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Review

Molecular dialogues between *Trichoderma* and roots: Role of the fungal secretome

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ABSTRACT

Trichoderma species are opportunistic fungi residing primarily in soil, tree bark and on wild mushrooms. *Trichoderma* is capable of killing other fungi and penetrating plant roots, and is commonly used as both a biofungicide and inducer of plant defence against pathogens. These fungi also exert other beneficial effects on plants including growth promotion and tolerance to abiotic stresses, primarily mediated by their intimate interactions with roots. In root–microbe interactions (both beneficial and harmful), fungal secreted proteins play a crucial role in establishing contact with the roots, fungal attachment, root penetration and triggering of plant responses. In *Trichoderma*–root interactions, the sucrose present in root exudates has been demonstrated to be important in fungal attraction. Attachment to roots is mediated by hydrophobin-like proteins, and secreted swollenins and plant cell wall degrading enzymes facilitate internalization of the fungal hyphae. During the early stage of penetration, suppression of plant defence is vital to successful initial root colonisation; this is mediated by small soluble cysteine-rich secreted proteins (effector-like proteins). Up to this stage, *Trichoderma*'s behaviour is similar to that of a plant pathogen invading root structures. However, subsequent events like oxidative bursts, the synthesis of salicylic acid by the plants, and secretion of elicitor-like proteins by *Trichoderma* spp. differentiate this fungus from pathogens. These processes induce immunity in plants that help counter subsequent invasion by plant pathogens and insects. In this review, we present an inventory of soluble secreted proteins from *Trichoderma* that might play an active role in beneficial *Trichoderma*–plant interactions, and review the function of such proteins where known.

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1. Introduction

Soil fungi belonging to the ascomycete genus *Trichoderma* have the potential to provide environmentally-friendly biocontrol of plant diseases. They directly antagonize many plant pathogens, while at the same time promoting plant growth and triggering resistance to subsequent pathogenic attack (Chet, 1987; Druzhinina *et al.*, 2011; Lorito *et al.*, 2010; Mukherjee *et al.*, 2013). *Trichoderma* spp. colonise and penetrate the surface of plant roots, where growth is then limited mostly to the apoplast, the epidermis and the first few cortical cell layers. Certain strains of *Trichoderma* are reported to be systemic endophytes (Druzhinina *et al.*, 2011). Promotion of root growth is commonly reported in the literature, and production/stimulation of phytohormones is also recorded (Contreras-Cornejo *et al.*, 2013). Though not identical, there are certain analogies between *Trichoderma* and ectomycorrhizae, as far as their interaction with roots is concerned (Harman *et al.*, 2004). Mycorrhizal fungi are tightly linked symbionts of plant roots. As such, they are able to colonise extracellularly (ectomycorrhizae) or intracellularly (endomycorrhizae), while evading the plant immune system (Zuccaro *et al.*, 2014). At the opposite end of the spectrum of fungal–plant interactions are the soil-borne pathogens that penetrate the root and cause diseases. The factors that define the outcome of fungal colonisation (endophytic, symbiotic or pathogenic) are not fully understood. It is clear, though, that the fungus is capable of following a wider range of lifestyles than it may exhibit in any one interaction. This outcome is determined by the fungal and host genotypes, among other factors. *Trichoderma* has been defined as an opportunistic symbiont based on the ability to grow saprophytically in the soil as well as in close association with plant roots (Harman *et al.*, 2004). Traditionally the host response has been postulated to be an induced systemic resistance (ISR) reaction (like that imparted by the rhizobacteria that grow on, and not inside the roots). However, *Trichoderma*-mediated induced defence has often been found to be ISR or SAR (SAR is the systemic acquired resistance triggered by biotrophic and hemibiotrophic pathogens, while ISR is employed more against necrotrophs), or both (probably in keeping with the ability to grow both on and in the roots). Intriguingly, it was recently shown that the progeny of *Trichoderma*-primed tomato plants can inherit a resistant state, providing protection from nematodes (Medeiros *et al.*, 2017). The molecular mechanisms of *Trichoderma*–root interactions are only beginning to be understood. The secretomes of *Trichoderma* species are rich in carbohydrate active enzymes (CAZymes), other enzymes, and many proteins with no obvious enzymatic activity including small secreted proteins (reviewed by de Mojana di Cologna *et al.* (2018). Small cysteine-rich secreted proteins belonging to the ceratoplatanin (CP) family have been studied from the functional to the structural levels as plant immunity stimulators (Djonovic *et al.*, 2007; Seidl *et al.*, 2006; Vargas *et al.*, 2008). The CP paralogs may have different roles depending on the plant species, the *Trichoderma* strain and the pathogen used to assay resistance in the plant (Crutcher, 2012; Crutcher *et al.*, 2015; Gaderer *et al.*, 2015; Salas-Marina *et al.*, 2015). Apart from these, many other secreted proteins, notably the hydrophobins and many CAZymes, have been found to be involved in the interaction between *Trichoderma* and roots (Moran-Diez *et al.*, 2009; Samolski *et al.*, 2012; Viterbo and Chet, 2006). In a new twist in the story, our recent findings point to the involvement of certain components of the *Trichoderma* secretome in inducing susceptibility in host plants – perhaps by suppressing initial plant resistance, which aids fungal root penetration (Lamdan *et al.*, 2015). Bioinformatic predictions suggest that some secreted *Trichoderma* proteins could have plant intracellular targets (Schmoll *et al.*, 2016), which provides a promising direction for future experiments. Thus, knowledge from pathogens and mycorrhizal fungi will be a valuable guide for future work on *Trichoderma*, while keeping in mind that the details will surely differ. All these issues are addressed and critically analysed in the current review. Since several *Trichoderma* genomes have been sequenced, and these include species from distinct ecosystems and lifestyles, we also analyse the genomic potential of the *Trichoderma* species in setting-up dialogue with plants.

2. *Trichoderma*-induced plant defence: interplay of signals/hormones

Root–microbe interactions can be either beneficial, as in the case of *Trichoderma* and mycorrhiza, or pathogenic. *Trichoderma* exerts beneficial effects on plants in terms of improvement or maintenance of soil productivity, increased percentages and rates of seed germination, nutrient uptake, growth promotion, alleviation of adverse effects caused by environmental damage and systemic defence stimulation against pathogen attack and abiotic stress, without the need of establishing any contact with the invader (Hermosa *et al.*, 2012; Rubio *et al.*, 2017a; Shoresh *et al.*, 2010). Systemic defence stimulation primes the plant immune response, acting against subsequent attack by any class of pathogens. Bacteria and fungi are the most familiar, however *Trichoderma* also primes defence against nematodes (Martínez-Medina *et al.*, 2017; Medeiros *et al.*, 2017; Sharon *et al.*, 2001), insects (Coppola *et al.*, 2017) and viruses (Elsharkawy *et al.*, 2013; Vitti *et al.*, 2016). Thus, as with mycorrhiza, plants do not perceive *Trichoderma* as an enemy. However, to achieve such “true-friend” status, *Trichoderma* had to develop opportunistic mechanisms for effective utilization of root exudate components (Vargas *et al.*, 2009) and overcoming the early plant defences (Moran-Diez *et al.*, 2012). Plants are capable of establishing immune responses that can be highly specific, with restricted self-reactivity, and that often generate a lifelong memory of the encountered attackers (Spoel and Dong, 2012). The first active line of defence, known as the innate immune response, occurs when evolutionarily conserved epitopes of microbe-derived molecules, called microbe-associated molecular patterns (MAMPs), such as beta-glucans and chitin (major components of the fungal cell wall), are detected by cell-surface pattern recognition receptors (PRRs). Similarly, PRRs also respond to molecules, such as cell wall oligomers or cuticular fragments, released by microbial hydrolytic activity on plant tissues, which are referred to as damage-associated molecular patterns (DAMPs).

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