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Review

Fungal proteins and genes associated with biocontrol mechanisms of soil-borne pathogens: a review

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ABSTRACT

Soil suppressiveness to soil-borne diseases relies mainly on microbial interactions. Some of them, *e.g.* antibiosis and mycoparasitism, are directly deleterious to pathogenic fungi; others indirectly affect microbial populations, pathogens included, when quite active non pathogenic microorganisms intensively exploit trophic or spatial resources. The mechanisms that govern the suppressive nature of the various known suppressive soils are often hypothetical. The objective of this article is to review the fungal proteins and corresponding genes directly or indirectly involved in antagonistic relationships between pathogens and non-pathogens and associated with biocontrol of soil-borne pathogens. The current hypothesis is that they contribute to soil suppressiveness. We assigned the proteins encoded by these genes to five function-based groups. The first group contains the proteins involved in host recognition and signaling pathways and the transcription factors involved in biocontrol activities. Proteins that protect antagonistic fungi against their own toxins and against other microorganisms are also included in this first group. The second group lists enzymes and proteins involved in the biosynthesis pathway of secondary metabolites, such as peptaibols, terpenes, polyketides, and gliotoxins that have antifungal activity towards soil-borne plant pathogens. The third group deals with proteins and molecules involved in competition for nutrients and root colonization. The fourth one contains the fungal cell wall-degrading enzymes secreted by antagonistic fungi during mycoparasitism. They are mainly chitin-degrading enzymes, glucanases and proteases. Finally, the last group gathers fungal proteins and molecules that induce plant defense reactions and prevent infection by plant pathogens. We conclude that the proteins involved or simply associated with the specific suppression of pathogens are not all known yet, but genes encoding a number of them or facilitating their expression are identified. Selecting candidate genes among them may help to understand the underlying mechanisms of soil suppressiveness when using metatranscriptomic analyses to identify functional groups.

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1. Introduction

Soil-borne diseases are still an acute problem for agriculture as means for pest and disease control are limited in such a complex environment. The traditional approach to control soil-borne diseases consists in trying to eradicate the pathogens from the soil. This has led to the use of very dangerous biocides whose side effects often result in increased phytosanitary risks related to the acquisition of resistance by pathogens or the emergence of new pest populations. As against that, approaches should be proposed to enhance the existing natural suppressive potential of every soil whether in the field or in protected crops under shelter (Alabouvette 1986; Raaijmakers *et al.*, 2009; Kyselková and Moënne-loccoz, 2012). The soil is not a neutral medium where pathogenic microorganisms interact freely with the roots of the host plant. Actually, microorganisms, and also the soil microfauna, directly or indirectly interact through parasitism or antibiosis, amensalism or competition for the exploitation of common resources. They also interact *via* plants by priming plant defense reactions and rhizodeposits that in turn may select microbial populations in the rhizosphere (Raaijmakers *et al.*, 2009; Aimé *et al.*, 2013). The soil interferes in several ways with the relationships between and among microorganisms, pathogens and plants, and it can modify the interactions among microorganisms themselves (Höper *et al.*, 1995; Janvier *et al.*, 2007). Different situations in which such biotic and abiotic interactions may play a role in plant health have been described all around the world. They correspond to soils in which disease caused by a type of pathogen to a given host plant type is very little or not at all expressed, *i.e.* almost constitutive disease suppression. In other situations, disease suppression is acquired gradually thanks to the use of farming practices including organic amendments and specific green fertilizers, appropriate crop rotation schemes or on the contrary extended monocultures. However, the outcomes of disease suppression management are frequently variable and not sustainable yet. Disease suppression has been demonstrated for a wide range of soil-borne plant pathogens including bacteria, nematodes, oomycetes and fungi (Stutz *et al.*, 1986; Becker *et al.*, 1997; Persson *et al.*, 1999; Shiomi *et al.*, 1999; Weller *et al.*, 2002; Rimé *et al.*, 2003; Borneman and Becker, 2007; Vos *et al.*, 2014).

All these situations fall within the concept of soil suppressiveness proposed by Cook and Baker (1983) that is a suppressive soil is a soil in which the pathogen does not establish, establishes but causes little or no damage, or establishes and causes disease for a while but thereafter the disease becomes less severe although the pathogen may persist in the soil. However, even if all these situations pertain to the same concept, each is very specific and involves different mechanisms, whether with different, unevenly distributed soil microorganisms or different functions encoded by genes of various taxonomic origins but expressed according to environmental conditions, or both. Apart from some cases of acquired soil suppressiveness, as for instance take-all disease for which, 2,4-diacetylphloroglucinol produced by *Pseudomonas* populations is involved in the suppression of *Gaeumannomyces graminis* var. *tritici* (Weller *et al.*, 2002), attempts at deciphering the mechanisms involved in soil suppressiveness have not revealed so many genes or proteins, enzymes or secondary metabolites (Mendes *et al.*, 2011). Conversely, studies of the modes of action of biocontrol agents and research efforts devoted to plant–pathogen interactions at the cellular and molecular levels have helped to highlight enzymes, secondary metabolites and signal molecules that may act alone or in interaction in pathogen suppression (Massart and Jijakli, 2007). Much work on the genetics of biological control using fungal antagonists have been done mainly with the genus *Trichoderma* (Viterbo *et al.*, 2001, 2010; Mukherjee *et al.*, 2004, 2012; Reithner *et al.*, 2005, 2014; Vinale *et al.*, 2008, 2013). Previous reviews focussed on this genus (Szekeres *et al.*, 2005; Sharma *et al.*, 2011) but expressed genes involved in the modes of action of many other biocontrol fungi including for example *Chlonostachys rosea*, *Coniothyrium minitans*, *Pseudozyma* sp., *Stachybotrys elegans*, *Verticillium biguttatum* and oomycete *Pythium oligandrum* were also described (McQuilken and Gemmell, 2004; Morissette *et al.*, 2006; Muthumeenakshi *et al.*, 2007; Mamarabadi *et al.*, 2008, 2009; Teichmann *et al.*, 2011; Horner *et al.*, 2012). The whole constitutes a complex database that would be interesting to use to better understand the successes but also the failures encountered in biological control (inoculation of a biological control agent in the soil) and in integrated pest management through agricultural practices. Indeed, most of these molecules also must probably operate in suppressive soils from which many biocontrol agents have been isolated (Harman, 2000; Alabouvette *et al.*, 2007).

This article reviews fungal and oomycetes proteins and the respective genes encoding these proteins associated with antimicrobial activity and pathogen or disease suppression. We classified the proteins into five function-based groups: 1) host recognition and genetic reprogramming, 2) antibiosis, 3) competition for nutrient and root colonization, 4) mycoparasitism and subsequent cell wall degradation and 5) induction of plant defense reactions. Depending on studies, genes or proteins have been identified. But biochemical characterization of proteins usually makes it possible to determine the gene coding for its expression, and on the other hand knowing the gene leads to the protein. That is why we name genes or proteins indifferently when we describe the mechanisms involved in interactions with the pathogens. Protein names, encoding genes and accession numbers are provided in the Tables.

2. Host recognition and genetic reprogramming of gene expression

Biocontrol agents antagonize pathogenic fungi in a variety of ways including antibiosis, mycoparasitism, competition for trophic and spatial resources, and induction of plant defense reactions. An antagonistic interaction starts with specific recognition of the target pathogen by the antagonistic fungus followed by genetic reprogramming of its gene expression and subsequent control or destruction of the pathogenic fungus. These two steps are critical because they define the nature and the intensity of the antagonistic activities implemented by the biocontrol agent.