



Soil treatment-induced differential gene expression in tomato: Relationships between defense gene expression and soil microbial community composition



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ABSTRACT

Soil management affects chemical and microbiological properties of soils in ways that impact plant growth. We examined effects of amendment treatments and contrasting management treatments on chemical and microbiological soil properties and on expression of selected defense genes in laboratory-grown tomatoes (*Solanum lycopersicum*). Treatments imposed on a conventionally managed Maury silt loam included: compost, manure, vetch (*Vicia villosa*), inorganic N, and non-treated control. Non-amended, organically managed Maury soil, collected from the same location was also studied. Compost, manure, and vetch increased total organic C (TOC) and permanganate oxidizable C (POXC) in soil. Organically managed soil also had greater TOC and POXC than the control treatment. Soil N was increased by compost, manure, vetch and inorganic N treatment. Microbial communities from compost, vetch and manure treatments differed from each other and from communities in the other treatments. Defense genes: *ChiB* (chitinase), *Osm* (osmotin), and *GluA* (β -1,3-glucanase) were generally expressed less in plants from manure treated soil and organically managed soil. The *PR1b* (pathogenesis-related protein PR1b) gene was expressed more in plants from compost, inorganic N, and vetch treatments. Defense gene expression was negatively related to Gram-negative bacterial biomarkers, which were greatest in manure treated soil and organically managed soil. These results suggest that increased relative abundance of Gram-negative members of soil microbial communities in manure treated or organically managed soils may indirectly reduce the steady state expression of defense genes in plants, allowing plants to shift resources from defense to other beneficial functions such as fruit or biomass production.

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1. Introduction

Soil management is a critical component of sustainable agroecosystems because it affects soil health and soil quality (Doran, 2002). Because the soil microbial community governs many key soil processes, including turnover of soil organic matter, formation of humus, nutrient cycling, and facilitating good soil structure (Kennedy and Papendick, 1995), understanding

management impacts on this community is important to those interested in sustainable management (Brussaard et al., 2007).

The use of organic amendments can affect the soil microbial community. For example, Larkin et al. (2006) found that animal manures increased bacterial numbers, particularly Gram-negative bacteria, while Buyer et al. (2010) found that a vetch cover crop increased microbial biomass and the proportions of phospholipid fatty acid biomarkers for actinomycetes, fungi, arbuscular mycorrhizal fungi (AMF), and bacteria. Saison et al. (2006) and Larkin et al. (2011) observed that compost affected microbial community composition. Amendment complexity can also affect the microbial community. Schutter and Dick (2001) used fatty acid methyl esters (FAMES) to examine soils amended with cellulose and found them to have elevated levels of fungal biomarkers relative to soils amended with more labile substrates such as glucose or gelatin. Lucas et al. (2014) built on these studies to show that amendments such as hairy vetch and dairy manure could be

Abbreviations: AMF, arbuscular mycorrhizal fungi; FAME, fatty acid methyl ester; MRPP, multi-response permutation procedure; NMS, non-metric multidimensional scaling; POXC, permanganate oxidizable carbon; qPCR, quantitative real-time polymerase chain reaction; SAR, systemic acquired resistance; TOC, total organic carbon.

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used to manipulate the soil microbial community for a specific purpose: promoting fungal proliferation in structurally degraded soils to enhance aggregation. These findings are important given the increased focus among researchers and producers on managing the soil microbial community to promote soil health within agroecosystems (Brussaard et al., 2007).

It has been suggested that soil management can be used to manipulate soil microbial communities to promote plant health (Chaparro et al., 2012). The existence of microorganisms that promote plant growth has been well documented (Glick, 1995; Bent, 2006). Some plant growth promoting soil microbes facilitate plant growth by producing plant hormones, such as cytokinins and gibberellins (Arshad and Frankenberger, 1998). Ryu et al. (2003) found that microbial cytokinin stimulated plant growth in *Arabidopsis* and Mattoo and Abdul-Baki (2006) suggest that microbial cytokinin may play a role in the vetch effect seen in tomatoes by Kumar et al. (2004). Fungi can also have growth promoting effects. Harman et al. (2004) note that some *Trichoderma* species promote plant growth and disease resistance by producing compounds that affect plant proteomics and metabolism. It has also been shown that plant growth promoting organisms affect gene expression in plants (Park and Kloepper, 2000; Bent, 2006). Research involving plant growth promoting microbes has focused on developing inoculants or amendments that promote growth or suppress disease (Sturz and Christie, 2003).

In addition to altering microbial communities, soil management practices have recently been shown to affect plant health via modulation of plant gene expression. Kumar et al. (2004) found that, compared to plants grown in black plastic mulch, tomatoes grown after a vetch cover crop showed a “distinct expression profile of select gene transcripts”. They observed plants grown after vetch to have increased expression of certain nitrogen responsive genes, defense response genes, hormone response genes, and chaperone genes. Kumar et al. (2004) found plants that followed vetch to be healthier, being more resistant to disease and exhibiting delayed leaf senescence. In other studies, Lu et al. (2005) found that some nitrogen response genes in wheat were differentially expressed between manure treated soil and soil fertilized with inorganic ammonium nitrate fertilizer while Kavroulakis et al. (2006) found that tomatoes grown in soils amended with disease suppressive compost had greater expression of pathogenesis related *PR* genes, possibly conferring enhanced disease resistance to the plants. Tenea et al. (2012) were able to differentiate between wheat grown in conventional soils or organically managed soils through ten differentially expressed gene transcripts.

In their review of crop genetic responses to management Mattoo and Abdul-Baki (2006) discuss implications of the work of Kumar et al. (2004), noting that in the “complex web of plant–soil interactions” it is likely that soil microbes play a role in eliciting favorable genetic responses in plants. The idea that microbes in a diverse soil ecosystem can directly benefit plants (beyond the well characterized symbioses involving mycorrhizae or legume-associated nitrogen fixers) has been a key tenet of modern sustainability initiatives (Brussaard et al., 2007). Lau and Lennon (2011) found that *Brassica rapa* L. plants were less productive when grown in artificial media inoculated with autoclaved soil when compared to those grown in media inoculated with nonsterilized soil, providing evidence that microorganisms can affect the health of plants in an agroecosystem. They suggest that the complexity of microbial communities can affect the natural selection of plant traits.

It has long been known that management practices that build soil C also increase microbial biomass and diversity (Kennedy et al., 2004). These microbial changes may play a role in the organic

matter mediated disease suppression described by Stone et al. (2004). As Kavroulakis et al. (2006) noted, some suppressive mechanisms may be related to changes in plant defense gene expression. Some have examined the idea of managing native microbial communities to develop disease suppressive soils (Mazzola, 2004), but little has been done to characterize how management induced microbial shifts affect plant gene expression. This is likely because soil microbial community characterizations are difficult, using indirect measures that may not capture changes within critical microbial functional groups, thus limiting the understanding of interactions between microbes, plants, and the environment. Mattoo and Abdul-Baki (2006) note that research is needed to understand the magnitude of, and mechanisms involved in, soil microbial community impacts on crop genetic responses to management. The conclusions of Kumar et al. (2004) and Mattoo and Abdul-Baki (2006) suggest that soil management-influenced changes in microbial community groups could affect plant health via genetic modulation. To our knowledge there have been no studies attempting to link soil management induced shifts in microbial community structure to changes in plant gene expression. This research was designed to begin to fill this information gap. The objective of this research was to evaluate effects of various amendments and contrasting soil management systems on the expression of selected defense genes in tomato and to examine relationships between differential gene expression and management influenced soil microbial groups. We hypothesized that amendment driven shifts in soil microbial community structure would be related to defense gene expression profiles in tomatoes. Understanding linkages between plant gene modulations and management-induced shifts in microbial communities would be useful to researchers and producers because this information could facilitate development of best management practices in sustainable agroecosystems.

2. Materials and methods

2.1. Soil collection and treatment preparation

In spring of 2012 soil (Maury silt loam: Fine, mixed, active, mesic Typic Paleudalfs) was collected from two fields at the University of Kentucky Horticulture Research Farm in Lexington, KY. One field had been managed conventionally for over 20 years while the other had been managed using certified organic practices since 2004. Management of the conventional soil included frequent, intensive tillage, herbicide treatment for weed control, chemical control of insects, and primary fertility management with inorganic fertilizers. The organically managed field was managed according to National Organic Program guidelines (USDA-AMS, 2000) and included shallow tillage for weed control and seedbed preparation along with the use of various cover crops. Fertility in the organically managed soil was supplemented with compost and manure at various points in its history. Basic properties of the Maury soil from each field are given in Supplemental Table S1. All soil was passed through an 8 mm sieve to remove coarse fragments and larger organic debris and stored at 4°C for two weeks before being used to prepare treatments

Six soil treatments were investigated: (1) control soil (unadulterated conventional Maury), (2) compost amended (3) manure amended, (4) vetch amended, (5) organically managed (non-amended), and (6) inorganic N fertilizer. Vetch was grown at The University of Kentucky Horticulture Research Farm (Lexington, KY), dairy manure came from the University of Kentucky Dairy Research Facility (Lexington, KY) and green-waste compost was purchased (Peaceful Valley Organic Supplies, Grass Valley, CA). Vetch and manure were dried at 65°C, ground, passed through a 2 mm sieve, and allowed to equilibrate to air-dry moisture content.

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