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Arbuscular mycorrhizal effects on plant water relations and soil greenhouse gas emissions under changing moisture regimes

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ABSTRACT

Increased nutrient and/or water uptake by AM symbiosis may affect soil biochemical properties and greenhouse gas (GHG) emissions. A greenhouse experiment was carried out to compare mycorrhizal tomato (76R MYC) and its non-mycorrhizal mutant (*rmc*) on the CO_2 and N_2O emissions from an organically-managed soil. Plants were grown for 10 weeks in pots with compost amended soil and subjected to two consecutive dry down cycles to simulate changing moisture regimes in the field. Dry downs were applied gradually through controlled watering treatments. The effects of AM and soil moisture in GHG emissions were assessed in root in-growth PVC cylinders installed in the pots. Gas samples were taken from the cylinders using static chambers 4 h after each watering event. Photosynthetic rates and stomatal conductance of the plants were assessed after watering using a field portable open flow infra-red gas analyzer. Soil moisture was monitored throughout the experiment. Plant biomass and total shoot N, P and K as well as soil content of DON, DOC, NH_4^+–N, NO_3^-–N and microbial biomass C, were assessed at harvest. For the same shoot growth and nutrient content, *rmc* plants allocated more resources to root biomass than mycorrhizal plants. AM symbiosis improved the capacity of the plants to adapt to changing soil moisture, increasing photosynthetic rates and stomatal conductance at high soil moisture but decreasing them when soil moisture was lower. In addition AM symbiosis helped to regulate N_2O emissions at high soil moisture. Control over N_2O emissions by AM plants seemed to be driven by a higher use of soil water and not by increased N uptake.

1. Introduction

Interactions between roots and soil microorganisms control nutrient availability and uptake by plants and affect soil greenhouse gas (GHG) emissions (carbon dioxide (CO_2) and nitrous oxide (N_2O)) (Jackson et al., 2008; Philippot et al., 2008; Frank and Groffman, 2009). Arbuscular mycorrhizal (AM) fungi constitute one of the most widespread root-microorganism symbiotic associations (Smith and Smith, 2011). This symbiosis increases the uptake of soil nutrients in exchange for photoassimilated carbon compounds (Kiers et al., 2011; Fellbaum et al., 2012). In addition to their well-known role in P nutrition, AM symbiosis mediate the uptake of several forms of soil N, particularly inorganic N (Mäder, 2008; Ruzicka et al., 2012). Using a wild-type mycorrhizal tomato plant and a closely related reduced mycorrhizal colonization mutant (*rmc*) (Barker et al., 1998), Ruzicka et al. (2012) showed that mycorrhizal roots use soil N differently than *rmc* plants based on the expression of different genes involved in N uptake. In addition, higher N uptake is generally observed in the mycorrhizal genotype (Cavagnaro et al., 2006, 2012). By enhancing N uptake and assimilation, AM symbiosis reduces the risk of N loss through nitrate leaching (Asghari and Cavagnaro, 2012), and could also reduce the loss of N from the ecosystem as N_2O. Yet, few studies have been conducted on the role of AM symbiosis on N_2O emissions (Veresoglou et al., 2012). Cavagnaro et al. (2012) observed that field-grown plants of the mycorrhizal tomato genotype had higher N uptake but no effect on soil N_2O emissions. This same study, reported higher CO_2 emissions in the mycorrhizal plants than in the non mycorrhizal mutants. It has been previously suggested that the AM symbiosis can influence soil CO_2 emissions either due to direct respiration of the fungi or due to indirect impacts on heterotrophic microorganisms (Johnson et al., 2002; Langley and Hungate, 2003; Zhu and Miller, 2003; Cavagnaro et al., 2008).

The AM symbiosis may also influence soil biogeochemical processes and GHG emissions through the change in soil physical properties such as soil water holding capacity (Augé, 2004;

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Cavagnaro et al., 2006). Soil GHG emissions are largely conditioned by the prevailing soil moisture. Soil water content has large influences in soil microbial communities altering mineralization, gas diffusivity, oxygen availability, nitrification and denitrification processes (Blagodatsky and Smith, 2012). Previous experiments in agricultural soils in California observed that CO_2 emissions peaked at 60% water-filled pore space (WFPS) whereas N_2O emissions were larger at higher soil moisture (>60% WFPS) (Burger et al., 2005). Besides the indirect effects on soil water retention, a large body of scientific evidence shows that AM symbiosis modifies plant water relations making them more resistant to water stress as compared to non-mycorrhizal plants (see review by Augé, 2001). When soil moisture decreases, stomatal conductance generally remains unaffected for longer in mycorrhizal than non-mycorrhizal plants (Duan et al., 1996). Similarly, mycorrhizal plants frequently exhibit higher photosynthetic rates at lower soil moisture conditions, showing a higher tolerance to drought and intrinsic water use efficiency (Augé, 2001; Ruiz-Lozano et al., 2012). The larger plant size typical of mycorrhizal plants may increase deeper exploration of soil water and nutrients by hyphae and thus result in a higher photosynthetic rate (Augé, 2001; Birhane et al., 2012). Nevertheless, differences in water relations between mycorrhizal and non-mycorrhizal plants are also observed between plants of similar size and nutrient content (Kothari et al., 1990). If mycorrhizal plants maintain higher stomatal conductance as soil dries, their greater water absorption could result in lower soil moisture compared to non-mycorrhizal plants, thus potentially altering soil biogeochemical cycles and GHG emissions (Augé, 2001, 2004).

The use of fungicides and tillage by intensive agriculture has shown to dramatically reduce the presence of the AM symbiosis (Kjøller and Rosendahl, 2000; Oehl et al., 2004). The role of AM symbiosis on plant and soil GHG emissions might be particularly important in organically-managed systems where the use of fungicides is avoided. Further, in these systems nutrient inputs are usually lower and provided in the form of slow-release organic fertilizers such as composted materials. Thus, the reliance on biological soil interactions for the release and uptake of plant nutrients is higher than in conventional cropping systems (Drinkwater et al., 1995). AM symbiosis of plant roots has the potential to increase water and nutrient use efficiency and thereby improve environmental quality in agroecosystems (Gianinazzi et al., 2010; Jackson et al., 2012). Understanding the role of this and other plant–microbe interactions in plant nutrition and biogeochemical cycles is therefore critical for the development of sustainable agricultural practices based in the intensification of naturally-existing ecological processes. This study examined how the AM symbiosis influenced the nutrition, water relations and physiology of tomato plants, as well as the emissions of CO_2 and N_2O from soil under changing soil moisture regimes and organic fertilization with compost. We hypothesized that mycorrhizal plants would decrease N_2O emissions as compared to plants with reduced mycorrhizal colonization through modulation of plant nutrient and water uptake and its effects on soil microbial and biochemical processes. To test this hypothesis, a controlled greenhouse experiment used the mycorrhizal and *rmc* genotypes described above. This allowed the study of the impacts of the AM symbiosis on plant and soil processes, without sterilization of the soil to establish a non-mycorrhizal control, thereby maintaining intact soil microbial processes in the field. In this experiment the two genotypes were grown in a compost-amended soil from an organic farm, rich in organic N, and were subjected to changes in soil moisture to mimic wet–dry cycles and the patchy moisture distribution typically found under field conditions (Burger et al., 2005).

2. Material and methods

2.1. Plants, soil and compost

The mycorrhizal defective tomato mutant with reduced mycorrhizal colonization (*rmc*) and its wild type progenitor *Solanum lycopersicum* cv. 76R MYC (Barker et al., 1998) were grown in a greenhouse pot study. Seeds were surface-sterilized and germinated in 72-well trays with peat moss and grown for 6 wk prior to transplanting. The soil, a fine-silty, mixed, superactive, calcareous, thermic Typic Endoaquepts (16.2% clay, 57.9% silt, 25.8% sand), was collected from an organically managed farm (Durst Organic Growers, Esparto, Yolo County, California) and subsequently sieved through a 1 cm mesh screen. Soil from this farm has been previously reported to provide mycorrhizal colonization of 15–25%, which is typical of well-colonized tomato (Cavagnaro et al., 2006; Ruzicka et al., 2012). After sieving, soil was mixed with sterilized sand in a 4:1 (soil:sand) ratio to increase soil particle size and facilitate gas diffusivity and watering in the greenhouse pots. Final particle size distribution was 9.8% clay, 34.1% silt, and 56% sand. The potting soil was subsequently amended with compost at a rate of 7.8 T ha^{-1} as recommended for processing tomato production in California (Hartz et al., 2008).

The compost was provided by Greenbelt Carriers (Dixon, Yolo County, California) and produced from a mixture of cow (40%), goat (20%), sheep (20%), and horse manure (15%), with oak shavings (5%). Soil and compost properties are summarized in Table 1. Compost amendment provided 34, 2 and 57 mg kg^{-1} of N, P and K respectively. The compost and potting soil were thoroughly mixed and incorporated into the 12 L pots at a bulk density of 1.1 g cm^{-3}, similar to typical field conditions. The effects of moisture regimes and mycorrhizal colonization on soil N_2O and CO_2 emissions from pots were assessed in root in-growth cylinders installed in the pots (Fig. 1). Cylinders were made from PVC pipe 10 cm in depth and 13.5 cm in diameter. Cylinders had 8 evenly spaced holes (3.5 cm in diameter) on the side of the cylinder to facilitate root growth. The bottom of the cylinder and the side holes were covered with plastic 1 mm mesh. Cylinders were filled with the same potting soil/compost mix as the rest of the pot. During pot set up, cylinders were buried 8.5 cm from the soil surface and 1.5 cm was above the surface.

Pots were watered with distilled water to field capacity which was 22% gravimetric soil moisture, prior to transplanting. Briefly, pots were gently watered until excess water started to drip through the bottom; pot weights were recorded after the excess water drained. Subsequently, one 6-wk old tomato seedling (76R MYC or *rmc*) was transplanted in each pot on 16 August, 2011. Seedlings were transplanted at least 5 cm away from the cylinders. There were 40 pots in total with 20 pots per genotype.

2.2. Moisture regimes

The pots were watered daily to 20% gravimetric soil moisture by replenishing water loss from a pre-set pot weight. Two moisture

Table 1
Physicochemical properties of the farmland soil (without compost) and the compost used in the experiment.

	Soil	Compost
Bulk density (g cm^{-3})	1.16	Not applicable
Total C (μg g dw^{-1})	$11.9 \cdot 10^3$	$175 \cdot 10^3$
Total N (μg g dw^{-1})	$1.7 \cdot 10^3$	$10.4 \cdot 10^3$
NH_4^+–N (μg g dw^{-1})	8.31	648.2
NO_3^-–N (μg g dw^{-1})	8.08	1.29
Olsen-P (μg g dw^{-1})	35.4	674
K (μg g dw^{-1})	$3 \cdot 10^3$	$18 \cdot 10^3$
$\delta^{15}N$	4.7	11.4