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Effect of *Bacillus thuringiensis* (*Bt*) maize cultivation history on arbuscular mycorrhizal fungal colonization, spore abundance and diversity, and plant growth

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ABSTRACT

Greenhouse studies have reported that maize expressing *Bacillus thuringiensis* (*Bt*) insecticidal toxins may have nontarget effects on symbiotic arbuscular mycorrhizal fungi (AMF), however, field studies have not detected the same pattern. This may be due to the short-term nature of previous field experiments, differences in soil properties between studies, or plant-soil feedbacks that influence AMF communities in roots and soil over time. In this field experiment, we used split plots to evaluate the effect of *Bt* or non-*Bt* maize cultivation history on AMF spore abundance, diversity, root colonization, and growth of seven different genotypes of *Bt* maize and five corresponding non-*Bt* parental (P) isolines. We found that *Bt* plants had higher leaf chlorophyll content when they were grown in plots that had been cultivated with *Bt* maize the previous year, and similarly, non-*Bt* plants had higher chlorophyll content when they were grown in plots with a non-*Bt* cultivation history, indicative of a positive feedback effect. There was a lower density of AMF spores in plots with a *Bt* maize cultivation history than in plots where P maize had been grown in the previous year, but no difference in spore diversity. Despite the differences in spore density, we found no significant differences in AMF colonization or root or shoot biomass between plots with a cultivation history of *Bt* and P maize. This study presents the first evidence of an effect of *Bt* maize cultivation on the soil ecosystem, but also provides further evidence that this effect is not necessarily large or easily detectable within the range of normal environmental variation. Management of agroecosystems will need to consider the potential effects of reduced numbers of AMF propagules in soil as this could have an effect on ecosystem processes including carbon sequestration, nutrient cycling, drought tolerance, soil aggregation, and plant resistance to pathogens. Taken together with greenhouse experiments, we can now make predictions on how *Bt* maize cultivation may affect AMF under different environmental conditions.

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1. Introduction

The relationship between genetically modified (GM) plants and arbuscular mycorrhizal fungi (AMF) is an important element of soil ecology research. AMF are ubiquitous in both natural and agroecosystems and form symbiotic relationships with most land plants (Wang and Qiu, 2006; Smith and Read, 2008). In the plant/AMF symbiosis, plants provide carbon to the fungi in the form of photosynthate and AMF provide nutrients (mainly P and N) and water to the plant by effectively increasing the surface area of plant roots (Smith and Read, 2008). While AMF are known to be sensitive to a variety of agricultural factors, including tillage (Douds et al., 1995; Galvez et al., 2001), pesticides (Trappe et al., 1984), and fertilizer applications (Johnson et al., 1991, 2008), it is not well understood how AMF may be impacted by the cultivation of *Bacillus thuringiensis* (*Bt*) protein expressing crops over time, including *Bt* maize (*Zea mays* L.).

Bacillus thuringiensis maize is genetically engineered to express one or more insecticidal toxins derived from *Bt* soil bacteria to protect plants against damage by insect pests including

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lepidopteran, coleopteran, and dipteran larvae (reviewed in Icoz and Stotzky, 2008; Cheeke, 2012). There are more than 60 *Bt* proteins that specifically target certain insect groups (reviewed in Icoz and Stotzky, 2008; Sanchis, 2011). Globally, *Bt* maize is one of the most widely cultivated genetically modified crops, and in 2012, GM varieties comprised 88% of all maize planted in the USA (USDA, 2012). *Bt* proteins work by binding to specific receptors in the guts of susceptible larvae, liquefying the gut and killing the insect (Federici, 1993; reviewed in Bravo et al., 2007). While specific in their mode of action, *Bt* proteins can also enter soil and waterways through root exudates, decomposing plant material, and/or pollen deposition (reviewed in Icoz and Stotzky, 2008; Cheeke, 2012) where they can remain biologically active for at least several months (Tapp and Stotzky, 1998; Zwahlen et al., 2003; Tank et al., 2010). Because of the widespread adoption of genetically modified *Bt* crops worldwide, questions have arisen about the short-term and long-term effects of transgenic crop cultivation on nontarget organisms in the soil ecosystem.

Although benefits of *Bt* crop cultivation may include reduced chemical insecticide use, less insect damage on plants, and lower exposure to insecticides for agricultural workers, recent studies have reported negative effects of some *Bt* plants on arbuscular mycorrhizal fungi (Turrini et al., 2004; Castaldini et al., 2005; Cheeke et al., 2011, 2012), nematodes (Hoss et al., 2008), and nontarget insect larvae (Dively et al., 2004; Rosi-Marshall et al., 2007). Other studies demonstrate no negative effect of *Bt* crop cultivation on AMF (de Vaufleury et al., 2007; Knox et al., 2008; Tan et al., 2011; Verbruggen et al., 2012; Cheeke et al., 2013) and other soil organisms (reviewed in Icoz and Stotzky, 2008; Cheeke, 2012). While there is no evidence of a direct effect of *Bt* proteins on AMF, genetic changes within a plant (either through genetic engineering or traditional approaches) may alter a plant's relationship with symbiotic organisms. For example, if genetic changes within a plant resulted in an alteration of plant root exudates (Bais et al., 2006; Broeckling et al., 2008), enzyme activity (Schaarschmidt et al., 2007), or chemical signals (Akiyama et al., 2005), AMF (and other soil organisms) may be affected. AMF require a plant for survival and obtain their carbon by living within root cells. Thus, AMF may be more sensitive to genetic changes within a plant than other soil organisms, even if they are not affected by *Bt* proteins directly.

Cropping history may contribute to feedbacks that can enhance or inhibit plant–microbe relationships in agricultural systems (Johnson et al., 1991; Bullock, 1992). In the Midwestern United States, crop rotations are commonly employed to mitigate problems associated with monocultures such as nutrient depletion, pathogen buildup, and pest resistance (Bullock, 1992; Kinkel et al., 2011). In natural systems, positive plant–soil feedbacks have been shown to reduce plant diversity while negative plant–soil feedbacks tend to increase plant diversity (Bever et al., 2012). Plant–soil feedbacks have also been shown to alter the AMF community (Bever, 2002; Bainard et al., 2009). For example, plants that have a higher dependence on AMF may lead to higher AMF infection potential of soils than those that do not form AMF associations (Stinson et al., 2006; Callaway et al., 2008; Mack and Rudgers, 2008; Bainard et al., 2009). Thus, a reduced or antagonistic association with AMF may reduce AMF propagules in the soil over time (Vogelsang and Bever, 2009), potentially affecting AMF colonization of roots in subsequent plantings (Gavito and Miller, 1998; discussed in Bever et al., 2012; Koide and Peoples, 2012).

To test whether AMF propagules in the soil are reduced over time in field plots with a history of *Bt* maize cultivation, field plots were cultivated in a single maize genotype in 2009 (Cheeke et al., 2013) and in the following year, paired *Bt*/non-*Bt* maize lines were grown in split plots with either a *Bt* or non-*Bt* cultivation history. We examined whether AMF spore abundance, diversity, or root colonization were lower in plots with a *Bt* cultivation history compared to plots with a non-*Bt* cultivation history and also investigated the effects of cultivation history on plant root biomass, shoot biomass, and leaf chlorophyll content. Based on previous greenhouse studies (Cheeke et al., 2011, 2012) that demonstrated reduced AMF colonization in the same genotypes of *Bt* maize tested here, we hypothesized that AMF propagules would be lower in plots with a history of *Bt* maize cultivation and that AMF colonization would be lower in *Bt* maize compared with their non-*Bt* parental isolines when grown in the same split-plots. We also hypothesized that plants with higher levels of AMF colonization would have higher leaf chlorophyll content and greater shoot biomass as a result of the symbiosis, and that *Bt* and non-*Bt* maize would have a more positive growth response when grown in plots previously cultivated with self than with non-self (i.e., positive feedback response). In this study, 14 different *Bt* and non-*Bt* maize genotypes were utilized to test the effect of plot cultivation history on the density and diversity of AMF propagules in soil, percent AMF colonization of roots, plant growth responses, and plant–soil feedback effects that may influence plant fitness.

2. Materials and methods

2.1. Study site

This field experiment was conducted from May to September 2010 in Corvallis, OR, USA. The Willamette Valley of Western Oregon has cool, wet winters and warm, dry summers. The mean annual low temperature is 5.6 °C, mean annual high temperature is 17.4 °C, and mean annual precipitation is 111 cm/year (NOAA, 2012). The soil at the field site has a clay loam texture (22% sand, 50% silt, and 27% clay), pH 5.7–6.1, medium levels of nitrogen (13–20 ppm NO_3-N) and potassium (333–438 ppm), and high levels of available phosphorus (27–32 ppm Weak Bray) (A & L Western Agricultural Laboratories, Portland, OR, USA) and is classified as Chehalis series fine-silty, mixed superactive, mesic Cumulic Ultic Haploxerolls (Natural Resources Conservation Service, 2012).

2.2. Maize cultivars

We used seven different genotypes of *Bt* maize (*Zea mays*) that exhibited reduced AMF colonization in previous greenhouse studies (Cheeke et al., 2012) and five corresponding non-*Bt* parental (P) base hybrids, representing both sweet corn and field corn (Table 1). The *Bt* genotypes differed in the *Bt* protein expressed (Cry1Ab, Cry34/35Ab1, Cry1F + Cry34/35Ab1, Cry1F, Cry3Bb1) and background genetics. Seeds were obtained from three companies (Syngenta Seeds Inc., Boise, ID, Monsanto Company, St. Louis, MO, and an anonymous seed industry supplier). The P maize seeds obtained from Monsanto Co., were described as non-*Bt* near isoline control hybrids, and the P maize seeds obtained from Syngenta and the other seed industry supplier were described as near isogenic parental base-hybrids or parental isolines.

2.3. Construction of plots

The field site measured 35 m × 5 m and had 28 plots arranged randomly in four incomplete blocks. In 2009, 24 plots were cultivated with a single *Bt* or non-*Bt* genotype to establish a *Bt* or non-*Bt* history and data were collected on AMF spore abundance, diversity, root colonization, and maize growth responses (Cheeke et al., 2013). In 2010, each plant genotype was matched with its *Bt* or non-*Bt* counterpart (Table 1) and grown in split-plots with either a *Bt* or non-*Bt* history. Four additional split-plots were added

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