



Impacts of compost application on the formation and functioning of arbuscular mycorrhizas



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ABSTRACT

With rising fertilizer costs, and concerns about the environmental impacts of excessive fertilizer use, organic matter is increasingly seen as an important source of nutrients in agriculture. This study investigated the impact of different rates of compost addition on the formation and functioning of arbuscular mycorrhizas (AM). A glasshouse experiment was conducted in which a mycorrhiza defective tomato mutant, and its mycorrhizal wild-type progenitor were grown in soil amended with a municipal greenwaste derived compost, at four rates of application. Impacts on the formation and functioning of AM were quantified. While compost addition at low levels of application had little effect on the formation of AM, at higher rates a small decrease in colonization of roots by AMF was observed. Both AM and compost application had a significant impact on plant growth and/or nutrition. Although the formation of AM had relatively little impact on plant growth, plants grew progressively better with increasing compost supply. In contrast, the formation of AM had a strong positive effect on plant P and Zn acquisition, especially at lower rates of compost application. AM and compost can have an important role in agricultural systems, especially those that place a strong emphasis on biologically regulated nutrient supply systems.

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1. Introduction

With rising fertilizer costs, and concerns about the environmental impacts of excessive fertilizer use, there has been increasing scrutiny of nutrient management on farms (Tilman et al., 2002). An important part of this scrutiny has been to identify nutrient sources that can be readily and reliably used to support plant growth (Conyers and Moody, 2009; Hargreaves et al., 2008). It has long been recognized that organic amendments, such as cover crop residues and composts, among many others, contain significant amounts of nutrients than can be used to maintain and enhance plant growth (Quilty and Cattle, 2011). To this end, many farming systems rely solely, or in large part, on organic sources of nutrients. Such farming systems include organic farming, hybrid organic–conventional farming, or as is the case for most of the world's farmers, subsistence farming (Cardoso and Kuyper, 2006; Nelson and Janke, 2007; Placea et al., 2003; Watson et al., 2002).

A major challenge in the use of organic amendments is ensuring that they provide a reliable and predictable supply of nutrients

(Quilty and Cattle, 2011; Rose et al., 2014). Whereas precise amounts of inorganic nutrients can be applied to the soil, and relatively accurate plant responses predicted, this is less often the case with organic amendments. This is because nutrients in organic forms need to be mineralized before they can be taken up by plants (Jackson et al., 2008; Paul, 2006). While this can provide a 'slow release' of nutrients over the course of the growing season, the actual amounts and timing of nutrient release are much less predictable than where inorganic fertilizers are used.

Composts, that is, humified organic matter produced via biologically-mediated oxidative processes (Hargreaves et al., 2008; Quilty and Cattle, 2011; Zmora-Nahum et al., 2007), are one of the most commonly used organic amendments in agriculture (see Quilty and Cattle, 2011, for recent review). In addition to providing an important source of nutrients, they can also increase soil carbon stocks, and help to improve soil structure and water retention (e.g. Caravaca et al., 2002; Raviv et al., 1998). Another key benefit of composts is that they can be readily made on small- or large-scales, and provide a means of disposing of a wide variety of organic waste streams, many of which are produced on farms. It is for this reason that composts have been identified as an important option for managing nutrients on farms.

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The capacity of plants to acquire nutrients is affected by many factors. The formation of arbuscular mycorrhizas (AM), associations between the roots of most terrestrial plant species and a relatively small group of soil fungi, can increase the capacity of plants to acquire nutrients from the soil (Smith and Read, 2008). The fungi do this by growing beyond the nutrient depletion zones that typically form around roots, and by greatly increasing the absorptive surface of the root system. Their rapid growth and high plasticity enables the fungi to exploit nutrient patches in the soil, and to better respond to the tremendously complex spatio-temporal dynamics of soil nutrients (Facelli and Facelli, 2002; Tibbett, 2000). Arbuscular mycorrhizal fungi (AMF) are able to take up nutrients in inorganic forms (Marschner and Dell, 1994). And, while there is some evidence to suggest that AM may access nutrients from organic sources (Hodge et al., 2001; Hodge and Fitter, 2010), this most likely occurs following the mineralization of nutrients in organic matter (see Smith and Smith, 2011 for discussion). Irrespective of the mechanisms involved, it is likely that AMF will be important in helping plants to acquire nutrients released from compost. Although insights have been gained into how compost addition affects the formation of AM, relatively few studies have considered impacts on the functioning of AM (Caravaca et al., 2003; Puschel et al., 2008; Roldan et al., 2006).

The formation of AM, typically measured as percent of root length colonized (Smith and Read, 2008), can be adversely affected when inorganic nutrients, especially P, are added to the soil in large amounts (Baon et al., 1992; Bolan et al., 1984; Watts-Williams and Cavagnaro, 2012). For example, for the mycorrhizal tomato genotype used in this study and grown in the same soil (see below), percent root length colonized was reduced from 85% through 60% to 40% when soil P was increased from 4, 20 and 76 mg plant-available P/kg dry soil. Effects of P supply on the formation of AM are especially relevant to farming systems where large amounts of inorganic fertilizer are added to the soil. In contrast, since composts (typically) provide a sustained release of nutrients over the course of a growing season (or seasons), rather than a large single pulse of nutrients, they may offer a way of supplying nutrients to plants that does not adversely affect the formation of AM. This, however, has not been widely assessed, and results are inconsistent, with compost addition resulting in an increase, a decrease, or no change in mycorrhizal colonization of roots (e.g. Caravaca et al., 2003; Duong et al., 2012; Puschel et al., 2008; Roldan et al., 2006). Furthermore, there is very little understanding of how different rates of compost addition impact upon the formation of AM (Copetta et al., 2011; Valarini et al., 2009). Taken together, if compost and AM are to both be part of on-farm nutrient management, there is need to develop an understanding of how compost applied at different rates affects the formation and functioning of AM.

Whether or not mycorrhizal plants outperform their non-mycorrhizal counterparts, in terms of growth and nutrient acquisition, in systems where composts are used is not well established (Caravaca et al., 2003; Puschel et al., 2008; Roldan et al., 2006). This in part can be explained by the complexities associated with the establishment of appropriate non-mycorrhizal treatments for comparison. Typically, non-mycorrhizal treatments are established by sterilizing the soil to eliminate AMF; however, in doing so other soil biota, including those involved in the decomposition of compost and nutrient mineralization, are also eliminated (Smith and Smith, 1982). While sterilized soils can be back-inoculated with bacterial filtrates after sterilization, this does not completely return all biota to the soil. Another challenge particular to studies using composts, is that even if appropriate non-mycorrhizal treatments are established in which AMF are eliminated and other soil biota are returned to the soil, the compost applied may bring with it

propagules of AMF. One solution for overcoming these issues is the use of mycorrhiza defective mutants that do not form AM and their wild-type progenitors that do form AM (Barker et al., 1998; Rillig, 2004; Watts-Williams and Cavagnaro, 2014). This genotypic approach to controlling for the formation of AM overcomes the need to sterilize soils to establish non-mycorrhizal treatments, thereby ensuring that the biological processes responsible for compost decomposition and nutrient mineralization are unaffected (Cavagnaro et al., 2006). This approach is also not compromised where the compost applied to the soil contains propagules of AMF.

Results of an experiment which investigated the impact of different rates of compost addition on the formation and functioning of AM are reported here. This study asked two specific questions:

1. Is the addition of compost to the soil, at various rates of application, associated with an increase, a decrease or no change in the formation of AM (measured as percent mycorrhizal colonization of roots)?
2. Where compost is applied to the soil at various rates, does formation of AM enhance plant nutrient acquisition and growth?

To answer these questions a glasshouse experiment was conducted in which a mycorrhiza defective mutant and mycorrhizal wild-type genotype pair of tomato (Barker et al., 1998) were grown separately in soil to which compost was applied at rates of 0, 12.5, 25 and 50 t/ha. Since AM play an important role in the acquisition of P and Zn, emphasis is placed on plant P and Zn nutrition. The tomato genotypes used in this study have been used extensively in the study of AM in the laboratory and field (e.g. Cavagnaro et al., 2008; Cavagnaro and Martin, 2011; Marschner and Timonen, 2005; Watts-Williams and Cavagnaro, 2012), but not with composts. Importantly, these genotypes are matched in terms of growth in the absence of AMF (Cavagnaro et al., 2004). Thus, this genotypic approach to controlling for the formation of AM provides a unique, and minimally invasive way, of studying AM-compost interactions with the wider soil biota interact.

2. Materials and methods

2.1. Soil, compost and plants

Plastic, free-draining pots (130 mm diameter) were filled with 1 kg of a 20:80 (W/W) soil:sand mixture. The field soil, which was collected from Wallenjoe Swamp State Game Park (Lat. = -36.471935, Long. = 144.868512) situated near Rochester in northern Victoria, Australia, is a loam. This soil has a pH of 6.4 ± 0.4 , a total C content of $1.9 \pm 1.1\%$, a total N content of $0.2 \pm 0.1\%$, and has low concentrations of plant available P (12.8 ± 7.4 mg P/kg soil) and diethylene triamine pentaacetic acid (DTPA)-extractable Zn (1.2 ± 0.7 mg Zn/kg soil). The sand was a coarse washed river sand. This soil:sand mixture, which is referred to as 'soil' hereafter, was used as it further reduces soil nutrient concentrations (plant-available (Colwell) P = 3.8 ± 1.5 mg P/kg soil; DTPA-extractable Zn 0.13 ± 0.3 mg Zn/kg soil), has a high AMF inoculum potential, and permits ready and complete extraction of fine roots at the time of harvest (Watts-Williams and Cavagnaro, 2012).

A municipal greenwaste compost was used in this study. Details of the preparation of the compost are given in Ng et al. (2014). Key physicochemical properties of the compost (Mean \pm S.E.) were: Plant-available (Colwell) P = 1459 ± 30 mg/kg, pH = 8.4 ± 0.1 , DTPA-extractable = Zn 82 ± 2 mg Zn/kg, Total C = $16.9 \pm 0.3\%$, Total N = $1.5 \pm 0.003\%$, C:N ratio 11.4 ± 0.2 . The compost was applied to the soil by placing a layer of compost on the surface of the soil in the pots at rates of 0, 29.9, 59.8 and 119.6 g of compost per pot, which

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