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Research Paper

Activity, diversity and function of arbuscular mycorrhizae vary with changes in agricultural management intensity

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ABSTRACT

Many beneficial soil microbes are sensitive to chemical and mechanical disturbances associated with conventional row crop agriculture, including arbuscular mycorrhizal (AM) fungi. AM fungi provide agricultural benefits through multiple mechanisms including increasing crop pathogen resistance, helping with crop nutrient acquisition, and increasing soil carbon storage. Conversion to less intensive row crop agricultural management systems such as biologically-based organic and no-till may reduce the negative effects of conventional management to AM fungi. In this study, AM fungus activity (via glomalin production), spore diversity, community structure, and community stability were surveyed over 20 years in no-till, biologically-based organic, and conventionally managed plots at the W.K. Kellogg Biological Station Long Term Ecological Research Site in Michigan, USA. A complementary greenhouse experiment tested for direct effects of AM fungal inocula from these different agricultural management treatments on growth of corn and wheat plants. Soil glomalin increased in no-till and organic management systems, most likely due to decreases in disturbance associated with tillage and chemical inputs. No-till management slightly increased AM fungus diversity and community stability. AM fungus community structure significantly differed between conventional and no-till treatments, with an indicator species analysis showing that *Acaulospora* spp. were characteristic of conventional management, while *Glomus* spp. and *Gigaspora* spp. were associated with no-till management. AM fungal inocula from organically-managed treatments increased wheat, but not corn, growth. Overall, conversion from long-term conventional row crop agricultural management to no-till or biologically-based organic systems increased soil glomalin, but did not uniformly improve AM fungus diversity or crop plant benefits. In the future, novel agricultural systems combining organic management with conservation tillage may further improve AM fungal benefits to soils and crops.

1. Introduction

Decades of ecological research have documented negative consequences on aboveground regional biodiversity and ecosystem services associated with intensive agricultural production (McLaughlin and Mineau, 1995; Grandy et al., 2006; Robertson and Vitousek, 2009; Power, 2010; Syswerda and Robertson, 2014). Intensive agricultural management has also been shown to reduce belowground biodiversity and ecosystem functioning across a wide variety of systems. For example, inorganic nitrogen fertilizer application reduced bacterial soil diversity associated with corn (Toljander et al., 2008). Similarly, conventional row crop agricultural management in the upper Midwest, USA reduced bacterial functional gene diversity (Xue et al., 2013). Loss of soil biodiversity has been shown to alter ecosystem function, for example by increasing greenhouse gas production and soil nutrient losses (de Vries et al., 2011). These types of changes may have current and future consequences for agriculture, as effects of climate change create uncertainty for conventional row crop agriculture in major areas of productivity (Funk et al., 2008; Culman et al., 2010).

Many soil microbes are sensitive to chemical and mechanical disturbances associated with agriculture, including arbuscular mycorrhizal (AM) fungi (Brito et al., 2012). AM fungi are root symbionts present in many terrestrial ecosystems and are known to form beneficial associations with nearly all agricultural crops (Douds and Millner, 1999), though commensal and negative

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associations are also possible, especially in high phosphorus or high nitrogen environments (Johnson et al., 2015). AM fungi can provide benefits to crop plants through multiple mechanisms including pathogen resistance and nutrient acquisition (Wehner et al., 2010; Veresoglou et al., 2012). AM fungi can also increase soil ecosystem function. For example, following colonization of the crop root, AM fungi typically create an extensive extra-radical hyphal (ERH) network to explore the soil and transfer nutrients. Both AM fungus spore and ERH cell walls contain a recalcitrant soil glycoprotein known as glomalin (Wright and Upadhyaya, 1996), which may contribute 4–8% of soil organic carbon in natural ecosystems (Treseder and Allen, 2000) and 2–4% of soil organic carbon in agricultural systems (Borie et al., 2006), and also contributes to formation of water stable soil aggregates (Piotrowski et al., 2004). Recent research in agricultural systems has shown positive correlations between AM fungus diversity and glomalin (Rillig, 2004a; Veresoglou et al., 2012). More diverse AM fungus communities are also known to increase plant productivity in natural grasslands (van der Heijden et al., 1998). Unfortunately, these and other potential benefits derived from soil biodiversity are often overlooked in favor of increased chemical and fertilizer inputs to maintain productivity (Drinkwater and Snapp, 2007).

Conversion to less intensive row crop agricultural management systems such as biologically-based organic and no-till may reduce the negative effects of conventional management to AM fungi (Kabir, 2005; Gosling et al., 2006). For example, a study in grain producing farmlands in England found AM fungus diversity increased under organic as compared to conventional management (van der Gast et al., 2011). Similarly, adopting no-till management increased AM fungus abundance, root colonization, and plant tissue N for corn grown in Canada (Kabir et al., 1998). However, these less intensive agricultural systems may still affect soil microbial communities through more limited combinations of chemical (fertilizer/biocides) and mechanical (tillage) disturbance. For example, Hijri et al. (2006) found low AM fungus diversity in both organically managed and intensive conventional row crop systems, possibly due to residual high soil P levels from previous conventional management. Further research is needed to understand how the AM fungus community responds long-term to implementation of different row crop management systems for previously cultivated land.

This study examines how AM fungus communities have responded following conversion from long-term conventional row crop agricultural management to less intensive systems. Specifically, this study asks, How have AM fungus activity, community diversity, stability, and function been altered by conversion to no-till or biologically-based organic management? It was expected that conversion from long-term conventional row crop management to less intensive agricultural management systems would a) increase AM fungus activity, especially when tillage ceases and allows more extensive AM fungus hyphal networks to develop (Kabir, 2005; Verbruggen and Kiers, 2010); b) increase AM fungus diversity, shift AM fungus composition towards more beneficial species, and increase community stability due to cessation of physical and chemical disturbances (e.g., studies in Douds and Millner, 1999; Jansa et al., 2002; Verbruggen and Kiers, 2010); and c) increase functional benefits of AM fungi to crops, especially in organic systems as AM fungus communities are known to be more beneficial in lower-fertility soils (e.g., Johnson et al., 2015). Alternatively, some studies have indicated that conventional row-crop agriculture management can increase the overall stability of AM fungus community structure (Wu and Xia, 2006; Li et al., 2013) and has relatively little effect on AM fungus activity and diversity (Franke-Snyder et al., 2001). Results from this study provide more understanding of how conversion to these reduced intensity row crop agricultural systems may influence AM fungus activity, community diversity, and related ecosystem functioning.

2. Methods

2.1. Site description

The W.K. Kellogg Biological Station Long Term Ecological Research (KBS-LTER) site located in Michigan, USA (42°24′N, 85°24′W) was established in 1989 to evaluate the ecology of row crop agricultural management typical of the north central USA grain producing region. LTER site soils are moderately fertile, well-drained Kalamazoo silt loam (mixed, mesic Typic Hapludalf, sandy to silty clay loam) and the region receives approximately 1000 mm precipitation annually (Crum and Collins, 1995). The Main Cropping Systems Experiment (MCSE) includes seven different annual and perennial agricultural management systems applied to one hectare plots and replicated five times in a randomized block design. The full site description and experimental design is detailed in Robertson (1991). This study focused on three annual agricultural cropping systems in a corn-soybean-wheat rotation: conventional management (CONV; high external chemical inputs with fertilizer and biocide application rates based on soil-test recommendations, and tillage), no-till (NT; high external chemical inputs, no tillage), and biologically-based organic (ORG; no external inputs, tillage and mechanical cultivation, cover-crop). CONV and ORG tillage consisted of moldboard plowing in the spring from 1989 to 1998, and chisel plowing in the spring from 1999 to present. Additional tillage consisted of disking before wheat planting and inter-row cultivation for soybean and corn. The cover crop in the ORG treatment from 1989 to 1993 was hairy vetch (*Vicia villosa* Roth) and from 1994 onward was red clover (*Trifolium pratense* L.) Site history prior to 1989 consisted of mixed agricultural and horticultural cropping for 100+ years, with the most recent years prior to experiment establishment dominated by conventionally managed continuous corn production.

Previous results from the MCSE show that crop yields have been higher in the no-till and conventional compared to the biologically-based organic treatment, especially for corn and wheat harvests. Soil quality is higher in no-till compared to conventional, and soil carbon is higher in biologically-based organic compared to the conventional treatment (Syswerda and Robertson, 2014; Bhardwaj et al., 2011). However, no work has characterized AM fungus responses to management, which may contribute to some of these previous findings.

2.2. Soil samples

In 2012, 50 g samples were taken from archived soils (pooled replicates) from each agricultural management system described above spanning 20 years (1989, 1990, 1991, 1992, 1994, 1998, 2003, and 2008; n = 24). Archived soils from this experiment were limited in volume, and so the eight sampling years were selected in consultation with LTER project managers to balance available soil volume with adequate time coverage. Crops planted in fields varied across sampling years; this study focused on corn and wheat as these were most frequently represented in the archive samples, and so the two samples from soy plantings (1991 CONV and NT) were excluded from all analyses (Table A.1 lists the planted crop associated with each sample). Original annual soil sampling dates were in March or April, with the exception of 1989 when samples were taken in November. Full details of the LTER soil sampling protocol are available at: lter.kbs.msu.edu/protocols/112. Briefly, five samples for each treatment were taken using a standard soil probe (2 cm × 30 cm) from five distinct sampling sites within each of five replicate fields. The original samples were pooled across