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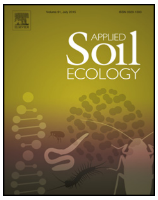

The occurrence of pathogen suppressive soils in Sweden in relation to soil biota, soil properties, and farming practices

Michael T. Löbmann[a], Ramesh R. Vetukuri[a], Levine de Zinger[a], Beatrix W. Alsanius[b], Laura J. Grenville-Briggs[a], Abigail J. Walter[a,*]

[a] *Department of Plant Protection Biology, Swedish University of Agricultural Sciences, 23053 Alnarp, Sweden*
[b] *Department of Biosystems and Technology, Swedish University of Agricultural Sciences, 23053 Alnarp, Sweden*

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ABSTRACT

Despite more than 50 years of research and their great potential for sustainable pest management, pathogen suppressive soils remain poorly understood. We conducted a study on suppression of root rot disease symptoms associated with *Pythium ultimum* in untreated and heat-sterilized soil from ten southern Swedish farms with six different cropping and management regimes. Physical and chemical soil properties, soil nematodes belonging to different trophic guilds, and the predominant soil oomycetes were analyzed for their potential as indicators of soil suppressiveness. Six of the ten sampled soils were suppressive to *P. ultimum* disease symptoms. Suppressive or conducive properties of the soils from sites with permanent soil cover were related to the presence of live soil biota, while soils from sites with interrupted soil cover had suppressive or conducive effects unrelated to live soil biota. In soils with biologically conducive effects, soils had high or low cation nutrient content, while biologically suppressive soils had intermediate nutrient levels. No relationship was found between disease symptoms and the soil nematode trophic community or the predominant soil oomycetes. Permanent soil cover and a balanced nutrient supply were correlated with biologically suppressive effects on *P. ultimum* disease symptoms.

1. Introduction

Management of soil-borne pathogens is a significant challenge in agriculture. Pathogen management often requires toxic pesticides, which strongly affect soil ecosystems (Carrascosa et al., 2015) or complex combinations of management techniques (Gamliel et al., 2000). Recent efforts to decrease the environmental impact of farming, such as the EU IPM directive (European Parliament and Council, 2009) as well as the complexity of non-chemical management strategies demonstrate a need for more sustainable pathogen control methods.

Suppressive soils are a promising avenue for pathogen control. Pathogen suppressive soils have been known for over 100 years (Chandrashekara et al., 2012), and suppressiveness may be mediated by biotic or abiotic mechanisms. Soils may be pathogen suppressive, where plant pathogens cannot survive, or disease suppressive, where the presence of pathogens does not result in disease. Biological suppressiveness may be general, where soil biodiversity suppresses pathogens via complex ecological interactions, or specific, where one or a few antagonists act against single pathogens (Cook and Baker, 1983). The mechanisms include abiotic soil conditions where pathogens cannot grow or survive or ecological interactions that reduce pathogen numbers or infectivity (Chen et al., 1987, 1988; Hoitink et al., 1997; Alabouvette and Steinberg, 2006; Brady and Weil, 2008).

In natural ecosystems, soil organisms stabilize the soil with a multitude of physical, chemical and structural processes such that plant growth is enhanced and single opportunistic organisms are less likely to dominate (Doran et al., 1996; Wall et al., 2012). High functional biodiversity is expected to increase ecosystem resilience by creating redundancy in ecosystem services, making soil less vulnerable to short-term changes in the environment. Thus, soil biodiversity may contribute to suppressiveness indirectly by creating a physical environment that favors the plant over the pathogen or directly by supporting high trophic level organisms that consume pathogens (Nitta, 1991; Reeleder, 2003; Stirling,

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* Corresponding author.
E-mail address: abigail.jan.walter@gmail.com (A.J. Walter).

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2014). For example, the natural enemies of an existing non-pathogenic soil oomycete community might also control an oomycete pathogen. Suppressive effects of soils and composts are positively correlated with factors like microbial activity and microbial biomass (Chen et al., 1988; van Os and van Ginkel, 2001).

Since the first discussions on suppressive soils (Baker and Snyder, 1965) attempts to build suppressiveness via inoculation biological control have been made (Fravel, 2005). However, Janczura et al. (2006) argue that the complexity of ecological and biochemical interactions between hosts and pathogens make this method unlikely to succeed. Changes in farming practices can enhance suppressiveness by creating environmental conditions that allow beneficial microorganisms to flourish. Unfortunately, large differences between soil ecosystems and farming practices make it difficult to understand the specific conditions needed to create and maintain suppressive properties of agricultural soils (Mazzola, 2002; Alabouvette and Steinberg, 2006). Summers et al. (2014) for example found that short term mechanisms that create suppressive soils depend largely on the local soils and weather conditions.

In agricultural soils, soil management directly influences soil biotic properties such as biodiversity (Buckley and Schmidt, 2003), microbial activity (Mbuthia et al., 2015) and microbial biomass (Pandey et al., 2015). Soil suppressiveness at the same site varies according to the long-term management practices employed (Tamm et al., 2010). Hence, manipulating soil management has a huge potential for increasing the ability of agricultural soils to suppress plant disease (Ghorbani et al., 2008). Current soil management recommendations for increased pathogen suppressiveness are mainly based on increasing organic inputs to the soil, reducing disturbances such as tillage, and diversifying crop rotation. Recommendations are very general and have varying results (Alabouvette and Steinberg, 2006; Mazzola, 2007; Brady and Weil, 2008; Ghorbani et al., 2008).

Recently, research has shown that factors such as the C/N ratio of organic amendments affected the balance between different groups of soil organisms, and this has cascading effects to the high trophic level organisms and pests (Stirling, 2014). Thus, in order to successfully enhance soil suppressiveness, it is necessary to understand how particular farming practices will influence key components of biodiversity and the soil ecosystem. Stirling et al. (2011) and Stirling (2013) showed that appropriate soil management including minimum tillage, organic amendments, mulching with crop residues, and appropriate crop rotation reduces plant pathogenic nematodes, and can be more productive and profitable than conventional strategies based on pesticides, synthetic fertilizers and extensive tillage.

Indicators for suppressive soils could be helpful tools for management of soil suppressiveness, and nematodes are attractive as potential indicators of general suppressiveness. Nematodes can be found in high numbers in most soils. They are representative of the soil ecosystem, sensitive to changes in the soil environment, and relatively easy to assess (Bongers and Bongers, 1998). Further, Stirling et al. (2011) found positive correlations between the abundance of herbivorous, bacterivorous, hyphal-feeding and predatory nematodes and the suppressiveness of soils to plant parasitic nematodes.

Pythium spp. are some of the most important soil-borne pathogens causing diseases in forest and agricultural systems associated with root lesions, damping-off, and root rot (White, 1986; Weiland, 2011). *Pythium* species are opportunistic pathogens that can depend on soil properties, microbial community and field history. They are known to cause disease rapidly when general suppressiveness of soil is reduced (Postma et al., 2000). Soil suppressive to *Pythium* spp. has been described before, and is usually associated with beneficial $\gamma-$Proteobacteria, and other bacterial strains, actinomycetes, oomycetes, and fungi, with suggested mechanisms including mycoparasitism, production of antibiotics or toxic metabolites, competition for nutrients or space, or induction of systemic resistance in the host plant (Martin and Hancock, 1986; Chen et al., 2012; Mavrodi et al., 2012; Kilany et al., 2015).

We hypothesize that soils with general suppressiveness to pathogens or disease exist in Swedish agricultural systems and that suppressiveness can be linked to the biotic or abiotic conditions or farming practices at the site. In this study, we tested soils taken from fields with different management regimes for biotic and abiotic disease suppressive properties and assessed the soil nematode community and the dominant oomycetes in the soils as potential bioindicators of suppressiveness. The oomycete pathogen *Pythium ultimum* attacking wheat seedlings was used as a model pathosystem to assess general suppressiveness of the soils. *P. ultimum* is a common soil-borne pathogen of many crops and causes damping-off and root rot disease in wheat leading to reduced plant growth or death of seedlings (Hendrix and Campbell, 1973), and has previously been used as a model for soil suppressiveness (Manici et al., 2005). This was an appropriate choice of model system because *P. ultimum* was not recovered from any of these soils, and no *P. ultimum*-associated symptoms were observed during sampling or mentioned during farmer interviews. However, other oomycetes were present. Thus we did not expect soil organisms to provide specific suppressiveness, and any observed effects should have been due to general suppressiveness. General suppressiveness has been previously described for *Pythium* spp. (Pane et al., 2011).

2. Material and methods

2.1. Collection of soil samples

Ten farms in Scania Province (Sweden) representing six management systems that differed as much as possible in their farming practices (Table 1), especially regarding on soil management, were chosen (Supplemental Material Table S1). Where possible, two farms were chosen for each management system. However, only one pasture and one strip tillage farm were included in the study. Semi-structured interviews were performed with the growers managing the sites in order to obtain information about the field history and management practices including soil disturbance, fertilization practices, chemical usage, and rotation schedule. In two cases, the information was acquired via email and telephone.

All soil was collected between 11 and 21 November 2014. On each farm, one field was chosen for the assessment. The field was divided into three areas of approximately 10 × 20 m, which were sampled separately as replicates for that site. The soil was sampled with a 2.0 cm diameter soil bore to a depth of 30 cm. Soil cores were taken in a W-pattern, except at the orchards. In the apple orchards, the soil cores were taken from areas in proximity to the trunk of the trees, where the soil was managed as described. Between 20 and 30 soil cores, representing approximately 2.5 kg of soil were taken from each replicate area, and mixed thoroughly.

Soil samples were transported and stored at 4 °C in darkness until they were processed. Each sample was mixed thoroughly and divided into parcels of approximately 300 ml for the pathogenicity assays, 500 ml for soil testing, and 250 g for nematode analysis. All sampled soils were tested for pH, P, K, Mg, K/Mg, Ca (AL-method, Swedish Standard SS 28310/SS028310T1 and ICP-OES), soil organic matter (SOM) (KLK nr 1 1965 mod.), clay, sand (SS OSO 11277 mod.), cation- and anion-exchange-capacity and base saturation (Eurofins Soil Testing Service, Lidköping, Sweden).