rhizosphere environments. *Trichoderma* has been proposed as a marker of healthy soils<sup>41</sup>. A core *Trichoderma* biome seems to be present in both endemic and cosmopolitan plants from different continents, in which endemic plant populations harbour a substantially higher proportion of antagonistic *Trichoderma* species<sup>42</sup>. The cultivation systems used and

the crops cultivated can have diverse effects on soil properties, which in turn influences fungal diversity (for both pathogenic and beneficial fungi)<sup>43–45</sup>. Microbiome diversity is highest in bulk soil and decreases in rhizosphere and endosphere samples<sup>44,45</sup>. However, with inoculations of *Trichoderma*, prokaryote and eukaryote populations are modified in bulk soil and in the two root-associated compartments. The use of *Trichoderma* strains alone or in combination with organic compost in crop plants has been reported to maintain plant growth and cause changes in the structure and function of microbial communities in the rhizosphere in terms of microbial community composition and effect on phosphorus solubilization (resulting in total rhizosphere soil microbial community changes and stimulation of potentially beneficial microbial consortia)<sup>46,47</sup>. Diverse organic amendments added to soil differentially influence the growth and disease suppression capacity of microorganisms, including beneficial fungi such as *Trichoderma*, and increase plant root proliferation<sup>48</sup>. *Trichoderma* can aid in the maintenance of microbiome diversity when growth conditions are compromised as was observed when the application of *Trichoderma* alone increased the number and diversity of many genera of beneficial plant bacteria in the wheat rhizosphere after the microbiome had been negatively affected by high doses of inorganic nitrogen fertilizers<sup>45</sup> or, similarly, when dual inoculations with *Trichoderma* and endophytes were found to enrich the microbiome of plants subjected to drought stress<sup>49</sup>.

The compatibility of *Trichoderma* with mycorrhizal fungi has been frequently questioned for three reasons: first, the high mycoparasitic potential of *Trichoderma* and its attack on arbuscular mycorrhizal fungi (AMF) in vitro<sup>50</sup>; second, the distinct and *Trichoderma* species-dependent VOC emission profiles against ectomycorrhizal fungi<sup>51</sup>; and third, the ability of AMF to compete for nutrients and colonization sites and boost the systemic defences of plants<sup>52</sup>, which might potentially hinder *Trichoderma* colonization in the rhizosphere. The behaviour of AMF reflects their ability to induce the systemic defences of plants and means that they can be effectively considered as indirect BCA. However, despite assumptions that *Trichoderma* and mycorrhizal fungi could not be applied simultaneously, their combined use has been noted to increase crop yields<sup>53</sup>, and greenhouse studies have proven their compatibility when applied together to tomato seedlings<sup>54,55</sup>. Furthermore, the application of *Trichoderma* aided AMF interactions with a

non-mycorrhizal *Brassica* host that improved rapeseed productivity<sup>56</sup>, and a single application of *Trichoderma* increased the levels of AMF in the wheat rhizosphere<sup>45</sup>. Importantly, compatibility studies need to be conducted for these two beneficial fungi and evaluated on a case-by-case basis, bearing in mind that root colonization by *Trichoderma* is much faster than that of mycorrhizal fungi.

Some *Trichoderma* spp. have been noted to produce harmful effects, including *T. aggressivum*, *T. pleuroti* and *T. pleurotica*, which have been reported as pathogens of edible mushrooms<sup>8,57</sup>. The production of the trichothecene toxin trichodermin by *Trichoderma brevicompactum* resulted in phytotoxic effects on tomato plants, thus invalidating the mycotoxin-producing strains as BCAs<sup>58</sup>.

With the ability to grow at high temperatures (37 °C), *Trichoderma longibrachiatum* has been noted as a human opportunistic pathogen in patients who are immunocompromised<sup>59</sup>. Fortunately, the undesirable activities observed with some *Trichoderma* do not correspond to those species commonly used in agriculture and commercially marketed. In addition, as a prerequisite for product registration, the microorganism must be tested and certified as not having any potential negative health effects.

Interestingly, *Trichoderma* can have deleterious effects on leaf-cutting ants (on the fungal gardens they grow for feeding as well as on their survival) owing to antagonism with their fungal symbiont. However, the endophytic colonization by *Trichoderma* of the plant material transported to the ant nests can act as an effective 'Trojan-horse' strategy that results in beneficial effects to the plant as it provides protection from these damaging agricultural and forestry pests<sup>60</sup>.

## Direct biocontrol in crop protection

*Trichoderma* can be considered as a multipurpose BCA owing to its combined potential actions, with direct antagonism to the target organism (Supplementary Table 1) and indirect activities through the plant host to stimulate a defence response to a multitude of biotic stress factors. The direct action of *Trichoderma* as a BCA (Fig. 2) has been extensively addressed in many reviews, including that by Harman et al.<sup>2</sup>. However, it is important to note that not all *Trichoderma* species or strains have the same capacity for pathogen or pest control, respond equally to diverse crops or cultivars<sup>61,62</sup>, function effectively in different geographic locations, or are able to maintain a consistent standard level of protection in all field conditions or over extended timeframes. In particular, the strains of *Trichoderma* that are of interest to agriculture<sup>63</sup> are principally distributed among species of the infrageneric groups ST (*T. atroviride*, *T. gamsii*, *T. viride*, *T. asperellum* and *T. asperelloides*) and HV (*T. harzianum* sensu lato, *T. afroharzianum*, *T. guizhouense* and *T. virens*)<sup>8</sup> (Box 1). In general, efficacy as a BCA depends on the biological characteristics of the *Trichoderma* strain, including rapid growth, prolific sporulation and opportunistic colonization of the environment, as well as on the biochemical arsenal of host cell wall-degrading enzymes (CWDEs)<sup>2,4,64</sup>, cumulative secondary metabolites<sup>65,66</sup> and released VOCs<sup>67</sup> (all of which affect interactions with the host plant<sup>68</sup>, influence the soil microbiome<sup>51,69</sup> and subsequently affect the biocontrol of plant attackers<sup>70</sup>).

The antagonism or direct biocontrol activity by *Trichoderma* of plant-damaging organisms can be attributed to the following five principal mechanisms<sup>2,71</sup>: parasitism, whereby *Trichoderma* is a predator that obtains nutrients from the target prey (that is, if the prey is a fungal phytopathogen, then *Trichoderma* is a mycoparasite feeding on a fungal disease agent); antibiosis, by production of secondary metabolites that inhibit competitors, limiting and impeding microorganism

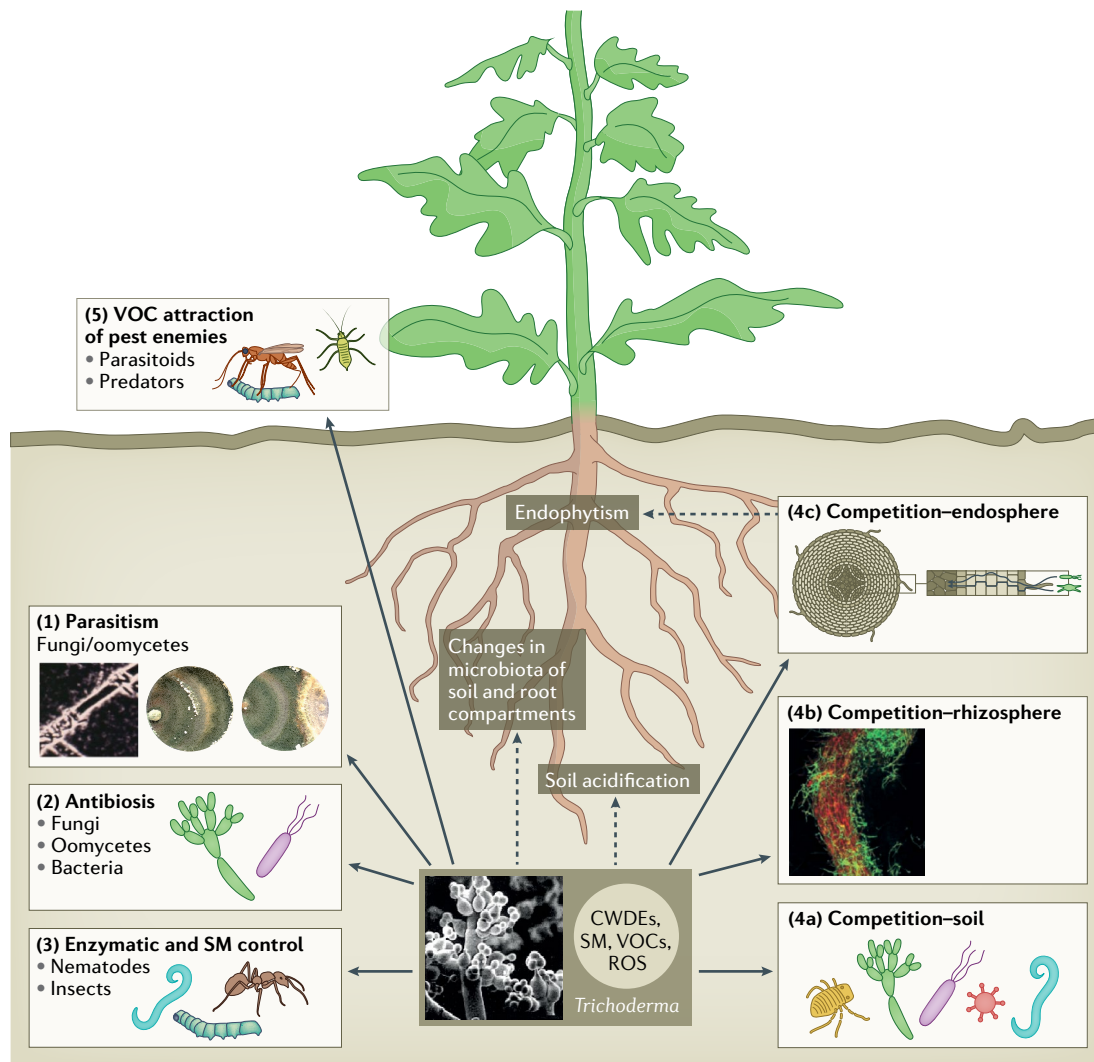
proliferation or plant pathogen attack; enzymatic activity (for example, chitinases) and production of secondary metabolites with biological activity against nematodes and insect pests; competition for ecological niches and resources (such as soil and mucigel nutrient uptake, ROS tolerance, growth on roots) that contribute to *Trichoderma* colonization of the soil, rhizosphere and endosphere (endophytism); and the production and release of VOCs can attract parasitoids and predators of insect pests. Moreover, a sixth mode of action for biocontrol (which is indirect rather than direct) involves the induction of immunity in the plant host, whereby *Trichoderma* activates plant defence responses and mechanisms that provide protection against biotic and abiotic stress (discussed below).

*Trichoderma* can directly control some economically important agricultural phytopathogen ascomycetes (*Botrytis*, *Colletotrichum*, *Erysiphe*, *Fusarium*, *Magnaporthe*, *Sclerotinia*, *Verticillium*), basidiomycetes (*Rhizoctonia*, *Athelia*, *Armillaria*, *Ustilago*, *Puccinia*) and oomycetes (*Pythium*, *Phytophthora*)<sup>72</sup>. Furthermore, different secondary metabolites can inhibit certain bacteria (*Clavibacter*, *Pseudomonas*, *Xanthomonas*)<sup>66,69,73</sup>. Genes associated with mycoparasitism, demonstrating transcriptional response to the prey<sup>4,74</sup>, and CWDEs produced by *Trichoderma* in interactions with phytopathogens have been extensively identified and have been proven to effectively inhibit spore germination, hyphal growth and the development of dormant fungal vegetative structures (such as sclerotia and chlamydospores) in a wide range of pathogens<sup>75</sup>. CWDEs, such as chitinases<sup>76</sup>, glucanases<sup>77–80</sup> and proteases<sup>74</sup>, alone or in combination<sup>81,82</sup>, have demonstrated their antagonistic role against plant pathogenic fungi and oomycetes (Supplementary Table 1).

*Trichoderma* produces >120 different types of secondary metabolite, with the most relevant chemical structures being terpenes, pyrones, polyketides and non-ribosomal peptides. Some of these secondary metabolites possess antibiotic activity, inhibiting the growth and multiplication of fungi<sup>66,83</sup>, oomycetes<sup>84,85</sup> and bacteria<sup>66,73</sup>. The application of purified secondary metabolites has biocontrol effects on target pathogens comparable to those obtained by using the living *Trichoderma* producer<sup>86</sup>. Secondary metabolites that can permeabilize cell membranes might work synergistically with CWDEs to promote cell disruption<sup>87</sup>. Although *Trichoderma* might be considered a necrotrophic mycoparasite that destroys its prey, microscopic evidence<sup>88</sup> demonstrates that the fungus might instead penetrate through open holes in the cell wall and not extensively damage the prey, thus using what might be called a hemi-biotrophic parasitic mode of action<sup>75</sup>.

*Trichoderma* has long been noted to have suppressive effects on *Meloidogyne* root-knot nematodes (RKN)<sup>89</sup>. Similar findings have been confirmed for other nematodes (*Heterodera*, *Haemonchus*, *Pratylenchus* or *Globodera*), whereby inhibition occurs via *Trichoderma* parasitism<sup>90</sup>, egg lysis by proteases<sup>91</sup> and chitinases<sup>92</sup>, or suppression of egg hatching by secondary metabolites<sup>73</sup>. Furthermore, *Trichoderma* has demonstrated direct biocontrol of insects through enzymatic activity on the midgut peritrophic matrix<sup>93</sup> and inhibition of cuticle formation<sup>94</sup>. In addition, extracts of secondary metabolites can have inhibitory effects on insect larvae<sup>95</sup>.

As competitors in the plant environment, *Trichoderma* spp. can interfere with or counteract the attack strategies used by phytopathogens to invade plants. For example, proteases secreted by *Trichoderma* can inhibit enzymes produced by pathogens to disrupt plant tissues for penetration<sup>96</sup>. Secondary metabolites produced by *Trichoderma* can downregulate the expression of pathogen genes involved in the pathogenicity process; for example, polyketides released by *Trichoderma arundinaceum* can modulate the phytotoxic sesquiterpenes



**Fig. 2 | *Trichoderma* as a direct biological control agent.** *Trichoderma* is found in the soil and plant root zone (rhizosphere), where it produces cell wall-degrading enzymes (CWDEs), secondary metabolites (SM), volatile organic compounds (VOCs) and reactive oxygen species (ROS), all of which permit the fungus to have diverse roles in crop protection. (1) Parasitism of phytopathogenic fungi and oomycetes. (2) Antibiosis by secondary metabolites inhibits growth of fungi, oomycetes and bacteria. (3) Control of nematodes and insects in the soil via enzymes (proteases, chitinases) and secondary metabolites. (4) *Trichoderma*

acidifies the soil and affects the structure and abundance of microbiota in soil and root compartments; in addition, its ability to take up nutrients, tolerate ROS and grow on roots, and its compatibility with other plant-beneficial microorganisms, enable it to compete successfully in the soil (4a), rhizosphere (4b) and endosphere (4c). *Trichoderma* colonization of the rhizosphere and root tissues (endophytism) inhibits the occupation of these spaces by potentially pathogenic microorganisms and nematodes. (5) VOCs produced by *Trichoderma* can attract parasitoids and predators of insect pests.

of *Botrytis cinerea* that are involved in virulence and growth<sup>97</sup>. A final biocontrol mechanism that is considered a direct effect by *Trichoderma* and not via the plant is the production of VOCs such as 6-PP, which are released in the environment and are able to attract parasitoids and predators of insect pests<sup>98</sup>.

## Indirect biocontrol and priming of defences

*Trichoderma* acts as an indirect BCA by activating plant immune responses (Fig. 3), resulting in a faster and stronger induction of defence mechanisms upon perception of a subsequent triggering stimulus (Box 2); this form of defence is known as priming<sup>99</sup>. By inducing priming, *Trichoderma* can provide the plant with long-lasting

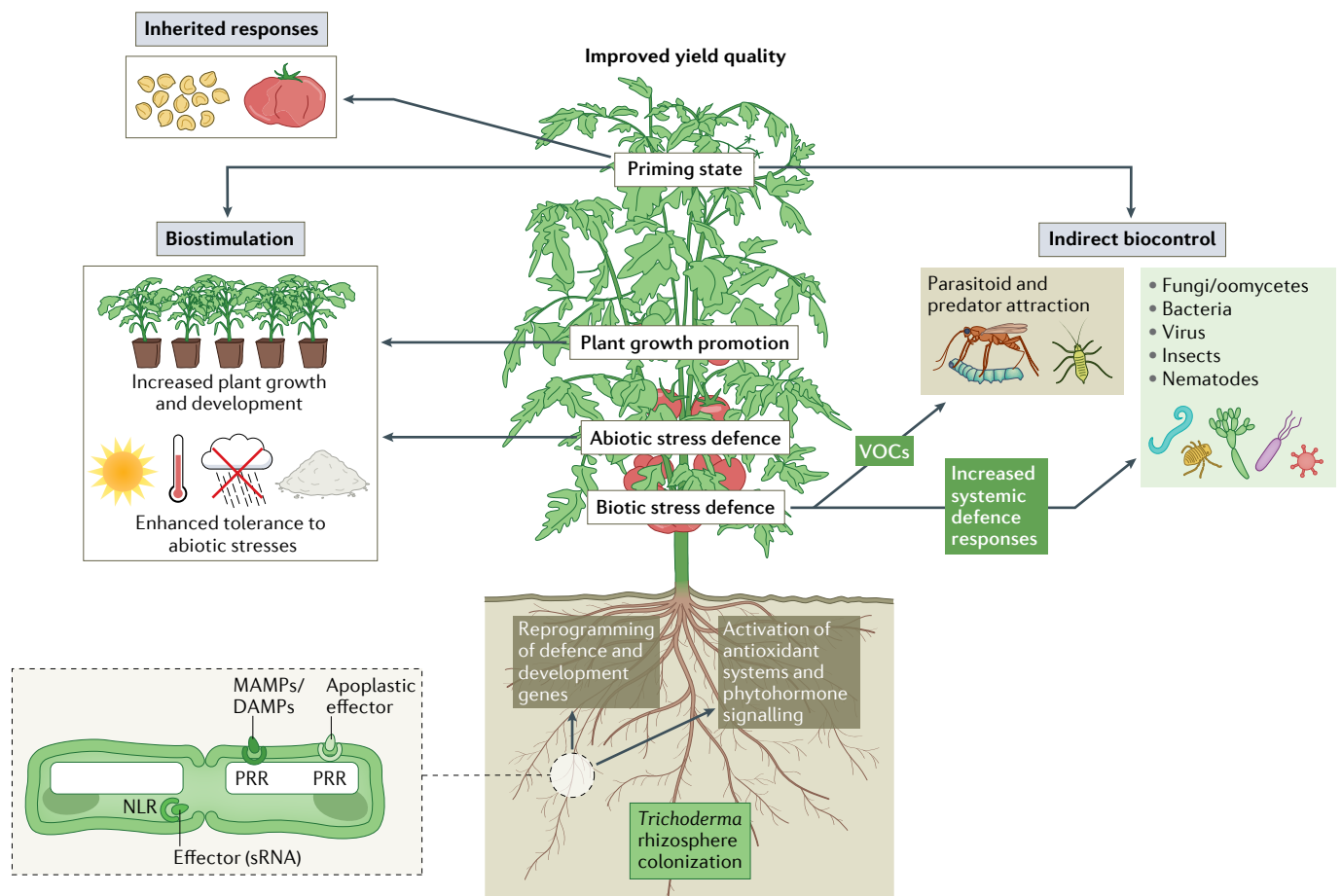
defence through the balance of different phytohormone-dependent pathways<sup>6</sup>. Priming is not exclusively associated with indirect biocontrol as reinforcement of plant responses to biotic and abiotic stresses are very similar in their genesis and establishment, although they are activated by stimuli of very different nature. The molecular interaction between *Trichoderma* and plants, and the manner in which signals are activated and systemically transmitted, have been the subject of several reviews<sup>6,7,100</sup>. Structural components of the *Trichoderma* cell wall and membrane (for example, chitin,  $\beta$ -glucans and sterols) act as microorganism-associated molecular patterns (MAMPs)<sup>36,101,102</sup>. Plant cell wall oligomers released by the hydrolytic activity of *Trichoderma* on plant tissues<sup>103</sup> or derivatives from its antagonistic biocontrol action of

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other microorganisms<sup>104</sup> might function as damage-associated molecular patterns, which, once recognized by pattern-recognition receptors (PRRs), activate MAMP-triggered immunity, which is stronger than pathogen-triggered immunity, thus conferring plant resistance<sup>3</sup>.

The plant reacts to the arrival of *Trichoderma* at the roots with an increase in levels of salicylic acid (a key phytohormone that controls early root colonization) to limit *Trichoderma* to the apoplastic space of the epidermis and cortex<sup>40,105</sup>. Next, *Trichoderma* increases the level of a second layer of plant immunity by means of an array of apoplastic effector proteins and metabolites such as xylanase EIX<sup>106</sup>, LysM protein Tal6 (ref.<sup>107</sup>), cerato-platanin Sm1 (ref.<sup>108</sup>), the peptaibol alamethicin<sup>109</sup>, and the terpenes trichodiene<sup>110</sup> and harzianum A<sup>111</sup>, among others<sup>112</sup>. The apoplastic effector-triggered defence is considered effector-triggered immunity regardless of whether it is activated at the PRR level.

The secreted effectors<sup>113</sup>, together with ROS tolerance, might enable endophytic colonization and allow *Trichoderma* to establish an avirulent relationship with the plant and long-lasting priming that keeps plant response at or just below the threshold for effective resistance<sup>3</sup> (Box 2). How the cytoplasmic nucleotide-binding site leucine-rich repeat (NLR) receptors interact with the effectors released by *Trichoderma* is not well understood. In tomato plants, NLR receptors are over-represented in the leaf proteome of plant roots inoculated with *T. atroviride* and *Rhizoctonia solani*<sup>114</sup>, and NLR genes have also been induced by harzianic acid released by *T. harzianum*<sup>86</sup>. NLR-like proteins are upregulated in the leaf maize proteome after the inoculation of roots with *T. afroharzianum*<sup>115</sup>. *Trichoderma* effectors are not known to be ligands for NLR, although the signal transduction and events that follow receptor activation by *Trichoderma* and their effects on plants



**Fig. 3 | *Trichoderma* as an indirect biological control agent, biostimulant and priming inducer.** Colonization of the rhizosphere by *Trichoderma* induces local and systemic defence responses in the plant. *Trichoderma* microorganism-associated molecular patterns (MAMPs) and damage-associated molecular patterns (DAMPs) are recognized by pattern-recognition receptors (PRRs) on the plant cell membrane, which also recognize apoplastic effectors secreted by *Trichoderma*. In addition, the release of small RNA (sRNA) by the fungus leads to upregulation of plant cytoplasmic nucleotide-binding site leucine-rich repeat (NLR) receptors. After *Trichoderma* recognition, the plant reprogrammes genes involved in defence and development, and activates antioxidant systems and phytohormone signalling that lead to biotic stress defence (indirect biocontrol) by increasing systemic immune responses to attack by fungi, oomycetes,

bacteria, viruses, insect herbivores and nematodes, as well as by releasing plant volatile organic compounds (VOCs) that are able to attract parasitoids and predators of insect pests; abiotic stress defence (biostimulation) that results in enhanced tolerance and adaptation to abiotic stresses (such as drought, salinity and extreme temperatures); plant growth promotion (biostimulation), whereby *Trichoderma* stimulates plant growth and development when the plant does not need the activation of the defence-immunity response; priming state, which activates a condition that provides long-lasting indirect biocontrol and biostimulation effects throughout the life of the plant; and inherited responses, in terms of defence and growth traits that can be passed on to offspring by transmission of genetic and epigenetic marks in the seeds. The overall positive results of *Trichoderma* in the soil are noted in improved crop yields and quality.

## Box 2

### Plant defence layers and the role of *Trichoderma* in priming defence

Plant cells individually auto-defend from invaders and then forward the defence signal to neighbouring cells, resulting in systemic transmission to the entire plant. The first layer of innate defence is regulated by pattern-recognition receptors (PRRs) situated on the plant cell surface that perceive structural components of the invaders known as pathogen-associated molecular patterns, microorganism-associated molecular patterns (MAMPs) and damage-associated molecular patterns (DAMPs; which are small molecules resulting from the hydrolytic action of the attackers on the plant or released by the action of biological control agents on their prey). MAMP-triggered immunity (MTI) or DAMP-triggered immunity is transmitted and amplified through cascades of mitogen-activated protein kinases, which convert external stimuli into intracellular responses, resulting in transcriptional reprogramming that leads to plant cell wall fortification; increases in levels of intracellular calcium; production of reactive oxygen species, antimicrobial secondary metabolites and pathogenesis-related proteins; and accumulation of defence phytohormones such as salicylic acid, jasmonic acid and ethylene. Attackers can overcome and suppress MTI by deploying specific effector proteins into the host cytoplasm. Plants activate a second specific defence layer, known as effector-triggered immunity (ETI), following cytoplasmic effector recognition by nucleotide-binding site leucine-rich repeat protein (NLR) receptors. ETI is quicker

and more intense than MTI and is associated with early oxidative burst and hypersensitive response cell death to prevent the invasion of pathogens.

Priming activated in the plant by *Trichoderma* (see figure) follows a different defence dynamic (green arrows) to the untreated control plant (red arrows). PRRs recognize *Trichoderma* MAMPs and host plant or *Trichoderma* prey DAMPs, which increases the level of MTI. *Trichoderma* induces a stronger and more intense defence than MTI via apoplastic effectors, which are also recognized by PRRs (ETI). The plant enters a state of priming in which defence responses are not activated but remain 'alert' around the threshold for effective resistance. With a stress challenge, there is a faster and stronger induction of plant defence from a level of resistance greater than that of the control plant. When the stress ceases, the *Trichoderma*-treated plant enters a post-challenge priming state in which the defence level is once again maintained around the threshold for effective resistance. The response events are stored in the 'transcriptional memory' of the plant, which discriminates between single and repeated stresses, and can modulate transcription of response genes to future stress during the current lifetime of the plant (to the dotted line). Subsequently, offspring from the *Trichoderma*-treated plant acquire an inherited memory, whereby, when exposed to stress, they can activate heritable priming also at a level of effective resistance.

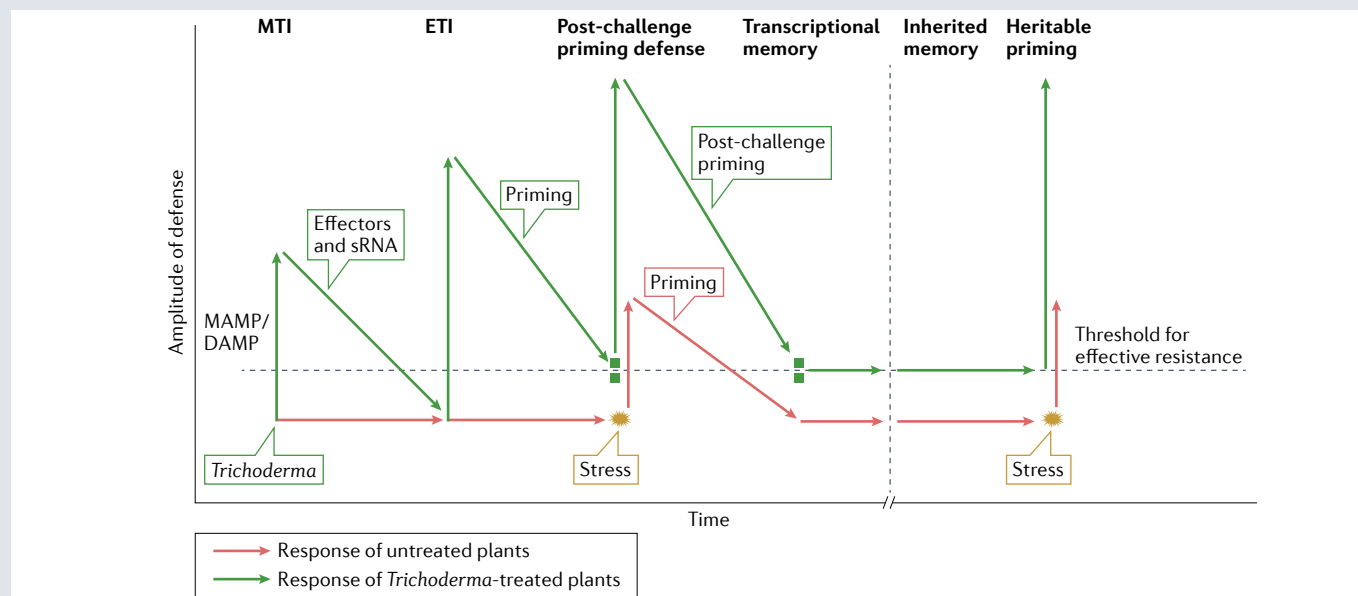


Figure adapted from ref.<sup>161</sup>, Springer Nature Limited; and based on knowledge of previous studies<sup>3121,132</sup>. sRNA, small RNA.

are increasingly being studied and understood, including the potential role of bidirectional cross-kingdom small RNA trafficking<sup>7,112</sup>.

The salicylic acid-dependent defences that limit early growth of *Trichoderma* can spread throughout the plant, constituting a defence

model known as systemic-acquired resistance, which has been found to be effective against biotrophic pathogens<sup>116</sup>. *Trichoderma* suppresses salicylic acid defences and induces jasmonic acid biosynthesis and jasmonic acid-responsive genes, which are expressed in the root cells, thus



generating a signal that spreads systemically<sup>102</sup>. This defence model is known as jasmonic acid–ethylene-dependent induced systemic resistance and is especially effective against necrotrophic pathogens and herbivore attack<sup>116</sup>. To colonize the roots, *Trichoderma* takes advantage of the antagonism between salicylic acid and jasmonic acid<sup>102</sup>. Pioneering work demonstrated that cucumber roots colonized by *T. asperellum* accumulated substantial levels of jasmonic acid and ethylene in 24 h (ref.<sup>117</sup>), supporting the notion that priming activated by beneficial microorganisms conforms to an induced systemic resistance response<sup>116</sup>. However, evidence suggests that *Trichoderma*-triggered defences against pathogenic fungi and even viruses are modulated by both jasmonic acid–ethylene and salicylic acid<sup>111,118,119</sup>.

Improved plant fitness, as promoted by *Trichoderma*, also prevents nematode access to the roots<sup>120</sup>. In tomato roots in which RKN complete their life cycle, *Trichoderma* reprogrammes plant immunity by adapting salicylic acid-dependent and jasmonic acid-dependent defences according to the nematode infection stage<sup>121,122</sup>. As a general mechanism, *Trichoderma* also primes defences by different means and at diverse frequencies in leaves and roots via small RNA-mediated gene silencing and by inducing the transcription of core components of the RNA-dependent DNA methylation machinery that sharpens the expression of both salicylic acid and jasmonic acid–ethylene defence-related genes<sup>123</sup>.

Another indirect biocontrol mechanism of *Trichoderma* is the activation of plant systemic defences by VOCs, in which their release results in an oxidative burst that is effective against aphids<sup>124</sup>. *Trichoderma* can also enhance the expression of genes encoding for protective enzymes against moths<sup>125</sup>. Furthermore, *Trichoderma* is able to alter plant metabolic pathways leading to the induction of various plant systemic defences<sup>126</sup> such as the production of phytochemicals that act as anti-feed deterrents<sup>127,128</sup> or negatively affect the insect gut proteome equilibrium<sup>129</sup>, activate the release of plant VOCs with high attractivity to parasitoids and predators of aphids<sup>124,130</sup>, or decrease feeding by herbivorous insects<sup>131</sup>.

The speed and efficiency at which plants adapt to their surroundings might also be facilitated by *Trichoderma* given that it has a role in balancing defences and growth as well as alleviating the effects of unfavourable environmental conditions. Abiotic stress-mediated phytohormones share common regulators with MAMPs and/or damage-associated molecular patterns. However, in natural settings in which plants are exposed to a mix of stimuli, PRR pathways display a substantial divergence in sensitivity to biotic or abiotic perturbations and signal transduction. Given that abiotic stresses modify water fluxes, solute concentrations and ion homeostasis, the Ca<sup>2+</sup> pumps or channels required for PRR-dependent defences have an important role in regulating potential gradients across membranes and conditioning plant immunity<sup>132</sup>. Abiotic stress sensing induces cytoplasmic Ca<sup>2+</sup> accumulation, leading to an extracellular ROS burst and activation of Ca<sup>2+</sup>-dependent protein kinase cascades; these mechanisms enable the plant to cope with the variation in ambient conditions by prioritizing functions involved with plant growth regulation and responses to environmental stresses<sup>132</sup>. A hydrophobin secreted by *Trichoderma* triggers the plant Ca<sup>2+</sup> signalling pathway<sup>133</sup>, which opens up an interesting line of research on G protein recognition and signalling activation and/or deactivation that is compatible with the effects that *Trichoderma* has on plants<sup>7</sup>.

Early studies described how *Trichoderma* favours the production of plant metabolites associated with increased drought tolerance<sup>37,134</sup> and how its enhancement of antioxidant defence delays the onset of a water-deficit response<sup>19</sup>. Numerous reports illustrated that *Trichoderma* could affect ROS scavenging and has 1-amino-1-cyclopropane-carboxylic

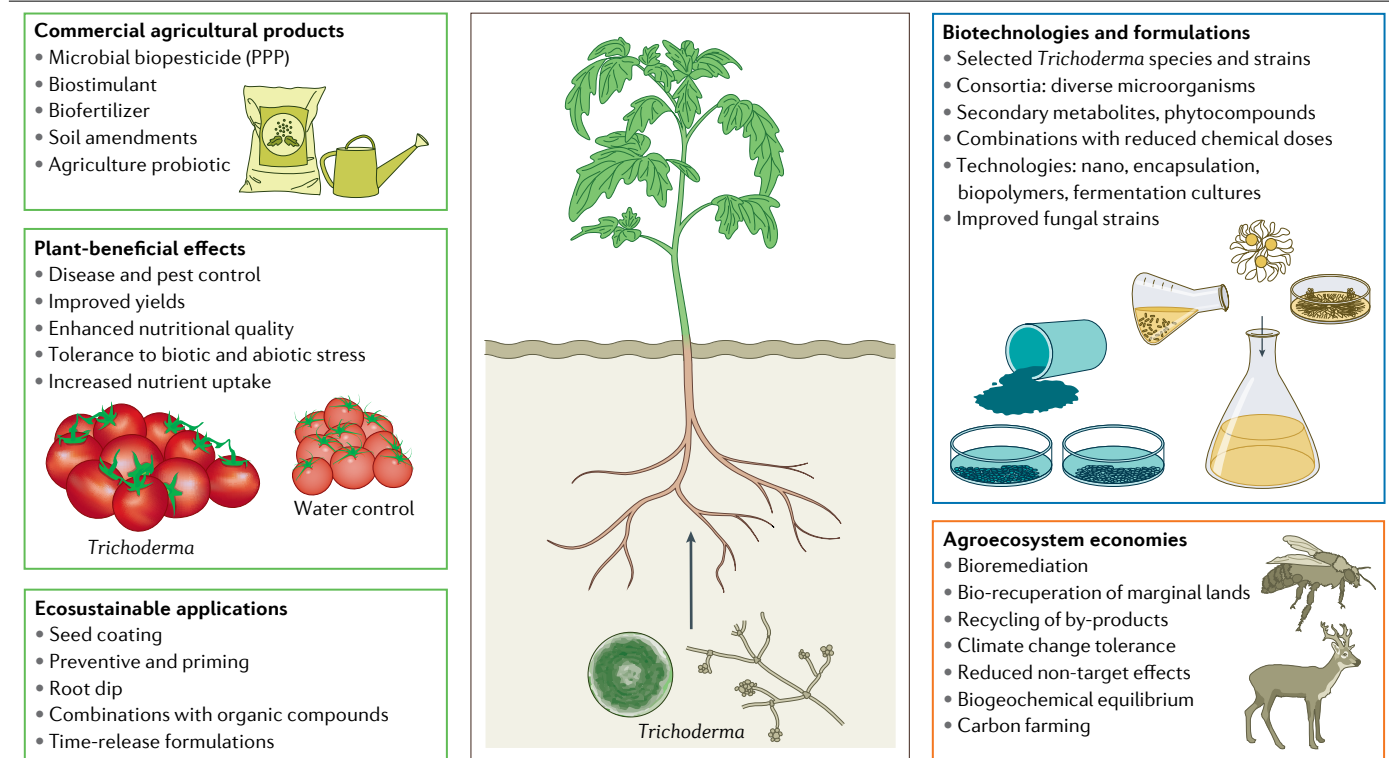
acid deaminase (ACCD) activity leading, respectively, to activation of plant antioxidant machinery and regulation of plant ethylene levels under drought, waterlogging, and osmotic, salinity, chilling, or heat stress<sup>135–138</sup>. *Trichoderma* also increased plant growth and salt tolerance by direct contact<sup>102</sup> or through VOCs<sup>139</sup>. However, the promotion of growth and development triggered by the combination of *Trichoderma* and inorganic fertilizers to salt-stressed plants led to a dysregulation of the phytohormone network as overstimulated plants in suboptimal conditions were unable to adapt to the contradictory signalling<sup>140</sup>. Without a doubt, plant–*Trichoderma* crosstalk is dynamic and the expression of salicylic acid and jasmonic acid–ethylene-dependent defence genes might overlap in an undulating pattern that responds to both biotic and abiotic stresses<sup>14,141</sup>. This plant effect disappears over time, becoming imperceptible several weeks after the plant has been in contact with *Trichoderma*<sup>142</sup>. Given that the plant–*Trichoderma* interaction varies with timing and the plant and/or fungal species-strain involved, time course studies are needed to determine which transduced signal for each specific plant response is prevalent at a given time.

Once the *Trichoderma*-activated priming signals gradually disappear, the plant activates a ‘transcriptional memory’, in which cells previously primed by a particular stimulus show increased rates of gene expression upon subsequent re-stimulation<sup>143</sup>. The capacity for defence priming can be inherited, generating a second level of memory known as ‘heritable priming’, that can be passed-on to the offspring (Box 2). These next-generation plants express a stronger defence response than offspring of un-primed plants<sup>144</sup>. The beneficial action that *Trichoderma* has on plants is modulated by molecular networks that condition the immediate and long-lasting systemic responses, orchestrating the metabolic trade-offs between plant growth and defence<sup>7</sup>; for example, in the *Trichoderma*–tomato–RKN interaction, the tomato progeny inherit both resistance to RKN as well as growth-promotion effects without compromising the level of defence in the plant offspring in responding to the nematode attack<sup>121</sup>.

## Applications in agriculture

Modern agriculture policies have been radically changed by the Sustainable Development Goals of the 2015 UN General Assembly, which were later focused on food and agriculture as the key factors to address concerns regarding fertilizer handling, pesticide use and management practices<sup>145</sup>. Climatic changes and intensive agricultural practices have created biodiversity loss, changes in the geographic distribution of plant-damaging pests and pathogens, and contamination of soil, air and water resources by chemicals that negatively impact not only the agroecosystem but also human health<sup>146</sup>. Progressive modifications in agricultural policies are aimed at reducing the use of synthetic chemical products; thus, the growing importance of plant-beneficial *Trichoderma* in this process is apparent from its increased use as a biological alternative to agrochemicals and the intensified research linking the fungus to ‘sustainable agriculture’ as noted in the recent literature searches conducted for this review<sup>38,44,48,71,72</sup>. *Trichoderma* has become a popular protagonist as the key component of plant biostimulants, bioprotectants, biofertilizers, soil amendments, soil integrators, biodegraders and bioremediators<sup>147</sup> (Fig. 4; Supplementary Table 2).

*Trichoderma* has remained as a renowned BCA of phytopathogens and as a mycoparasite that uses direct antagonism and other mechanisms in the biocontrol of important plant diseases. Therefore, it is of no surprise that *Trichoderma* is the active BCA substance in many commercial preparations registered as plant protection products (PPPs). In general, authorization as a microbial BCA can only be



**Fig. 4 | Overview of the (potential) contribution of *Trichoderma* to eco-sustainable agriculture.** Green border: available commercial products containing *Trichoderma*, their plant-beneficial effects and different application approaches for efficient and sustainable use of resources. Blue border: potential strategies for producing more efficient *Trichoderma* products by using biotechnologies based

on industrial fermentation processes, or manipulation of different living plant-beneficial microorganisms and bioactive components in formulation preparations. Orange border: prospective uses of *Trichoderma* applications to enhance agricultural sustainability, improve agroecosystem equilibrium, and contribute to green and circular economies. PPP, plant protection product.

provided by the appropriate designated institutions after passing a rigorous evaluation process (for efficacy and safety) to support its claims as a PPP, a procedure following that used for chemical phytosanitary products. The usefulness of *Trichoderma* is demonstrated by the increase from 21 BCA registrations, with strains of 8 *Trichoderma* species, worldwide in 2014 (ref.<sup>72</sup>) to 144 global registrations in 40 countries, comprised of 11 *Trichoderma* species and 44 strains, that are available in 10 diverse product formulations (as noted in an internet search conducted for this Review (2022); Supplementary Table 2). This survey indicated that Brazil has the most active market (28% of total registrations), followed by Colombia (18%), then consolidated European Union (15% in 22 countries). The information provided about the manufactured products from India and China, the biggest Asian consumers of *Trichoderma*-based products, as well as the developing markets in Central and South America are not fully complete owing to the diverse registration procedures used by the regulatory authorities in comparison to the European and North American counterparts. For instance, in India, many governmental research institutions are funded to isolate and test 'agriculturally important microbes' for bioefficacy and to then develop the dossier for registration by the Central Insecticides Board and Registration Committee. Any company can buy the dossier, strain, technology transfer and training, submit for registration, and then manufacture their own product. Currently, in India, this process is only possible for the species *T. viride* and *T. harzianum*. The product claims for the *Trichoderma* microbial biofungicide correspond

to the control of phytopathogens as previously mentioned for direct BCAs and for use in a large variety of crops, including vegetables, field crops (such as wheat, rice, bean and soya), soft fruits, ornamentals and flowers, herbs and aromatics, golf course turf, arboriculture, coffee, orchards and grapevines (Supplementary Table 2).

Although many *Trichoderma* species and strains have been registered for use as PPPs and have recognized plant growth-promotion effects, by definition, they cannot be registered or commercially distributed as plant biostimulants in Europe<sup>147</sup>. The regulatory framework varies by country and, in some nations, *Trichoderma* strains are allowed to be marketed with claims as plant inoculants, strengtheners or biostimulants, irrespective of whether the active substances exert direct or indirect biocontrol and without an evaluation process verifying efficacy. Policy-makers are still investigating whether the multipurpose use of *Trichoderma* species, as both PPPs and biostimulants, is possible and how this can be regulated given that the capacity of many *Trichoderma* strains to exert indirect biocontrol and to act as biostimulants is determined by the plant host, depending upon which process the plant exploits (defence versus growth), and by various stimuli in the agroecosystem. This dilemma with *Trichoderma* is an important issue to be faced for future regulation revisions. Given that scientific evidence supports the validity of *Trichoderma* applications both for biocontrol and biostimulation effects together (and just singly), it is time to unify the legal framework regarding these non-harmful and agriculturally useful fungi, defining them as 'plant-beneficial microorganisms'.

## Eco-sustainable agriculture

To increase the general success and implementation of biological products in eco-sustainable agriculture, the focus needs to be on improving their shelf life, efficacy and standards to a level similar to that of chemical products used to date<sup>71</sup>. Strategies aimed at improving the yield of conidia and chlamydospores and their stress tolerance are of great importance for the development of cost-effective and durable agricultural applications of *Trichoderma*. Technologies to produce an ideal *Trichoderma* product for agriculture should exploit its multipurpose assets by selecting species or strains that have potential biocontrol, rhizosphere competence, endophytic colonization characteristics, and can induce disease resistance and/or promote plant growth (Box 3 and Fig. 4). Components of microbial consortia can include *Trichoderma* species or strains alone with different capabilities, or compatible combinations with other plant-beneficial microorganisms such as biocontrol bacteria (*Bacillus*, *Pseudomonas*) and/or other fungi (*Coniothyrium*, non-pathogenic *Fusarium* or *Rhizoctonia*), entomopathogenic fungi (*Beauveria*, *Metarhizium*), nematode trapping fungi (*Arthrobotrys*, *Dactylellina*, *Drechslerella*), mycorrhizal fungi (AMF, ectomycorrhizal fungi, *Serendipita*), and/or plant growth-promoting rhizobacteria (*Azotobacter*, *Azospirillum*, *Bacillus*, *Pseudomonas*)<sup>47</sup> (Supplementary Table 2). Bioformulations could contain living *Trichoderma* plus bioactive compounds from other microbial and/or botanical sources (such as algae or phyto-extracts) or with natural carriers to improve application efficacy<sup>72</sup>. For example, *Trichoderma*, its secondary metabolites (such as 6-PP), phytohormones, plant extracts and polymers (such as cellulose, galactomannan or chitosan) have been tested successfully for biocontrol and/or plant growth-promotion effects<sup>148–150</sup>. To this end, the search, selection and practical use of synthetic communities generated from *Trichoderma*-based root microbiomes<sup>20</sup> or synthetic communities from *Trichoderma*-fostered microbiomes<sup>47</sup> will be important in developing new generation biofertilizers and agricultural probiotics to aid microbiota recruitment or restoration, particularly where intensively cultivated lands suffer from soil fatigue.

With regard to future agricultural mandates aimed at reducing the use of chemical products in farm management, the selection of *Trichoderma* strains tolerant to agrochemicals and compatible with inorganic fertilizers will be a useful strategy<sup>151</sup>. Industrial processes can use technologies to improve *Trichoderma* qualities by inducing the production of bioactive compounds responsible for the beneficial effects in agricultural production or protecting these qualities during fermentation<sup>152,153</sup>. Other innovations include encapsulation and nanoparticle technologies<sup>154</sup> for the delivery and dissemination of *Trichoderma* spore inoculum and/or the compounds produced, which could be important during the preparation of fermentation culture supernatants and application over extensive cultivated areas. *Trichoderma* has a role in the present transitions in agriculture towards a green economy (to reduce environmental impacts and ensure food safety) and a circular economy (to recycle agri-food waste to produce value-added products, such as substrate sources to cultivate plant-beneficial microorganisms, including *Trichoderma*, or organic matter formulations, with/without these microorganisms, for direct application as soil amendments). Biotechnological advances might permit the safe and widespread use of *Trichoderma* gene expression in plants to confer increased resistance to pathogens<sup>155</sup> and tolerance to abiotic stresses<sup>156</sup>, thus reducing the use of agrochemicals and improving the ability of crops to overcome adverse environmental conditions.

The ongoing findings in *Trichoderma* research prompt a reflection on the effective use of this fungus in agriculture and the development of practical uses with selected potential strains (Fig. 4). New applications

include crop cultivation in marginal lands, improved crop resilience to unfavourable climate changes<sup>157</sup>, bioremediation for the reduction of pollutants in contaminated sites<sup>158</sup>, and a general contribution to the reduction of methane and carbon dioxide emissions in the atmosphere<sup>38</sup>.

## Conclusions

This article has provided an overview of the advances in *Trichoderma* research that support its applications as a successful BCA and plant biostimulant for improved crop protection and production. Notable changes have occurred in the systematics of the genus-species complex that will affect the nomenclature and how the fungal group is recognized and nominated, subsequently influencing species or strain selection for use in biotechnological development. Progress is also noted in scientific investigations regarding the multitrophic, interkingdom relationships that *Trichoderma* establishes in the agroecosystem; the evolutionary events that have given rise to rhizosphere and endophytic colonization of the host plant; and interactions with the plant microbiota and other non-target organisms that affect the surrounding soil ecology, influence plant growth, and contribute to environmental and human well-being. However, the most exciting scientific discoveries – made possible with modern omics techniques – are those offering insights into the plant

### Box 3

## Ideal characteristics of a *Trichoderma*-based product for future sustainable agriculture

The ideal commercial product based on *Trichoderma* will be multifunctional and capable of the following diverse beneficial effects for agriculture:

1. Direct biocontrol of plant pathogens and pests, thus reducing the need for chemical pesticides
2. Multiple capabilities for crop protection in a single product, exhibiting a broad spectrum of biocontrol activity against pathogenic microorganisms, nematodes and insects
3. Activation of plant defence mechanisms providing indirect biocontrol of plant pathogens and pests
4. Activation of plant defence mechanisms that increase tolerance to abiotic stress
5. Activation of plant defence priming against biotic and abiotic stresses at the time of attack or damage, which can activate over time and has a long-term duration
6. Provision of heritable beneficial traits in seedbed and nursery plants
7. Stimulation of plant growth to increase crop productivity and yields
8. Improvement of soil nutrient availability and fertilization, leading to increased plant uptake and assimilation
9. Improvement of quality of harvested products by increasing nutritional values and storage attributes
10. Decreased use of chemical products in agriculture, thus reducing risks to the environment and consumer health

## Glossary

### Agroecosystem

An ecosystem subjected to anthropological activities that are finalized in agricultural production involving the continuous manipulation of biotic and abiotic components to obtain maximum yields and quality of the produce such as food, textile and biofuel plant products, and animal goods.

### Biofertilizers

Products that contain living organisms that promote plant growth by increasing the supply or availability of primary nutrients to the host plant.

### Biological control agent

(BCA). A natural enemy or antagonistic organism used in plant protection that can inhibit or eliminate harmful organisms and their negative effects through direct or indirect mechanisms of parasitism, antibiosis, competition or induced plant defence.

### Bioprotectants

Biological tools providing the protection of plants or the environment from biotic and/or abiotic stress by methods of biocontrol or bioremediation.

### Biostimulant

A biological product used to improve plant nutrient use efficiency, tolerance to abiotic stress, quality traits or availability of confined nutrients in the soil by using components of microbial or non-microbial origins.

responses to this fungus guest, including induced defence responses that provide indirect biocontrol to a variety of phytopathogens, the effects on priming and plant memory, and increased tolerance to a diverse range of biotic and abiotic stresses. *Trichoderma* is a model system for studying and deciphering the beneficial microorganism–plant and microorganism–microorganism interactions that these fungi establish among themselves and their surroundings.

Without a doubt, *Trichoderma* is a fascinating microorganism – an opportunist that is versatile and in continuous evolution, a true survivor of the multitude of ecological changes over the millennia. The main question that arises is, how can we harness *Trichoderma* diversity to develop long-term efficient strategies to improve agricultural production and protection? Can adverse climatic conditions be counteracted with *Trichoderma*? Can *Trichoderma* help assure global food security? Can agriculture truly become auto-sufficient by using alternative biological solutions such as *Trichoderma* without the implementation of synthetic

### Eco-sustainable agriculture

A system that generates increasing prosperity by reducing chemical inputs and implementing alternative methods to minimize negative impacts to the environment, biodiversity, and human and animal health, thus permitting the renewal of natural resources.

### Plant protection products

(PPPs). Products consisting of an approved active substance (chemical or biological) with the capacity to protect plants or plant products against harmful organisms, that positively influence the life processes of plants, preserve plant products, destroy undesired plants or parts of plants, or control or prevent undesired growth of plants.

### Priming

An adaptive strategy improving plant defence capacity whereby an initial stimulus activates the physiological, transcriptional, metabolic and epigenetic mechanisms that enable the plant to respond more rapidly and/or efficiently to subsequent exposure to biotic or abiotic stress.

chemicals? How can optimal *Trichoderma* species or strains be selected, formulated and applied to obtain consistent efficacy? At present, the major bottleneck to the development of innovative *Trichoderma*-based products is how to overcome the restrictions imposed by registration and authorization procedures, including inflexible terminology and definitions; inadequate consideration of the variable characteristics of living biological organisms (they are not single purified elements) and the differing effects depending upon interactions between organisms; slow dossier evaluation; and limited communication among researchers, policy-makers, stakeholders and end users. These restrictions are in direct contrast to the legislative policies for agriculture of the future, as mandated by many governments globally, aiming to find solutions in the short-term that provide alternatives to synthetic chemicals, minimize negative impacts to the environment, develop green and circular economies, and implement a One Health approach (a concept that aims to optimize the health of people, animals and the environment). Multidisciplinary investigations are needed to understand the multipurpose properties of *Trichoderma* to maximize the benefits from this green fungus, thus leading to improved quality of life and safe, eco-sustainable agriculture.

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## References

1. Chaverri, P., Castlebury, L. A., Overton, B. E. & Samuels, G. J. *Hypocrea/Trichoderma*: species with conidiophore elongations and green conidia. *Mycologia* **95**, 1100–1140 (2003).
2. Harman, G. E., Howell, C. R., Viterbo, A., Chet, I. & Lorito, M. *Trichoderma* species-opportunistic, avirulent plant symbionts. *Nat. Rev. Microbiol.* **2**, 43–56 (2004).
3. Lorito, M., Woo, S. L., Harman, G. E. & Monte, E. Translational research on *Trichoderma*: from 'omics to the field. *Annu. Rev. Phytopathol.* **48**, 395–417 (2010).  
**Review of early *Trichoderma* expressomes that have led to a better understanding of their complex interactions with other living organisms and their potential importance in agriculture and industry.**
4. Kubicek, C. P. et al. Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome Biol.* **12**, R40 (2011).
5. Druzhinina, I. S. et al. *Trichoderma*: the genomics of opportunistic success. *Nat. Rev. Microbiol.* **9**, 749–759 (2011).
6. Hermosa, R., Viterbo, A., Chet, I. & Monte, E. Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* **158**, 17–25 (2012).  
***Trichoderma*–plant cross-talk model showing phytohormone homeostasis in the control of plant development and immune responses.**
7. Morán-Díez, M. E., Martínez de Alba, Á. E., Rubio, M. B., Hermosa, R. & Monte, E. *Trichoderma* and the plant heritable priming responses. *J. Fungi* **7**, 318 (2021).  
**Description of *Trichoderma*-induced priming stages in plants and summary of the main regulatory nodes in the transcriptional network of systemic defence and growth promotion triggered by *Trichoderma*.**
8. Cai, F. & Druzhinina, I. S. In honor of John Bissett: authoritative guidelines on molecular identification of *Trichoderma*. *Fungal Divers.* **107**, 1–69 (2021).  
**Unified criteria for molecular identification and systematics of *Trichoderma* species.**
9. Chaverri, P. & Samuels, G. J. Evolution of habitat preference and nutrition mode in a cosmopolitan fungal genus with evidence of interkingdom host jumps and major shifts in ecology. *Evolution* **67**, 2823–2837 (2013).
10. Druzhinina, I. S. et al. Massive lateral transfer of genes encoding plant cell wall-degrading enzymes to the mycoparasitic fungus *Trichoderma* from its plant-associated hosts. *PLoS Genet.* **14**, e1007322 (2018).
11. Kubicek, C. P. et al. Evolution and comparative genomics of the most common *Trichoderma* species. *BMC Genomics* **20**, 485 (2019).
12. Vajda, V. & McLoughlin, S. Fungal proliferation at the cretaceous-tertiary boundary. *Science* **303**, 1489 (2004).
13. Wen, C., Xiong, H., Wen, J., Wen, X. & Wang, C. *Trichoderma* species attract *Coptotermes formosanus* and antagonize termite pathogen *Metarhizium anisopliae*. *Front. Microbiol.* **11**, 653 (2020).
14. Rubio, M. B. et al. Identifying beneficial qualities of *Trichoderma parareesei* for plants. *Appl. Environ. Microbiol.* **80**, 1864–1873 (2014).  
**The beneficial effects of *Trichoderma* are more apparent in plants subjected to some type of stress; *Trichoderma*-induced plant phytohormone signalling follows an undulating dynamic, which decreases in amplitude with time.**
15. Vargas, W. A. et al. Role of gliotoxin in the symbiotic and pathogenic interactions of *Trichoderma virens*. *Microbiology* **160**, 2319–2330 (2014).
16. Montero-Barrientos, M., Hermosa, R., Cardoza, R. E., Gutiérrez, S. & Monte, E. Functional analysis of the *Trichoderma harzianum nox1* gene, encoding an NADPH oxidase, relates production of reactive oxygen species to specific biocontrol activity against *Pythium ultimum*. *Appl. Environ. Microbiol.* **77**, 3009–3016 (2011).

17. Villalobos-Escobedo, J. M. et al. The fungal NADPH oxidase is an essential element for the molecular dialog between *Trichoderma* and Arabidopsis. *Plant J.* **103**, 2178–2192 (2020).
18. Lombardi, N. et al. Root exudates of stressed plants stimulate and attract *Trichoderma* soil fungi. *Mol. Plant Microbe Interact.* **31**, 982–994 (2018).
19. Mastouri, F., Björkman, T. & Harman, G. E. *Trichoderma harzianum* enhances antioxidant defense of tomato seedlings and resistance to water deficit. *Mol. Plant Microbe Interact.* **25**, 1264–1271 (2012).
20. Pedrero-Méndez, A. et al. Why is the correct selection of *Trichoderma* strains important? The case of wheat endophytic strains of *T. harzianum* and *T. simmonsii*. *J. Fungi* **7**, 1087 (2021).
21. Hernández-Oñate, M. A., Esquivel-Naranjo, E. U., Mendoza-Mendoza, A., Stewart, A. & Herrera-Estrella, A. H. An injury-response mechanism conserved across kingdoms determines entry of the fungus *Trichoderma atroviride* into development. *Proc. Natl Acad. Sci. USA* **109**, 14918–14923 (2012).
22. Pola-Sánchez, E. et al. A global analysis of photoreceptor-mediated transcriptional changes reveals the intricate relationship between central metabolism and DNA repair in the filamentous fungus *Trichoderma atroviride*. *Front. Microbiol.* **12**, 724676 (2021).
23. Montero-Barrientos, M. et al. Overexpression of a *Trichoderma* HSP70 gene increases fungal resistance to heat and other abiotic stresses. *Fungal Genet. Biol.* **45**, 1506–1513 (2008).
24. Ruocco, M. et al. Identification of a new biocontrol gene in *Trichoderma atroviride*: the role of an ABC transporter membrane pump in the interaction with different plant-pathogenic fungi. *Mol. Plant Microbe Interact.* **22**, 291–301 (2009).
25. Vinale, F. et al. Harzianic acid: a novel siderophore from *Trichoderma harzianum*. *FEMS Microbiol. Lett.* **347**, 123–129 (2013).
26. Sarkar, D. & Rakshit, A. Bio-priming in combination with mineral fertilizer improves nutritional quality and yield of red cabbage under Middle Gangetic Plains, India. *Sci. Hortic.* **283**, 110075 (2021).
27. Li, R. X. et al. Solubilisation of phosphate and micronutrients by *Trichoderma harzianum* and its relationship with the promotion of tomato plant growth. *PLoS ONE* **10**, e0130081 (2015).
28. Bononi, L., Chiamonte, J. B., Pansa, C. C., Moitinho, M. A. & Melo, I. S. Phosphorus-solubilizing *Trichoderma* spp. from Amazon soils improve soybean plant growth. *Sci. Rep.* **10**, 2858 (2020).
29. Vinale, F. et al. A novel role for *Trichoderma* secondary metabolites in the interactions with plants. *Physiol. Mol. Plant Pathol.* **72**, 80–86 (2008).
- Demonstration of the role of *Trichoderma*-produced secondary metabolites on the plant for biological control of pathogens, induced plant resistance and plant growth promotion.**
30. Garnica-Vergara, A. et al. The volatile 6-pentyl-2H-pyran-2-one from *Trichoderma atroviride* regulates *Arabidopsis thaliana* root morphogenesis via auxin signaling and ETHYLENE INSENSITIVE 2 functioning. *N. Phytol.* **209**, 1496–1512 (2016).
31. Guzmán-Guzmán, P., Porras-Troncoso, M. D., Olmedo-Monfil, V. & Herrera-Estrella, A. *Trichoderma* species: versatile plant symbionts. *Phytopathology* **109**, 6–16 (2019).
32. Illescas, M., Pedrero-Méndez, A., Pitorini-Bovolini, M., Hermosa, R. & Monte, E. Phytohormone production profiles in *Trichoderma* species and their relationship to wheat plant responses to water stress. *Pathogens* **10**, 991 (2021).
33. Contreras-Cornejo, H. A., Macías-Rodríguez, L., Cortés-Penagos, C. & López-Bucio, J. *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in Arabidopsis. *Plant Physiol.* **149**, 1579–1592 (2009).
- Demonstration of the important role of auxin signalling in plant growth promotion by *Trichoderma*.**
34. Pelagio-Flores, R., Esparza-Reynoso, S., Garnica-Vergara, A., López-Bucio, J. & Herrera-Estrella, A. *Trichoderma*-induced acidification is an early trigger for changes in Arabidopsis root growth and determines fungal phytostimulation. *Front. Plant Sci.* **8**, 822 (2017).
35. Samolski, I., Rincón, A. M., Pinzón, L. M., Viterbo, A. & Monte, E. The *gid74* gene from *Trichoderma harzianum* has a role in root architecture and plant biofertilization. *Microbiology* **158**, 129–138 (2012).
36. Malmierca, M. G. et al. Trichodiene production in a *Trichoderma harzianum* *erg1*-silenced strain provides evidence of the importance of the sterol biosynthetic pathway in inducing plant defense-related gene expression. *Mol. Plant Microbe Interact.* **28**, 1181–1197 (2015).
37. Bae, H. et al. The beneficial endophyte *Trichoderma hamatum* isolate DIS 219b promotes growth and delays the onset of the drought response in *Theobroma cacao*. *J. Exp. Bot.* **60**, 3279–3295 (2009).
38. Harman, G. E. & Uphoff, N. Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. *Scientifica* **2019**, 9106395 (2019).
39. Tseng, Y. H. et al. An endophytic *Trichoderma* strain promotes growth of its hosts and defends against pathogen attack. *Front. Plant Sci.* **11**, 573670 (2020).
40. Carrero-Carrón, I. et al. Interactions between *Trichoderma harzianum* and defoliating *Vectidinium dahliae* in resistant and susceptible wild olive clones. *Plant Pathol.* **67**, 1758–1767 (2018).
41. Zachow, C. et al. Fungal diversity in the rhizosphere of endemic plant species of Tenerife (Canary Islands): relationship to vegetation zones and environmental factors. *ISME J.* **3**, 79–92 (2009).
42. Zachow, C., Berg, C., Müller, H., Monk, J. & Berg, G. Endemic plants harbour specific *Trichoderma* communities with an exceptional potential for biocontrol of phytopathogens. *J. Biotechnol.* **235**, 162–170 (2016).
43. Zhang, F. et al. *Trichoderma* biofertilizer links to altered soil chemistry, altered microbial communities, and improved grassland biomass. *Front. Microbiol.* **9**, 848 (2018).
44. Fiorentino, N. et al. *Trichoderma*-based biostimulants modulate rhizosphere microbial populations and improve N uptake efficiency, yield, and nutritional quality of leafy vegetables. *Front. Plant Sci.* **9**, 743 (2018).
45. Illescas, M. et al. Effect of inorganic N top dressing and *Trichoderma harzianum* seed-inoculation on crop yield and the shaping of root microbial communities of wheat plants cultivated under high basal N fertilization. *Front. Plant Sci.* **11**, 575861 (2020).
46. Ros, M., Raut, I., Santísima-Trinidad, A. B. & Pascual, J. A. Relationship of microbial communities and suppressiveness of *Trichoderma* fortified composts for pepper seedlings infected by *Phytophthora nicotianae*. *PLoS ONE* **12**, e0174069 (2017).
47. Qiao, C. et al. Reshaping the rhizosphere microbiome by bio-organic amendment to enhance crop yield in a maize-cabbage rotation system. *Appl. Soil Ecol.* **142**, 136–146 (2019).
48. Bonanomi, G., Lorito, M., Vinale, F. & Woo, S. L. Organic amendments, beneficial microbes, and soil microbiota: toward a unified framework for disease suppression. *Annu. Rev. Phytopathol.* **56**, 1–20 (2018).
49. He, C. et al. Dual inoculation of dark septate endophytes and *Trichoderma viride* drives plant performance and rhizosphere microbiome adaptations of *Astragalus mongholicus* to drought. *Environ. Microbiol.* **24**, 324–340 (2022).
50. Rousseau, A., Benhamou, N., Chet, I. & Piche, Y. Mycoparasitism of the extramatrical phase of *Glomus intraradices* by *Trichoderma harzianum*. *Phytopathology* **86**, 434–443 (1996).
51. Guo, Y. et al. *Trichoderma* species differ in their volatile profiles and in antagonism toward ectomycorrhiza *Laccaria bicolor*. *Front. Microbiol.* **10**, 891 (2019).
52. Cameron, D. D., Neal, A. L., van Wees, S. C. & Ton, J. Mycorrhiza-induced resistance: more than the sum of its parts? *Trends Plant Sci.* **18**, 539–545 (2013).
- This article reflects that mycorrhizae are not only microbial plant biostimulants but also induce plant systemic defences and might be considered indirect biological control agents.**
53. Buysens, C., César, V., Ferrais, F., Dupré de Boulois, H. & Declerck, S. Inoculation of *Medicago sativa* cover crop with *Rhizophagus irregularis* and *Trichoderma harzianum* increases the yield of subsequently-grown potato under low nutrient conditions. *Appl. Soil Ecol.* **105**, 137–143 (2016).
54. Martínez-Medina, A., Roldán, A., Albacete, A. & Pascual, J. A. The interaction with arbuscular mycorrhizal fungi or *Trichoderma harzianum* alters the shoot hormonal profile in melon plants. *Phytochemistry* **72**, 223–229 (2011).
55. Minchev, Z., Kostenko, O., Soler, R. & Pozo, M. J. Microbial consortia for effective biocontrol of root and foliar diseases in tomato. *Front. Plant Sci.* **12**, 756368 (2021).
56. Poveda, J., Hermosa, R., Monte, E. & Nicolás, C. *Trichoderma harzianum* favours the access of arbuscular mycorrhizal fungi to non-host Brassicaceae roots and increases plant productivity. *Sci. Rep.* **9**, 11650 (2019).
57. Samuels, G., Dodd, S. L., Gams, W., Castlebury, L. A. & Petrini, O. *Trichoderma* species associated with the green mold epidemic of commercially grown *Agaricus bisporus*. *Mycologia* **94**, 146–170 (2002).
58. Tijerino, A. et al. Overexpression of the *Trichoderma brevicompactum* *tri5* gene: effect on the expression of the trichodermin biosynthetic genes and on tomato seedlings. *Toxins* **3**, 1220–1232 (2011).
59. Kredics, L. et al. Clinical importance of the genus *Trichoderma*. A review. *Acta Microbiol. Immunol. Hung.* **50**, 105–117 (2003).
60. Rocha, S. L. et al. Recognition of endophytic *Trichoderma* species by leaf-cutting ants and their potential in a Trojan-horse management strategy. *R. Soc. Open Sci.* **4**, 160628 (2017).
61. Tucci, M., Ruocco, M., de Masi, L., de Palma, M. & Lorito, M. The beneficial effect of *Trichoderma* spp. on tomato is modulated by the plant genotype. *Mol. Plant Pathol.* **12**, 341–354 (2011).
62. Bazghaleh, N., Prashar, P., Woo, S. & Vanderberg, A. Effects of lentil genotype on the colonization of beneficial *Trichoderma* species and biocontrol of *Aphanomyces* root rot. *Microorganisms* **8**, 1290 (2020).
63. Chaverri, P. et al. Systematics of the *Trichoderma harzianum* species complex and the re-identification of commercial biocontrol strains. *Mycologia* **107**, 558–590 (2015).
- Identification of *Trichoderma* strains used as active matter in commercial products, highlighting the need for re-identification of those included in patents and registrations present and future.**
64. Vos, C. M., De Cremer, K., Cammue, B. P. & De Coninck, B. The toolbox of *Trichoderma* spp. in the biocontrol of *Botrytis cinerea* disease. *Mol. Plant Pathol.* **16**, 400–412 (2015).
65. Vinale, F. et al. Major secondary metabolites produced by two commercial *Trichoderma* strains active against different phytopathogens. *Let. Appl. Microbiol.* **43**, 143–148 (2006).
66. Xiao-Yan, S. et al. Broad-spectrum antimicrobial activity and high stability of trichokonins from *Trichoderma koningii* SMF2 against plant pathogens. *FEMS Microbiol. Lett.* **260**, 119–125 (2006).
67. Stoppacher, N., Kluger, B., Zeilinger, S., Krška, R. & Schuhmacher, R. Identification and profiling of volatile metabolites of the biocontrol fungus *Trichoderma atroviride* by HS-SPME-GC-MS. *J. Microbiol. Methods* **81**, 187–193 (2010).
68. Lee, S., Yap, M., Behringer, G., Hung, R. & Bennett, J. W. Volatile organic compounds emitted by *Trichoderma* species mediate plant growth. *Fungal Biol. Biotechnol.* **3**, 7 (2016).
69. Li, N., Islam, M. T. & Kang, S. Secreted metabolite-mediated interactions between rhizosphere bacteria and *Trichoderma* biocontrol agents. *PLoS ONE* **14**, e0227228 (2019).
70. Martínez-Medina, A., Van Wees, S. C. M. & Pieterse, C. M. J. Airborne signals from *Trichoderma harzianum* stimulate iron uptake responses in roots resulting in priming

- of jasmonic acid-dependent defences in shoots of *Arabidopsis thaliana* and *Solanum lycopersicum*. *Plant Cell Environ.* **40**, 2691–21705 (2017).
71. Collinge, D. B. et al. Biological control of plant diseases — what has been achieved and what is the direction? *Plant Pathol.* **71**, 1024–1047 (2022).
  72. Woo, S. L. et al. *Trichoderma*-based products and their widespread use in agriculture. *Open Mycol. J.* **8**, 71–126 (2014).
- An overview of *Trichoderma*-based products on the global commercial market, species utilized as active substances, companies, product claims, formulations, countries where used, and registrations.**
73. Baazeem, A. et al. In vitro antibacterial, antifungal, nematocidal and growth promoting activities of *Trichoderma hamatum* FB10 and its secondary metabolites. *J. Fungi* **7**, 331 (2021).
  74. Morán-Díez, M. E. et al. Transcriptomic analysis of *Trichoderma atroviride* overgrowing plant-wilting *Verticillium dahliae* reveals the role of a new M14 metalloprotease CPA1 in biocontrol. *Front. Microbiol.* **10**, 1120 (2019).
  75. Mukherjee, P. K., Mendoza-Mendoza, A., Zeilinger, S. & Horwitz, B. A. Mycoparasitism as a mechanism of *Trichoderma*-mediated suppression of plant diseases. *Fungal Biol. Rev.* **39**, 15–33 (2022).
  76. Zeilinger, S. et al. Chitinase gene expression during mycoparasitic interaction of *Trichoderma harzianum* with its host. *Fungal Genet. Biol.* **26**, 131–140 (1999).
  77. de la Cruz, J., Pintor-Toro, J. A., Benitez, T. & Llobell, A. Purification and characterization of an endo- $\beta$ -1,6-galactanase from *Trichoderma harzianum* that is related to its mycoparasitism. *J. Bacteriol.* **177**, 1864–1871 (1995).
  78. Migheli, Q., González-Candelas, L., Delessi, L., Camponogara, A. & Ramón-Vidal, D. Transformants of *Trichoderma longibrachiatum* overexpressing the  $\beta$ -1,4-endoglucanase gene *egl1* show enhanced biocontrol of *Pythium ultimum* on cucumber. *Phytopathology* **88**, 673–677 (1998).
  79. Ait-Lahsen, H. et al. An antifungal exo- $\alpha$ -1,3-galactanase (AGN13.1) from the biocontrol fungus *Trichoderma harzianum*. *Appl. Environ. Microbiol.* **67**, 5833–5839 (2001).
  80. Djonovic, S., Pozo, M. J. & Kenerley, C. M. Tvbgn3, a  $\beta$ -1,6-galactanase from the biocontrol fungus *Trichoderma virens*, is involved in mycoparasitism and control of *Pythium ultimum*. *Appl. Environ. Microbiol.* **72**, 7661–7670 (2006).
  81. Thrane, C., Tronsmo, A. & Jensen, D. F. Endo-1,3- $\beta$ -galactanase and cellulase from *Trichoderma harzianum*: purification and partial characterization, induction of and biological activity against plant pathogenic *Pythium* spp. *Eur. J. Plant Pathol.* **103**, 331–344 (1997).
  82. Almeida, F., Cerqueira, F. M., Silva, R. D. N., Ulhoa, C. J. & Lima, A. L. Mycoparasitism studies of *Trichoderma harzianum* strains against *Rhizoctonia solani* evaluation of coiling and hydrolytic enzyme production. *Biotechnol. Lett.* **29**, 1189–1193 (2007).
  83. Rubio, M. B., Hermosa, R., Reino, J. L., Collado, I. G. & Monte, E. The *Thc1f* transcription factor of *Trichoderma harzianum* is involved in 6-pentyl-2H-pyran-2-one production and antifungal activity. *Fungal Genet. Biol.* **46**, 17–27 (2009).
  84. Howell, C. R. & Stipanovic, R. D. Gliovirin, a new antibiotic from *Gliocladium virens*, and its role in the biological control of *Pythium ultimum*. *Can. J. Microbiol.* **29**, 321–324 (1983).
  85. Bae, S.-J. et al. *Trichoderma* metabolites as biological control agents against *Phytophthora* pathogens. *Biol. Control.* **92**, 128–138 (2016).
  86. Manganiello, G. et al. Modulation of tomato response to *Rhizoctonia solani* by *Trichoderma harzianum* and its secondary metabolite harzianic acid. *Front. Microbiol.* **9**, 1966 (2018).
  87. Di Pietro, A., Lorito, M., Hayes, C. K., Broadway, R. M. & Harman, G. E. Endochitinase from *Gliocladium virens*: isolation, characterization, and synergistic antifungal activity in combination with gliotoxin. *Phytopathology* **83**, 308–313 (1993).
  88. Lace, B. et al. Gate crashing arbuscular mycorrhizas: *in vivo* imaging shows the extensive colonization of both symbionts by *Trichoderma atroviride*. *Environ. Microbiol. Rep.* **7**, 64–77 (2015).
  89. Yang, H., Powell, N. T. & Barker, K. R. The influence of *Trichoderma harzianum* on the root-knot *Fusarium* wilt complex in cotton. *J. Nematol.* **8**, 81–86 (1976).
  90. Sharon, E. et al. Parasitism of *Trichoderma* on *Meloidogyne javanica* and role of the gelatinous matrix. *Eur. J. Plant Pathol.* **118**, 247–258 (2007).
  91. Suárez, B., Rey, M., Castillo, P., Monte, E. & Llobell, A. Isolation and characterization of PRA1, a trypsin-like protease from the biocontrol agent *Trichoderma harzianum* CECT 2413 displaying nematocidal activity. *Appl. Microbiol. Biotechnol.* **65**, 46–55 (2004).
  92. Sahebani, N. & Hadavi, N. Biological control of the root-knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. *Soil. Biol. Biochem.* **40**, 2016–2020 (2008).
  93. Berini, F. et al. Effects of *Trichoderma viride* chitinases on the peritrophic matrix of Lepidoptera. *Pest Manag. Sci.* **72**, 980–989 (2016).
  94. da Silveira, A. A. et al. Larvicidal potential of cell wall degrading enzymes from *Trichoderma asperellum* against *Aedes aegypti* (Diptera: Culicidae). *Biotechnol. Prog.* **37**, e3182 (2021).
  95. Podder, D. & Ghosh, S. K. A new application of *Trichoderma asperellum* as an anopheline larvicide for eco friendly management in medical science. *Sci. Rep.* **9**, 1108 (2019).
  96. Kapat, A., Zimand, G. & Elad, Y. Effect of two isolates of *Trichoderma harzianum* on the activity of hydrolytic enzymes produced by *Botrytis cinerea*. *Physiol. Mol. Plant Pathol.* **52**, 127–137 (1999).
  97. Malmierca, M. G. et al. Trichothecenes and aspinolides produced by *Trichoderma arundinaceum* regulate expression of *Botrytis cinerea* genes involved in virulence and growth. *Environ. Microbiol.* **18**, 3991–4004 (2016).
  98. Contreras-Cornejo, H. A. et al. *Trichoderma atroviride*, a maize root associated fungus, increases the parasitism rate of the fall armyworm *Spodoptera frugiperda* by its natural enemy *Campoletis sonorensis*. *Soil Biol. Biochem.* **122**, 196–202 (2018).
  99. Conrath, U., Beckers, G. J., Langenbach, C. J. & Jaskiewicz, M. R. Priming for enhanced defense. *Annu. Rev. Phytopathol.* **53**, 97–119 (2015).
  100. Mendoza-Mendoza, A. et al. Molecular dialogues between *Trichoderma* and roots: role of the fungal secretome. *Fungal Biol. Rev.* **32**, 62–85 (2018).
  101. Mathys, J. et al. Genome-wide characterization of ISR induced in *Arabidopsis thaliana* by *Trichoderma hamatum* T382 against *Botrytis cinerea* infection. *Front. Plant Sci.* **3**, 108 (2012).
  102. Brotman, Y. et al. *Trichoderma*-plant root colonization: escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. *PLoS Pathog.* **9**, e1003221 (2013).
  103. Moran-Díez, E. et al. The ThPG1 endopolygalacturonase is required for the *Trichoderma harzianum*-plant beneficial interaction. *Mol. Plant Microbe Interact.* **22**, 1021–1031 (2009).
  104. Hermosa, R. et al. The contribution of *Trichoderma* to balancing the costs of plant growth and defense. *Int. Microbiol.* **16**, 69–80 (2013).
  105. Alonso-Ramírez, A. et al. Salicylic acid prevents *Trichoderma harzianum* from entering the vascular system of roots. *Mol. Plant Pathol.* **15**, 823–831 (2014).
- Salicylic acid is key to controlling *Trichoderma* early root colonization as without the support of this phytohormone the plants cannot prevent the fungus from entering the vascular system and spreading to the aerial parts.**
106. Rotblat, B., Enshel-Seiffers, D., Gershoni, J. M., Schuster, S. & Avni, A. Identification of an essential component of the elicitation active site of the EIX protein elicitor. *Plant J.* **32**, 1049–1055 (2002).
  107. Romero-Contreras, Y. J. et al. Tal6 from *Trichoderma atroviride* is a LysM effector involved in mycoparasitism and plant association. *Front. Microbiol.* **10**, 2231 (2019).
  108. Djonovic, S., Pozo, M. J., Dangott, L. J., Howell, C. R. & Kenerley, C. M. Sm1, a proteinaceous elicitor secreted by the biocontrol fungus *Trichoderma virens* induces plant defense responses and systemic resistance. *Mol. Plant Microbe Interact.* **19**, 838–853 (2006).
  109. Engelberth, J. et al. Ion channel-forming alamethicin is a potent elicitor of volatile biosynthesis and tendrils coiling. Cross talk between jasmonate and salicylate signaling in lima bean. *Plant Physiol.* **125**, 369–377 (2001).
  110. Malmierca, M. G. et al. Production of trichothecenes by *Trichoderma harzianum* alters the perception of this biocontrol strain by plants and antagonized fungi. *Environ. Microbiol.* **17**, 2628–2646 (2015).
  111. Malmierca, M. G. et al. Involvement of *Trichoderma* trichothecenes in the biocontrol activity and induction of plant defense-related genes. *Appl. Environ. Microbiol.* **78**, 4856–4868 (2012).
  112. Ramirez-Valdespino, C. A., Casas-Flores, S. & Olmedo-Monfil, V. *Trichoderma* as a model to study effector-like molecules. *Front. Microbiol.* **10**, 1030 (2019).
  113. Lamdan, N., Shalaby, S., Ziv, T., Kenerley, C. M. & Horwitz, B. A. Secretome of the biocontrol fungus *Trichoderma virens* co-cultured with maize roots: role in induced systemic resistance. *Mol. Cell Proteom.* **14**, 1054–1063 (2015).
  114. Marra, R. et al. Study of the three-way interaction between *Trichoderma atroviride*, plant and fungal pathogens by using a proteomic approach. *Curr. Genet.* **50**, 307–321 (2006).
  115. Shores, M. & Harman, G. E. The molecular basis of shoot responses of maize seedlings to *Trichoderma harzianum* T22 inoculation of the root: a proteomic approach. *Plant Physiol.* **147**, 2147–2163 (2008).
  116. Pieterse, C. M. et al. Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* **52**, 347–375 (2014).
  117. Shores, M., Yedidia, I. & Chet, I. Involvement of jasmonic acid/ethylene signaling pathway in the systemic resistance induced in cucumber by *Trichoderma asperellum* T203. *Phytopathology* **95**, 76–84 (2005).
  118. Luo, Y. et al. Antimicrobial peptides induce defense responses and systemic resistance in tobacco against tobacco mosaic virus. *FEMS Microbiol. Lett.* **313**, 120–126 (2010).
  119. Salas-Marina, M. A. et al. Colonization of *Arabidopsis* roots by *Trichoderma atroviride* promotes growth and enhances systemic disease resistance through jasmonic acid/ethylene and salicylic acid pathways. *Eur. J. Plant Pathol.* **131**, 15–26 (2011).
  120. TariqJaveed, M., Farooq, T., Al-Hazmi, A. S., Hussain, M. D. & Rehman, A. U. Role of *Trichoderma* as a biocontrol agent (BCA) of phytoparasitic nematodes and plant growth inducer. *J. Invertebr. Pathol.* **183**, 107626 (2021).
  121. Medeiros, H. A. et al. Tomato progeny inherit resistance to the nematode *Meloidogyne javanica* linked to plant growth induced by the biocontrol fungus *Trichoderma atroviride*. *Sci. Rep.* **7**, 40216 (2017).
- Plant responses to *Trichoderma* are heritable in terms of both induction of defence and growth promotion, and the expression of these traits in the offspring depends on the treatment to which the parental plant was subjected.**
122. Martínez-Medina, A. et al. Shifting from priming of salicylic acid- to jasmonic acid-regulated defences by *Trichoderma* protects tomato against the root knot nematode *Meloidogyne incognita*. *N. Phytol.* **213**, 1363–1377 (2017).
  123. Rebollo-Prudencio, O. G. et al. The small RNA-mediated gene silencing machinery is required in *Arabidopsis* for stimulation of growth, systemic disease resistance, and suppression of the nitrile-specifier gene *NSP4* by *Trichoderma atroviride*. *Plant J.* **109**, 873–890 (2022).
  124. Coppola, M. et al. Transcriptome and metabolome reprogramming in tomato plants by *Trichoderma harzianum* strain T22 primes and enhances defense responses against aphids. *Front. Physiol.* **10**, 745 (2019).
  125. Coppola, M. et al. *Trichoderma atroviride* P1 colonization of tomato plants enhances both direct and indirect defense barriers against insects. *Front. Physiol.* **10**, 813 (2019).
- Demonstration of both direct and indirect biological control of sucking and chewing insects feeding on *Trichoderma*-treated plants.**

126. Gupta, S. et al. Inoculation of barley with *Trichoderma harzianum* T-22 modifies lipids and metabolites to improve salt tolerance. *J. Exp. Bot.* **72**, 7229–7246 (2021).
127. Arnold, A. E., Praprotnik, E. & Lončar, J. Testing virulence of different species of insect associated fungi against yellow mealworm (Coleoptera: Tenebrionidae) and their potential growth stimulation to maize. *Plants* **10**, 2498 (2021).
128. Kaushik, N. et al. Chemical composition of an aphid antifeedant extract from an endophytic fungus, *Trichoderma* sp. EF1671. *Microorganisms* **8**, 420 (2020).
129. Li, Y. et al. Impacts on silkworm larvae midgut proteomics by transgenic *Trichoderma* strain and analysis of glutathione S-transferase sigma 2 gene essential for anti-stress response of silkworm larvae. *J. Proteom.* **126**, 218–227 (2015).
130. Battaglia, D. et al. Tomato below ground-above ground interactions: *Trichoderma longibrachiatum* affects the performance of *Macrosiphum euphorbiae* and its natural antagonists. *Biomed. Res. Int.* **26**, 1249–1256 (2013).
131. Contreras-Cornejo, H. A., Macías-Rodríguez, L., del-Val, E. & Larsen, J. The root endophytic fungus *Trichoderma atroviride* induces foliar herbivory resistance in maize plants. *Appl. Soil Ecol.* **124**, 45–53 (2018).
132. Saijo, Y. & Loo, E. P. Plant immunity in signal integration between biotic and abiotic stress responses. *N. Phytol.* **225**, 87–104 (2020).
133. Moscatiello, R. et al. The hydrophobin HYTL01 secreted by the biocontrol fungus *Trichoderma longibrachiatum* triggers a NAADP-mediated calcium signalling pathway in *Lotus japonicus*. *Int. J. Mol. Sci.* **19**, 2596 (2018).
134. Bailey, B. A. et al. Fungal and plant gene expression during the colonization of cacao seedlings by endophytic isolates of four *Trichoderma* species. *Planta* **224**, 1449–1464 (2006).
135. Mastouri, F., Björkman, T. & Harman, G. E. Seed treatment with *Trichoderma harzianum* alleviates biotic, abiotic, and physiological stresses in germinating seeds and seedlings. *Phytopathology* **100**, 1213–1221 (2010).
- Pioneering work describing that *Trichoderma* reduces the damage caused by ROS in the plant, resulting in the alleviation of a range of biotic, abiotic and physiological stresses.**
136. Ghorbanpour, A., Salimi, A., Ghanbary, M. A. T., Pirdashti, H. & Dehestani, A. The effect of *Trichoderma harzianum* in mitigating low temperature stress in tomato (*Solanum lycopersicum* L.) plants. *Sci. Hortic.* **230**, 134–141 (2018).
137. Zhang, S., Xu, B. & Gan, Y. Seed treatment with *Trichoderma longibrachiatum* T6 promotes wheat seedling growth under NaCl stress through activating the enzymatic and nonenzymatic antioxidant defense systems. *Int. J. Mol. Sci.* **20**, 3729 (2019).
138. Rauf, M. et al. Molecular mechanisms of the 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase producing *Trichoderma asperellum* MAP1 in enhancing wheat tolerance to waterlogging stress. *Front. Plant Sci.* **11**, 614971 (2021).
139. Jalali, F., Zafari, D. & Salari, H. Volatile organic compounds of some *Trichoderma* spp. increase growth and induce salt tolerance in *Arabidopsis thaliana*. *Fungal Ecol.* **29**, 67–75 (2017).
140. Rubio, M. B. et al. The combination of *Trichoderma harzianum* and chemical fertilization leads to the deregulation of phytohormone networking, preventing the adaptive responses of tomato plants to salt stress. *Front. Plant Sci.* **8**, 294 (2017).
- Combined applications of *Trichoderma* and chemical fertilizer might have positive synergistic effects for plants but overstimulation leads to dysregulation of phytohormone networking if under stress conditions.**
141. Rivera-Méndez, W., Obregón, M., Morán-Díez, M. E., Hermosa, R. & Monte, E. *Trichoderma asperellum* biocontrol activity and induction of systemic defenses against *Sclerotium cepivorum* in onion plants under tropical climate conditions. *Biol. Control.* **141**, 104145 (2020).
142. Domínguez, S. et al. Nitrogen metabolism and growth enhancement in tomato plants challenged with *Trichoderma harzianum* expressing the *Aspergillus nidulans* acetamidase *amdS* gene. *Front. Microbiol.* **7**, 1182 (2016).
143. Liu, N. & Avramova, Z. Molecular mechanism of the priming by jasmonic acid of specific dehydration stress response genes in *Arabidopsis*. *Epigenetics Chromatin* **9**, 8 (2016).
144. Slaughter, A. et al. Descendants of primed *Arabidopsis* plants exhibit resistance to biotic stress. *Plant Physiol.* **158**, 835–843 (2012).
145. FAO. The State of Food and Agriculture 2019. *Moving Forward on Food Loss and Waste Reduction 1–182* (Food and Agriculture Organization of the United Nations, 2019).
146. DeClerck, F. A. J. et al. A whole earth approach to nature positive food: biodiversity and agriculture. *United Nations Food Systems Summit 2021 – Scientific Group 1–26* (CGIAR, 2021).
147. Woo, S. L. & Pepe, O. Microbial consortia: promising probiotics as plant biostimulants for sustainable agriculture. *Front. Plant Sci.* **9**, 1801 (2018).
148. Carillo, P. et al. Application of *Trichoderma harzianum*, 6-pentyl- $\alpha$ -pyrone and plant biopolymer formulations modulate plant metabolism and fruit quality of plum tomatoes. *Plants* **9**, 771 (2020).
149. Comite, E. et al. Bioformulations with beneficial microbial consortia, a bioactive compound and plant biopolymers modulate sweet basil productivity, photosynthetic activity and metabolites. *Pathogens* **10**, 870 (2021).
150. Lanzuise, S. et al. Combined biostimulant applications of *Trichoderma* spp. with fatty acid mixtures improve biocontrol activity, horticultural crop yield and nutritional quality. *Agronomy* **12**, 275 (2022).
151. Ons, L., Bylemans, D., Thevissen, K. & Cammue, B. P. A. Combining biocontrol agents with chemical fungicides for integrated plant fungal disease control. *Microorganisms* **8**, 1930 (2020).
152. Vinale, F. et al. Co-culture of plant beneficial microbes as source of bioactive metabolites. *Sci. Rep.* **7**, 14330 (2017).
153. Karuppiiah, V., Sun, J., Li, T., Vallikkannu, M. & Chen, J. Co-cultivation of *Trichoderma asperellum* GDFS1009 and *Bacillus amyloliquefaciens* 1841 causes differential gene expression and improvement in the wheat growth and biocontrol activity. *Front. Microbiol.* **10**, 68 (2019).
154. Fraceto, L. F. et al. *Trichoderma harzianum*-based novel formulations: potential applications for management of next-gen agricultural challenges. *J. Chem. Technol. Biotechnol.* **93**, 2056–2063 (2018).
155. Lorito, M. et al. Genes from mycoparasitic fungi as a source for improving plant resistance to fungal pathogens. *Proc. Natl Acad. Sci. USA* **95**, 7860–7865 (1998).
156. Montero-Barrientos, M. et al. Transgenic expression of the *Trichoderma harzianum* hsp70 gene increases *Arabidopsis* resistance to heat and other abiotic stresses. *J. Plant Physiol.* **167**, 659–665 (2010).
157. Kashyap, P. L., Rai, P., Srivastava, A. K. & Kumar, S. *Trichoderma* for climate resilient agriculture. *World J. Microbiol. Biotechnol.* **33**, 155 (2017).
158. Zafra, G., Moreno-Montano, A., Absalon, A. E. & Cortés-Espinoza, D. V. Degradation of polycyclic aromatic hydrocarbons in soil by a tolerant strain of *Trichoderma asperellum*. *Environ. Sci. Pollut. Res.* **22**, 1034–1042 (2015).
159. Robbertse, B. et al. Improving taxonomic accuracy for fungi in public sequence databases: applying ‘one name one species’ in well-defined genera with *Trichoderma/Hypocrea* as a test case. *Database* **2017**, 1–14 (2017).
160. Rossman, A. Y. et al. Genera in bionectriaceae, hypocreaceae, and nectriaceae (Hypocreales) proposed for acceptance or rejection. *IMA Fungus* **4**, 41–51 (2013).
161. Jones, J. D. G. & Dangl, J. L. The plant immune system. *Nature* **444**, 323–329 (2006).

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## Author contributions

S.L.W. and M.L. conceptualized the idea of this manuscript. S.L.W. and R.H. collected data, designed the content for the article, designed figures and drafted the tables. S.L.W., R.H., M.L. and E.M. contributed substantially to the discussion of the content. S.L.W. and E.M. wrote the article. All authors reviewed and edited the final version of the draft and agreed to the published version of the manuscript.

## Competing interests

The authors declare no competing interests.

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