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Volatile-mediated suppression of plant pathogens is related to soil properties and microbial community composition

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ABSTRACT

There is increasing evidence that the soil microbial community produces a suite of volatile organic compounds that suppress plant pathogens. However, it remains unknown which soil properties and management practices influence volatile-mediated pathogen suppression. The aim of this study was to relate soil properties to growth suppression of three plant pathogens by soil volatiles. We measured the effect of volatiles emitted from a broad range of agricultural soils on the *in vitro* growth of the plant pathogenic fungi *Rhizoctonia solani* and *Fusarium oxysporum*, and the oomycete *Pythium intermedium*. Growth suppression of pathogens by soil volatiles could be linked to various soil properties, and some aspects of microbial community composition and field history, using multiple linear regression. Volatile-mediated suppression of mycelial development occurred for each pathogen type, but the magnitude of inhibition differed among soils as well as pathogens. On average *R. solani* and *P. ultimum* appeared more sensitive to volatile suppression than *F. oxysporum*. Suppression of *R. solani* by volatiles was positively correlated with organic matter content, microbial biomass and proportion of litter saprotrophs in the microbial community, but negatively correlated with pH, microbial diversity (Shannon), and the proportion of *Acidobacteria* in the community. *R. solani, F. oxysporum,* and *P. intermedium* suppression by volatiles was affected by various management practices occurring in the soil's field history, such as reduced tillage, the presence of certain crops in the crop rotation, and the application of solid manure. *P. intermedium* suppression was also negatively correlated with soil sulphur content. This study identifies pathogen-specific drivers of growth-suppressive volatiles, a critical step in integrating soil volatiles into prediction and management of soil-borne plant diseases.

1. Introduction

Soil-borne fungal and oomycetal pathogens are a major threat to agricultural crops globally, reducing yields through plant disease and often requiring the use of pesticides for management (Oerke, 2006). Stimulation of natural suppression mechanisms is considered a promising strategy for sustainable disease management (Bailly and Weisskopf, 2017; Chaparro et al., 2012), but the soil properties and management practices associated with these mechanisms remain largely unidentified. It has been suggested that these properties will be to a large extent (micro)biological, but that future studies need to investigate whole soil microbial communities (Van Bruggen and Semenov, 2000), their reliance on various substrates, and their interactions with abiotic properties. In a review of abiotic properties associated with disease suppression, relationships have been found to be multidirectional and inconsistent with frequently studied properties including pH, nitrogen and organic carbon content (Höper and Alabouvette, 1996; Janvier et al., 2007). The most studied management practices in the context of disease suppression focus on organic matter level manipulation via amendment (Bailey and Lazarovits, 2003;

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Hoitink and Boehm, 1999; Termorshuizen et al., 2006) or pathogen population control through crop rotation (Bailey and Lazarovits, 2003; Peters et al., 2003), with varying degrees of effectiveness; the intensity of suppression can vary among agricultural fields and between growing seasons. Therefore, identifying an indicator of a soil's potential for natural suppression that could be applied across soil types would be useful to incorporate into field crop planning and pre-growing season management decisions.

A major aspect of disease suppression is the general phenomenon of fungistasis, which occurs when a pathogen's germination and/or hyphal extension is diminished by the soil microbial community either through competition for resources or the production of antifungal compounds (Watson and Ford, 1972). The latter may be particularly effective in the form of volatile organic compounds (VOCs), which currently are receiving increasing attention having been identified through fungistasis assays as important causal agents in pathogen suppression (Asari et al., 2016; Bailly and Weisskopf, 2017; Garbeva et al., 2011; Tyc et al., 2016). VOCs diffuse quickly through the soil, resulting in a greater effective range relative to other suppressive compounds or organisms (Schmidt et al., 2015). Previous work has found a significant positive relationship between direct inhibition of germination of fungal spores by incubation in 146 soils (direct contact) and the inhibition of spore germination by volatiles emitted from these soils, indicating the important role of volatiles in fungistasis (Chuankun et al., 2004). Furthermore, disinfestation of an agricultural soil has been shown to tremendously reduce the production of VOCs inhibiting the growth of oomycetal pathogens (Van Agtmaal et al., 2015), suggesting that soil's capacity for fungistasis was also altered by the change in soil management. This pathogen-growth inhibition may be beneficial to emerging seedlings, which are particularly susceptible to infestation (Noble and Coventry, 2005).

Common agricultural management practices such as tillage, cover cropping, organic matter input or removal, and fertilization influence soil quality in multiple ways, which has been shown to be reflected by the microbial community structure (García-Orenes et al., 2013), which in turn affects VOC composition and quantity (Insam and Seewald, 2010; Van Agtmaal et al., 2015). Soil VOCs are a heterogeneous combination of compounds producing a soil-specific profile. The quality and availability of organic substrates for microorganisms may influence the spectrum of VOCs and the rate at which they are produced (Fiddaman and Rossall, 1994; Gray et al., 2010; Insam and Seewald, 2010; Leff and Fierer, 2008). While many studies use some form of soluble organic C as an indicator of microbial substrate availability, recent studies have shown that further partitioning of soil dissolved organic C (DOC) may explain more variation in microbial activity rates (Straathof et al., 2014).

The effect of VOCs has been tested on *in vitro* hyphal growth of several phylogenetically different, agronomically important fungal and oomycetal soil-borne plant pathogens including *Rhizoctonia solani, Fusarium* spp. (Garbeva et al., 2014; Kai et al., 2009) and *Pythium* spp. (Chaurasia et al., 2005; Garbeva et al., 2014). In addition to having been previously studied, these species or genera are known to be present across temperate agricultural soils (Smith et al., 1988) and the aforementioned fungi have been identified as particularly pertinent to plant pathological study (Dean et al., 2012). The growth of these pathogens has been shown to be inhibited by both mixtures and isolates of VOCs released by various bacteria and fungi (Fiddaman and Rossall, 1994; Kai et al., 2007; Pandey et al., 1997; Weisskopf and Bailly, 2013; Werner et al., 2016). However, most volatile-pathogen interaction studies have been performed with bacterial isolates on artificial media, outside the indigenous environment of both the volatile-producers and the pathogens (Campos et al., 2010; Schmidt et al., 2015). Studies performed with isolates inherently limit the conclusions that can be drawn about volatiles emitted by the indigenous soil microbial community metabolizing substrates available to them *in situ*. Because of the myriad of influences the soil environment can have on both production and release of VOCs (Peñuelas et al., 2014), it is important to compare the release of pathogen-suppressing VOCs from a variety of soils under a range of management practices. Furthermore, investigating the link between pathogen suppression, soil properties, and management requires comparisons of soils ranging in their capacity for VOC-associated suppression. So far, no comprehensive survey has been done on potential factors explaining variation in pathogen suppression among soils or across multiple pathogen-types.

We conducted a survey of agricultural soils with the following objectives: 1) determine the effect of VOCs emitted from agricultural soils on *in vitro* biomass production of the soil-borne plant pathogens *R. solani, F. oxysporum,* and *P. intermedium*, and 2) statistically relate this effect to a range of soil variables potentially steering VOC production, i.e. abiotic soil properties, substrate (DOC) chemical properties, microbial community structure, field management, and crop history. By statistically relating *in vitro* suppression by VOCs to inherent and manageable soil properties and management practices, the outcome of this survey will inform both further hypothesis-driven bioassays and field trials, and inspire more mechanistic explorations.

2. Materials and methods

2.1. Field selection, soil sampling and pre-treatment

A total of 50 arable fields were sampled across the Netherlands (Fig. S1), covering a wide range of soil properties, e.g. texture, pH, and organic matter content. These sites were selected at random from a database of sites previously characterized for texture, pH, and organic matter by BLGG Agroexpertus, The Netherlands. Sampling took place in February–March 2013, after ground-thaw and shortly before the growing season; this sampling period before crop emergence or even before seeding was selected as the most pertinent time to capture natural disease control of seedling infections (Noble and Coventry, 2005) and is when most farmers send soil for biochemical analysis to inform management decisions in temperate regions. Soil sampling was performed by taking 60 subsamples (0–20 cm cores) in a double W-pattern from an area of about 2 ha in each field. These subsamples were pooled and manually homogenized, resulting in a 3 kg sample per field, which was kept at 4 °C during transportation.

Upon arrival in the lab, soils were processed immediately: they were split in two parts for determining (1) chemical soil properties, (2) DOC fractions, microbial biomass N, respiration, microbial community composition, and the *in vitro* suppression of pathogen growth by volatiles released by the soil. Part (1) was oven-dried (40 °C), ground, and analysed by Eurofins Agro (Wageningen, The Netherlands) according to standard procedures (Table 1). Part (2) was sieved to 4 mm. Per soil, two 1 g subsamples were taken and stored at −20 °C for DNA extractions. Soil moisture was determined on basis of weight loss after drying the soil at 105 °C for 24 h. After taking the subsamples for DNA extraction and soil moisture determination, part (2) was separated into three equally sized samples per field. These three samples were then incubated for 3 days at 9 °C and 60% water-holding capacity (WHC). By equilibrating each soil under the same conditions, the effects of variable temperature and moisture conditions between different fields over the four weeks of sampling were minimized. After separation and incubation, measurements of soil properties were performed in triplicate and the averages of the three replicate samples were used as input data.

2.2. Determination of soil properties

A brief summary of all measured soil properties and the respective methodological references can be found in Table 1. To isolate fractions of DOC, one part fresh soil (mass of dry-weight equivalent (DWE)) was suspended in two parts ultra-pure water. Samples were equilibrated for 1 h on a horizontal shaker, centrifuged 20 min at 3000 g, and ultracentrifuged 10 min at 11,700 g. The supernatant was filtered through a

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