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Effects of *Paenibacillus polymyxa* inoculation on below-ground nematode communities and plant growth

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ABSTRACT

Paenibacillus polymyxa has been shown to have great potential as a bio-fertiliser and biocontrol agent, however information regarding its effect on below-ground biota when used as a soil additive is scarce. Below-ground biota provide vital services to boost plant performance and thus knowledge regarding their response to bio-fertiliser and biocontrol agents is critical for future crop management.

Here, we extracted below-ground nematode (N) and microbial communities (M) and reassembled them in presence and absence of *P. polymyxa* soil inoculation (P). We then assessed the impacts of each of the three components, individually and in combination, on nematode community structure and plant growth.

The main pattern was a gradual shift in the below-ground nematode community from those with increased abundances of omnivorous and plant parasitic nematodes towards those with increased abundances of predatory nematodes along the treatment gradient from N, to N,M to N,P to N,M,P. This shift from increased abundances of omnivores and plant parasitic nematodes to increased abundances of predatory nematodes was significantly positively correlated with plant growth.

In conclusion, our study demonstrates for the first time that inoculation of soil with *P. polymyxa* changes the below-ground nematode community resulting in significant changes to plant growth.

1. Introduction

Meeting the increasing demand for food caused by global population and economic growth is one of the major challenges of the 21st century (FAO et al., 2012). It is predicted that maintaining global food security will require a doubling of agricultural outputs (Tubiello et al., 2007; FAO et al., 2012) and a shift towards the use of more sustainable and eco-friendly bio-fertiliser and biocontrol agents made from plant beneficial microbes. One determinant for plant growth is the intricate interplay between plants and the below-ground biota (van der Heijden et al., 2008; Ferris et al., 2012). It is therefore critical to understand the effect of plant beneficial microbes, when applied as soil inoculum, on below-ground biota. *Paenibacillus polymyxa* is a plant beneficial soil bacterium, that shows great potential for development as a bio-fertiliser and biocontrol agent due to its plant growth promoting traits including nitrogen fixation, phosphorus solubilisation, production of phytohormones and protection against plant pathogens (Lal and Tabacchioni, 2009; Eastman et al., 2014; Grady et al., 2016). Yet information regarding its impact on the below-ground biota and associated processes is scarce.

Nematodes are an abundant and diverse below-ground metazoan community (Bernard, 1992). They provide significant ecosystem services and as such serve as useful indicators for soil quality (Neher, 2001). To date, the impact of *P. polymyxa* on nematodes has only been studied in artificial binary interactions involving a single trophic nematode group where it was observed to have nematicidal activity against plant parasitic nematodes and thereby suppresses plant diseases such as root galling and wilting (Khan et al., 2008; Son et al., 2009). Below-ground nematode communities however, are comprised of 5 different trophic groups: i) *bacterivores*; ii) *fungivores*; iii) *plant parasitic nematodes*; iv) *predators*; v) *omnivores* (Yeates et al., 1993; Bongers and Bongers, 1998). Combined they play important roles below ground e.g. they contribute to nutrient cycling through the mineralisation of nitrogen, they distribute microbes through the soil, they serve as food source for other soil dwelling organisms, and they both contribute to and antagonise plant diseases (Ferris et al., 2012). They also interact with the microbial community within the soil. These interactions can be beneficial to the microbial community, for example root infestation by

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plant parasitic nematodes can lead to 'leakage' of nutrients from damaged plant root systems which results in an enhanced microbial biomass (Yeates et al., 1998) or detrimental, for example bacterivorous nematode activity can lead to a significant decrease in microbial biomass (Bardgett et al., 1999). However, little is known about how the different nematode trophic groups interact and we lack any information on how they are affected by *P. polymyxa*.

In this study we conducted a factorial experiment in controlled conditions which allowed us to assess changes to the below-ground nematode community structure and the resulting effect on plant growth in response to i) the native below-ground microbial community, and to ii) inoculation by *P. polymyxa*. We hypothesised, based on the outcomes of previous binary interaction studies (Khan et al., 2008; Son et al., 2009), that *P. polymyxa* would reduce the abundance of plant parasitic nematodes leading to further changes within the below-ground nematode community. We further hypothesised that this reduction in plant parasitic nematodes would have a beneficial effect on plant growth.

2. Material and methods

2.1. Extraction of nematodes and soil microbial communities

Nematodes were extracted from 5.2 kg of multipurpose compost using a modification of Cobb's decanting and sieving method (Van Bezooijen, 2006) followed by the Baermann funnel methods (Barker, 1985). To remove large particles, soil was washed through a 4 mm aperture sieve. The remaining soil suspension was then stirred vigorously, left to settle for 15 s and then passed through a 250 µm sieve, followed by a 53 µm sieve. The contents of these sieves were then washed into a nematode extraction container lined with a 20 cm Easy Flow Bonded Fibre Milk Filter (GD Textile). This was attached to a glass vial at the bottom for the eventual collection of nematodes (nematode wash). Samples were left for 24 h at 23 °C. The remaining soil suspension was passed through a 35 µm sieve in order to collect the microbial community (microbial wash). The contents of this sieve were washed into test tubes with water. Both the nematode and the microbial extractions were then divided into 4 equal measures for the resulting treatments.

2.2. Sterilisation of seeds and seedling preparation

Arabidopsis thaliana Col-0 seeds were sterilised by immersion in 70% ethanol followed by 50% bleach solution for 10 min and then rinsed twice with autoclaved ddH_2O. Sterilised seeds were germinated on a solid 1/2× Murashige and Skoog medium (Sigma M5524) supplemented with 1.5% agar. For vernalisation, the seeds were incubated at 4 °C for 2 days before growth at 25 °C with 80% relative humidity and a photoperiod of 16h light/8h dark. After 4 days, seedlings were potted into soil, see *Soil treatment*.

2.3. Preparation of the Paenibacillus polymyxa inoculum

Paenibacillus polymyxa strain ATCC 842 (Bacillus Genetic Stock Center) was grown in SOC medium at 30 °C overnight with shaking. The overnight culture was washed twice with Ringer's solution and adjusted to 10^5 colony forming units before being used as soil inoculum, see *Soil treatment*.

2.4. Soil treatment

Multipurpose compost was autoclaved in small batches and a subsample was checked for the presence of nematodes. The nematode free autoclaved compost was then potted into 56 pots (140g per pot). These pots were subjected to the following treatments: C = control (autoclaved soil); M = below-ground microbial community only; P = *P. polymyxa* only; M,P = below-ground microbial community and *P. polymyxa*; N = below-ground nematode community only; N,M = below-ground nematode and microbial communities; N,P = below-ground nematode communities and *P. polymyxa*; N,P,M = below-ground nematode and microbial communities and *P. polymyxa*. N,M hereby represents the most natural condition since both N and M were extracted directly from the soil, while in contrast P was used as external inoculum. Moreover, all individual components originated from the same pool of either N, M, or P respectively, enabling us to directly compare treatments. As defined by the treatment, in addition to *Arabidopsis thaliana* Col-0 seedlings, each pot received 6 mL of nematode wash, 6 mL of microbial wash, 6 mL of 10^5 *Paenibacillus polymyxa* in ringers solution, 6 mL of water (as a control for N and M) or 6 mL of ringers solution (as a control for P). All treatments had 7 replicates except N and N,P which both had 6 replicates. The pots were then incubated in a growth chamber at 25 °C with 80% relative humidity and a photoperiod of 16 h light/8 h dark. Pots were watered daily to field capacity. After one week, we removed all the seedlings and quantified plant growth using plant height which we measured as the height of each seedling from the bottom of the stem to the top of the main plant stem.

Where nematodes were added, we extracted the nematodes using the method detailed above. Each nematode extraction was diluted to 20 mL. The extraction was then mixed thoroughly and 1 mL was placed onto a 1 mL cytometer slide. Nematodes were counted and identified using a Leica M165 C stereo-microscope (Leica Microsystems, Heerbrugg, Switzerland). Identification of the different trophic groups was carried out by observing mouth structure and movement behaviour (Dindal, 1990; Yeates et al., 1993). Using the total nematode count from the 1 mL subsample, we scaled up to obtain the total nematode count for 20 mL. Nematode trophic group frequencies were recorded and a total for the whole nematode extraction (20 mL) was calculated.

2.5. Analysis methods

2.5.1. Nematode trophic group abundance

We used a generalised least-squares approach to test for difference in the abundances of each trophic group between all treatments and the nematode only treatment. Each treatment was categorised using two factors: whether or not below-ground microbial communities were added, and whether or not *P. polymyxa* inoculum was added. We included both factors, as well as the interaction between them, into the model as fixed effects. We also accounted for heterogeneity of variances within the models using the varIdent function (Zuur et al., 2009).

2.5.2. Plant growth

We used linear models to look for difference in plant growth between a) the control group b) the nematode treatment, and c) all the other treatments. Each treatment was categorised using two factors: whether or not below-ground microbial communities, nematodes or both below-ground microbial and nematode communities were added, and whether or not *P. polymyxa* was added. We included both factors, as well as the interaction between them, into the model as fixed effects. As a post-hoc test, we used a Tukey's honest significant difference to test for differences in plant growth between the treatments. Additionally, we correlated the axis one and axis two loadings from the PCoA with plant growth using Pearson's moment correlation tests.

2.5.3. Nematode community composition

We used a Hellinger transformation on the nematode trophic group abundance data to allow Euclidean-based ordination methods to be used. Hellinger transformations are recommended because they do not strongly weight rare species in the analysis (Legendre and Gallagher, 2001). We then used Principal Coordinates Analysis (PCoA) to summarise the effect of the different treatments on the nematode trophic group composition. We extracted the axis one and axis two loadings for each assay for further analysis.

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