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Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production

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ABSTRACT

The abundance and metabolic footprints of soil nematodes were quantified during four of eight years of an intensive organic vegetable production system. Treatment variables included cover crop mixtures and compost application rates. The abundances of bacterivore and fungivore nematodes were enhanced by the annual use of winter cover crops but showed no relationship to the level of residual soil organic matter. Metabolic footprints, based on biomass and respiratory activity, were calculated for functional guilds and ecosystem services of the nematode assemblage. The enrichment footprint, representing the ecosystem service of nutrient mineralization, was related to the level of soil organic carbon. It was strongly related to the metabolic footprint of bacterivore nematodes and both were enhanced in treatments that were cover cropped annually. Cover-cropped treatments also had a slightly higher herbivore footprint, suggesting support of some taxa of plant-feeding nematodes. The structure footprint, reflecting the metabolic activity of higher trophic level nematodes, including the predators of opportunistic species, did not differ among cover crop and compost amendment treatments. However, enrichment footprints were correlated with bacterivore footprints, which represented the predominantly bacterivore resources available to predators. Abundance of predators increased as a function of the abundance of those nematode prey that can be amplified by organic inputs. The functional connectance, represented by spatial co-location, between predators and amplifiable prey was greater in treatments with a greater abundance of predators. The functional connectance between predators and herbivore prey, representing a management target, was strongly related to the functional connectance between predators and amplifiable prey. We conclude that cover crops not only affect organisms at the entry level of the web but that resources are also transferred to higher trophic links which increases top-down pressure on plant-parasitic nematodes.

1. Introduction

A fundamental goal of organic agriculture is stewardship of the functions of the soil food web to optimize essential ecosystem services. Important among such services are the mineralization of molecules from organic to inorganic forms available to plants, and the regulation or suppression of pest species (Ferris et al., 1998; Ingham et al., 1985; Sánchez-Moreno and Ferris, 2007). During mineralization, organic molecules are metabolized by rhizosphere organisms to release energy and to obtain elements essential for their growth. In the regulatory process, feeding by generalist and specialist predators affects the abundance and biomass of organisms that are assimilating resources at the entry level of the soil food web, including herbivores (Sánchez-Moreno et al., 2009). To achieve adequate levels of such ecosystem services, it is necessary to have sufficient biomass and activity of appropriate functional guilds in the soil food web. That requires a frequent or consistent supply of new organic material to fuel the system (Ferris, 2010a).

Through use of cover crops that are incorporated into the soil or mulched on the surface, and the application of composts and manures, soil carbon and soil microbial biomass are usually higher in organic than in conventional agricultural systems (DuPont et al., 2010). Over time, organic systems, with their greater overall C input, retain soil C in progressively more recalcitrant forms and in the elevated biomass of soil organisms. Increased soil C is usually associated with higher soil moisture content, greater retention of essential minerals and improved soil quality (Clark et al., 1999; Glover et al., 2010; Pimentel et al., 2008).

Whereas the nutrient status of soils in conventionally-managed systems can be precisely adjusted with mineral fertilizers, that of organic systems is more difficult to accurately calibrate due to seasonal differences in rates of cover crop growth, differences in their C:N ratios and decomposition rates, and differences in

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compost quality. In conventional systems, chemical fertilizers are often at extremely high concentrations in the water films around soil particles. Such concentrations are toxic to sensitive organisms inhabiting those small volumes of water (Tenuta and Ferris, 2004). Among the nematodes, sensitive taxa include the slow-reproducing, large-bodied predator species that contribute to the regulation of population levels of pest species (Bongers and Ferris, 1999; Ferris, 2010a). The cover crop residues, composts and supplemental fertilizers of organic systems decompose through the metabolic activities of bacteria and fungi. Minerals released slowly from organic amendments are unlikely to achieve levels toxic to soil organisms. Unless organisms that feed on bacteria and fungi are present in abundance, nutrients may become bound in the organic molecules that comprise the biomass of decomposers and, consequently, be unavailable for plant uptake (Ferris et al., 2004).

A stronger conceptual base for soil ecology will emerge from application of broader ecological concepts in interpretation of soil processes (Barot et al., 2007). Applications of synoptic assessments that are explanatory or predictive of ecosystem functions and environmental impacts range from community respiration, the net carbon flux of a system, to the ecological footprint, the area necessary to provide the resources for, and to assimilate the wastes of, a population (Costanza, 2000; Ngao et al., 2012; Regaudie-de-Gioux and Duarte, 2012). Environmental effects of the metabolic activity of microbes, expressed through their production of extracellular metabolites, are described as their metabolic footprint (Mapelli et al., 2008). In soil systems, Mulder et al. (2008) propose faunal biomass flux and distribution as descriptors of ecosystem function. The structure of the nematode assemblage is a useful bioindicator of decomposition pathways, soil nutrient status, environmental quality, and the effects of contaminants (Bongers, 1990; Ferris et al., 2001; Höss et al., 2004; Heininger et al., 2007; Yeates et al., 2009). Besides utilization of C in body and egg production, nematodes have size-dependent metabolic costs (Ferris et al., 1995; Klekowski et al., 1972, 1974). Since both nematode biomass and respiration can be calculated from published morphometric parameters (Andrássy, 1956; Atkinson, 1980), Ferris (2010b) derived the nematode metabolic footprint (NMF). The NMF is a metric of metabolic activity and ecosystem function based on carbon utilization in production and respiration. When integrated with other faunal analysis tools, the NMF infers the activity level of functional guilds.

Food web structure and function are determined by resource supply and by predation and competition among trophic levels of organisms. The diverse organisms in a functional guild may occupy different niches and differ in attributes so that each contributes in a complementary manner to the system function. Consequently, there is a positive relationship between magnitude of the function and diversity within a functional guild (Loreau, 2004; Loreau and Hector, 2001) and loss of biodiversity has negative effects on ecosystem functioning (Heemsbergen et al., 2004). Further, a functional guild is not comprised of a single group of organisms; organisms of different taxonomic groups perform similar functions and services. Diversity thus underpins functional resilience whereby an ecosystem service continues even if conditions become unfavorable for some components of the guild (Ferris, 2010a; Loreau, 2004).

High values of land in the Salinas Valley of California (rental costs currently US \$3000–7000 ha^{-1} yr^{-1}) typically necessitate the production of two or more crops per year to maintain economic viability. Winter cover cropping to improve nutrient cycling and add organic matter to soil is considered a "best management practice" in high-input, intensive vegetable systems in California (Hartz, 2006; Wyland et al., 1996). However, winter cover cropping in addition to production of two cash crops can be challenging because of the time needed to incorporate the cover crop into the soil and allow adequate decomposition before planting subsequent cash crops. The overall objective of this research is to establish a sound basis for stewardship of the structure and function of the soil food web in an intensive organic agricultural system producing two vegetable crops per year and supported by winter cover crops, composts and supplemental organic fertilizers. We explore the application of some novel analyses to interpret and illustrate soil food web structure and function.

2. Materials and methods

2.1. Field characteristics

The field site of this experiment is in the Salinas Valley of California at 36° 37′ 20.82″, 121° 32′ 55.32″. The Salinas Valley is an area of intensive irrigated vegetable production with climate moderated by proximity to the ocean. Between 2003 and 2011, the average air temperature during the winter cover cropping period (October–March) was 11 °C and during the vegetable cropping period (May–September) was 15 °C. (http://wwwcimis.water.ca.gov, Station #89, Salinas South). The average annual rainfall during the eight years of the experiment was 302 mm, concentrated between October and March. The soil type at the experimental site is a uniform Chualar loamy sand (fine-loamy, mixed, thermic Typic Argixerol). The field was used for conventional oat hay production and mixed vegetable and sugar beet trials from 1990 to 1996. Organic production with mixed vegetable and cover crops began at the site in 1997 and the field has been certified organic by California Certified Organic Farmers since 1999. Since organic certification, the field has been in cover crops and in the current experiment.

2.2. Cropping sequence

A legume–rye mixture cover crop was grown on the experimental site in the winter of 2002–2003 and a buckwheat (*Fagopyrum esculentum*) cover crop during the following summer. The Salinas Organic Cropping Systems experiment was initiated by planting cover crops and applying compost treatments (per treatment list, Table 1) in October, 2003; these treatments were repeated each fall. Two cash crops were grown each summer, starting in 2004. Cover crops were incorporated in February or March and followed by a transplanted spring lettuce crop (May–June or June–July) and a summer crop of either spinach (July–August, 2004) or transplanted broccoli (July–September/October 2005 to 2010). Each lettuce crop received preplant supplemental organic fertilizers at a total N application rate of 73 kg ha^{-1} from a combination of pelleted poultry manure and drip-irrigation-applied liquid fish emulsion. Each broccoli crop received 134–168 kg N ha^{-1} from the same pelleted and liquid sources. Green-waste compost (7.6 Mg ha^{-1} d.w., C:N ratio ≈22) was applied to all treatments before each spring and summer crop, except for Treatment 1, which never received compost. Treatments 1 and 2 were fallow during all winter periods except 2006–2007 and 2010–2011, when they were cover cropped with the legume-rye mixture at the high seeding rate. Treatments 3–8 were cover cropped each winter (Table 1). Cover crops in Treatments 4, 6 and 8 were seeded at three times the rate of Treatments 3, 5 and 7 (Brennan and Boyd, 2012a,b).

2.3. Experimental design

The experimental design was a randomized complete block with the eight treatments arranged in each of four blocks in an area 49 m wide and 156 m long. Each plot was 19.5 m long and 12.2 m wide. During the vegetable crops, each treatment area consisted of 12 beds, 102 cm wide. The center 10 beds were used for data collection and the outer beds functioned as inter-plot buffers. Drip irrigation