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Changes in available nitrogen and nematode abundance in response to *Brassica* seed meal amendment of orchard soil

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ABSTRACT

A better understanding of the effects of Brassicaceae seed meals on resident soil microbial communities is necessary to predict the efficacy of these plant residues as either a biofumigant or organic fertilizer. This study analyzed the influence of high (*Brassica juncea*) and low (*Brassica napus*) glucosinolate content seed meals in addition to myrosinase-inactive derivatives on soil microbial community function with respect to nitrogen (N) cycling. All of the seed meal amendments stimulated nitric oxide (NO) generation in an orchard soil. N-mineralization occurred in response to *B. juncea* seed meal application but the amount of mineralization was reduced by the presence of active myrosinase and corresponding generation of allyl isothiocyanate. Microbial communities responded differentially to seed meal amendments: nematode abundance was enhanced by seed meals with either low glucosinolate or no myrosinase activity whereas fungal and bacterial abundance in soil did not exhibit significant changes in response to any seed meal amendment. In addition to changes in overall abundance, nematode diversity was also modified in response to seed meal amendment and differed among the amendments that enhanced nematode abundance. Collectively, these results indicate that microbial communities and overall soil function respond differentially to both seed meal type/glucosinolate content and isothiocyanate generation. These findings have significance for the efficient use of Brassicaceae residues as a source of plant available nitrogen.

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1. Introduction

Brassicaceae plant residues contain glucosinolates which upon hydrolysis by endogenous myrosinase yield bio-active compounds such as isothiocyanates (ITC), ionic isothiocyanate (SCN^-), organic cyanides, and nitriles (Cole, 1976). These compounds have biocidal activity toward numerous plant pests (Brown and Morra, 1997) including parasitic nematodes (Buskov et al., 2002; Henderson et al., 2009; Izzo and Mazzola, 2007; Zasada and Ferris, 2004) and pathogenic fungi and oomycetes (Manici et al., 1997; Mazzola et al., 2007). As such, soil incorporation of *Brassica* residues has been promoted as an alternative means to attain control of soil-borne plant pathogens in agro-ecosystems through the process termed biofumigation (Kirkegaard et al., 1993; Matthiessen and Kirkegaard, 2006). *Brassica* residues have been most commonly introduced to an agricultural soil system through the traditional technology of green manuring (Matthiessen and Kirkegaard, 2006). However, *Brassica* seed meals, a waste product of the oil extraction process, have emerged as a practical alternative due to higher glucosinolate content and ease of application relative to green manures. The efficacy of seed meal amendments in control of soil-borne plant pathogens is influenced by a number of factors not limited to seed meal particle size (Mazzola and Zhao, 2010), glucosinolate hydrolysis product chemistry and volatility (Bending and Lincoln, 2000), and sensitivity of specific organisms to the released compounds.

Brassicaceae seed meals have differential impacts on a range of organisms resident in agricultural soils not only in their overall influence on the community from a quantitative perspective but also with regard to the duration and spectrum of suppressive effects (Mazzola et al., 2007). Regardless of glucosinolate content, the seed meals *Brassica juncea* (*Bj*SM), *Brassica napus* (*Bn*SM), and *Sinapis alba* (*S. alba*) have been shown to effectively suppress *Rhizoctonia solani* and *Pratylenchus penetrans*, members of the apple replant disease pathogen complex, although only *Bj*SM demonstrates

Abbreviations: *Bj*SM, *Brassica juncea* seed meal; *Bn*SM, *Brassica napus* seed meal; A-*Bj*SM, autoclaved *Bj*SM; A-*Bn*SM, autoclaved *Bn*SM; NO, nitric oxide; qPCR, quantitative polymerase chain reaction; T-RFLP, terminal restriction fragment length polymorphism.

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sustained nematode suppression (Mazzola et al., 2001, 2007). Comparatively, of the three seed meals only *Bj*SM was non-stimulatory to *Pythium* sp. (Mazzola et al., 2009, 2007). Other elements of the soil microbial community are preferentially enhanced by seed meal amendments including *Trichoderma* sp., *Mortierella* sp. (Weerakoon et al., 2012), *Streptomyces* sp. (Cohen and Mazzola, 2006b; Mazzola et al., 2007), and *Pseudomonas* sp. which are enhanced or diminished depending on the source cultivar of the seed meal and the rate of application (Mazzola et al., 2001).

Brassicaceae seed meals can also provide a plant-accessible and economically viable form of nitrogen (N) for organic crop production (Balesh et al., 2005; Borek and Morra, 2005; Snyder et al., 2009). The N content of Brassicaceae seed meals is approximately 6% and significant levels (1–2%) of phosphorous, potassium and sulfur are also present (Mazzola et al., 2007). The availability of N applied in organic forms such as seed meal to plants depends in part upon the activity of soil fauna including bacterivorous nematodes. Microbiovorous nematodes excrete ammonium (NH_4^+) and other nitrogenous compounds through metabolism (Wright and Newall, 1976) and have been shown to increase organic N mineralization and stimulate nitrification (Bouwman et al., 1994). The effect of *Brassica* plant residues on soil fauna has generally been regarded from a plant parasitic nematode perspective, however there are also likely to be significant effects on elements of the free-living nematode population and thus N-cycling.

Mineralization of seed meal N proceeds rapidly, but the rates of N mineralization differ among Brassicaceae seed meal types (Snyder et al., 2010). These differences likely result from varied effects of different glucosinolate hydrolysis products on microbial populations involved in the mineralization process. Studies have demonstrated suppression of bacterial nitrifier abundance (Bending and Lincoln, 2000) and inhibition of nitrification (Brown and Morra, 2009) in response to the application of Brassicaceae tissues and subsequent generation of various glucosinolate hydrolysis products. Although bacteria and archaea are consistently the subject of examination in terms of nitrification and/or denitrification, fungi may also have a prominent role in the N cycle in certain soils (Laughlin and Stevens, 2002). *Fusarium* sp. and *Cylindrocarpon* sp., two fungal genera known to possess denitrification activities (Shoun and Tanimoto, 1991; Usuda et al., 1995), are abundant in orchard soil and exhibit differential responses in density when exposed to seed meal amendments derived from different Brassicaceae species (Mazzola and Brown, 2010; Mazzola et al., 2001).

The complexity of the N cycle in soils imparts an equally diverse set of points in the process with potential to be positively or negatively affected by seed meal amendments. The efficiency of N utilization in agricultural systems employing Brassicaceae seed meals will be dependent not only on the competence of N mineralization processes but also may be influenced indirectly in a time-based manner. The purpose of this study was to determine the effect of Brassicaceae seed meal amendment and myrosinase activity on N mineralization, denitrification and microbial populations resident in orchard soil.

2. Methods

2.1. Soil treatments

Studies were conducted in soil from the Columbia View Research and Demonstration (CV) orchard near Orondo, WA, USA (latitude 47° 37′ 33″ N, longitude 120° 13′ 31″ W) in which the dominant soil type is Burch sandy loam, pH 7.1 (Mazzola, 1998). Soil was collected from a region of the orchard that had not received prior seed meal amendment. Collection occurred in early October 2011 to coincide with enhanced nematode and microbial activity and stored at room temperature (RT) in the dark. Soil was homogenized by hand and aliquoted into seven bins prior to application of amendments. Seed meal from *B. juncea* cv. Pacific Gold (*Bj*SM) and *B. napus* cv. Athena (*Bn*SM) were selected for use based on the relatively high and low glucosinolate contents of 178 μmol g^{-1} (Handiseni et al., 2012) and 25.5 μmol g^{-1} defatted seed meal (Cohen and Mazzola, 2006b), respectively. The N content of *Bj*SM is 6.1% (Hoagland et al., 2008) and *Bn*SM is 5.8% (Cohen and Mazzola, 2006b), and further characteristics of these seed meals have been previously described (Cohen and Mazzola, 2006b; Mazzola et al., 2009). “Powdered” seed meal particle size (Cohen and Mazzola, 2006a) was obtained by sieving through a 1 mm metal mesh. Seed meals were added to soil at a rate of 0.3% (wt dry wt^{-1}) which is equivalent to approximately 183 mg N kg^{-1} dry soil for *Bj*SM and 174 mg N kg^{-1} dry soil for *Bn*SM. To provide a no nematode comparison, the nematicide fenamiphos (Nemacur®) was applied to soil at 50 μg a.i. (active ingredient) g^{-1} soil when specified. The average soil moisture for treated soils was 15.1 ± 3.1%. Soils were homogenized by hand and aliquoted as 125 g into 30 Saranex bags™ (17.8 × 20.3 cm, Bitran® Series “S” bags, Com-Pac International Carbondale, IL). The bags were sealed and incubated at RT for 57 days. Soils that were amended with seed meal and treated with fenamiphos were prepared as above, incubated in duplicate 12.5 g aliquots and analyzed after 21 days for nitric oxide (NO) generation and fungal and bacterial abundance.

Denatured seed meals with diminished capacity to yield isothiocyanate (ITC) (referred to as A-*Bj*SM and A-*Bn*SM) were prepared by autoclaving on a gravity load at 121 °C with 15 psi for 15 min to effectively inactivate the endogenous myrosinase enzyme (Handiseni et al., 2011). To determine whether ITC generation was abolished, soil amended with 6.0% wt dry wt^{-1} heat-treated *Bj*SM was transferred to 160 ml serum vials sealed with rubber septa and incubated at RT for 48–72 h prior to headspace analysis for allyl isothiocyanate (AITC) production as determined by gas chromatography per published protocol (Mazzola et al., 2007). Although the high temperature and pressure treatment undoubtedly altered other chemistries of the seed meal, including glucosinolate (Maheshwari et al., 1980), it was the only treatment of the four tested methods including 2 min microwave step, 6 h 85 °C or 20 h 99 °C treatments, that effectively diminished generation of AITC in *Bj*SM amended soil (data not shown). Retention of AITC by the Saranex bags was determined by incubating 10 g of 0.3% (wt dry wt^{-1}) *Bj*SM-amended soil in Saranex or polyethylene bags in 250 ml flasks sealed with several layers of parafilm. AITC was quantified from the headspace after an overnight incubation at RT.

2.2. N analysis

For each treatment, replicate bags of soil were sampled destructively at nine time points for analysis of NO emission from soil as an estimate of denitrification or loss of N from the system. Soils were mixed well and 5 g samples from each bag were transferred to two 18 × 150 mm glass test tubes. The tubes were sealed with several layers of parafilm and stored at room temperature for 20 h. Tubes were vortexed briefly and NO was measured from the headspace using a Sievers 280i Nitric Oxide Analyzer in which the maximum value was recorded. The remaining soil was frozen at −40 °C. Soil from time points which showed major changes in NO generation was analyzed for NO_3–N and NH_4–N. Triplicate bags of soil from days 3, 21 and 30-post seed meal application were thawed at room temperature for 3 h, dried at 40 °C overnight, extracted in 1 M potassium chloride (KCl) and filtered with a Whatman 40 filter. Ammonium and nitrate were quantified using an Astoria Analyzer (Astoria-Pacific International, Clackamas, OR) equipped with a 305D digital detector, 303A analytical cartridge, 302D

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