

Effects of mycorrhizal roots and extraradical hyphae on ^{15}N uptake from vineyard cover crop litter and the soil microbial community

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Abstract

The objectives of this study were to evaluate the contribution of arbuscular mycorrhizal (AM) fungal hyphae to ^{15}N uptake from vineyard cover crop litter (*Medicago polymorpha*), and to examine the soil microbial community under the influence of mycorrhizal roots and extraradical hyphae. Mycorrhizal grapevines (*Vitis vinifera*) were grown in specially designed containers, within which a polyvinyl chloride (PVC) mesh core was inserted. Different sizes of mesh allowed mycorrhizal roots (mycorrhizosphere treatment) or extraradical hyphae (hyphosphere treatment) to access dual labeled ^{15}N and ^{13}C cover crop litter that was placed inside the cores after 4 months of grapevine growth. Mesh cores in the bulk soil treatment, which served as a negative control, had the same mesh size as the hyphosphere treatment, but frequent rotation prevented extraradical hyphae from accessing the litter. Grapevines and soils were harvested 0, 7, 14, and 28 days after addition of the cover crop litter and examined for the presence of ^{15}N . Soil microbial biomass and the soil microbial community inside the mesh cores were examined using phospholipid fatty acid analysis. ^{15}N concentrations in grapevines in the hyphosphere treatment were twice that of grapevines in the bulk soil treatment, suggesting that extraradical hyphae extending from mycorrhizal grapevine roots may have a role in nutrient utilization from decomposing vineyard cover crops in the field. Nonetheless, grapevines in the mycorrhizosphere treatment had the highest ^{15}N concentrations, thus highlighting the importance of a healthy grapevine root system in nutrient uptake. We detected similar peaks in soil microbial biomass in the mycorrhizosphere and hyphosphere treatments after addition of the litter, despite significantly lower microbial biomass in the hyphosphere treatment initially. Our results suggest that although grapevine roots play a dominant role in the uptake of nutrients from a decomposing cover crop, AM hyphae may have a more important role in maintaining soil microbial communities associated with nutrient cycling.

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1. Introduction

Arbuscular mycorrhizal (AM) fungi benefit grapevines (*Vitis vinifera*) in terms of improved shoot and root growth (Schubert et al., 1988; Biricolti et al., 1997; Linderman and Davis, 2001), higher tissue concentrations of P (Biricolti et al., 1997), and the production of a more compact, highly branched root system (Schellenbaum et al., 1991). In the field, AM fungi naturally colonize grapevine roots, as demonstrated by studies on indigenous AM fungi in California vineyards (Menge et al., 1983; Cheng and

Baumgartner, 2004b) and in other grape-growing regions (Possingham and Groot-Obbink, 1971; Deal et al., 1972; Nappi et al., 1985). When AM fungi do not naturally colonize grapevine roots, such as after soil fumigation, they may suffer severe nutrient deficiencies (Menge et al., 1983). The results of these studies collectively support the hypothesis that AM fungi play essential roles in grapevine nutrition.

Vineyard cover crops have been shown to enhance indigenous populations of AM fungi in vineyard soils and grapevine roots (Baumgartner et al., 2005; Cheng and Baumgartner, 2005). Vineyard cover crops host AM fungi, with the notable exception of *Brassica* species (e.g. *B. nigra* (L.) Koch) (Schreiner and Koide, 1993). In California,

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planting cover crops in between vineyard rows is a common practice during the dormant season, used mainly to reduce soil erosion from winter rains, and also to improve soil fertility and structure (Ingels et al., 1998). Overlap of grapevine and cover crop roots may encourage interactions among grapevines, cover crops, and AM fungi, such as the formation of common mycorrhizal networks.

Previously, we found evidence of direct nutrient transfer from cover crops to grapevines via AM fungal links (Cheng and Baumgartner, 2004a). N transfer was significantly greater from the grass, *Bromus hordeaceus* L. ssp. *molliformis* (Lloyd) Maire & Weiller cv. Blando, to the grapevine than from the legume, *Medicago polymorpha* L. cv. Santiago, to the grapevine. Our findings demonstrated that certain cover crop species may be better than others at enhancing AM fungi-mediated nutrient transfer from cover crops to grapevines, possibly by hosting different AM fungal species or by supporting a greater root biomass.

Cover crop management practices, specifically mowing and tilling, may also affect AM fungi-mediated nutrient transfer from vineyard cover crops to grapevines. In spring, no-till cover crops are mowed and their root systems remain intact, whereas the shoots and roots of tilled cover crops are incorporated into the soil. Grapevines have been shown to utilize N from cover crops soon after tilling (Patrick et al., 2004). Extraradical hyphae extending from mycorrhizal roots may absorb nutrients from decomposing cover crops, given their abilities to accelerate decomposition and acquire N directly from complex organic materials, such as grass shoots (Hodge et al., 2001). In addition, they can proliferate organic materials and recycle mineralized nutrients efficiently, thereby improving host nutrient uptake from decomposed organic materials (St John et al., 1983; Aristizábal et al., 2004). Therefore, grapevines with higher mycorrhizal colonization may have a greater capacity to utilize nutrients from decomposing cover crop material than grapevines with minimal root colonization.

AM fungi may affect other soil microbes associated with decomposition of cover crops, given that their extraradical hyphae distribute photosynthesis-derived carbon (C) to the soil and, thus, contribute to the labile pool of C that other soil microbes utilize. The AM fungal hyphosphere, the zone of soil affected by the extraradical hyphae (Marschner, 1995), may support a distinct microbial community within the mycorrhizosphere, the zone of soil affected by both the root and hyphal components of a mycorrhiza (Linderman, 1988). Distinctions in the microbial communities between the mycorrhizosphere and hyphosphere may be attributed to differences in C and other nutrients derived from plant roots and hyphae. Extraradical hyphae, which grow extensively in root-free soil and form networks between adjacent host plants, are the most dynamic and functionally diverse, but the most poorly understood, components of the symbiosis (Staddon et al., 2003; Leake et al., 2004). Their functional significance within the mycorrhizosphere and as part of the soil microbial

community has long been ignored until recently with the application of advanced techniques (Leake et al., 2004), such as the use of isotope tracers and phospholipid fatty acid (PLFA) markers.

The goal of this study was to examine AM fungi-mediated nutrient uptake from a tilled vineyard cover crop, *M. polymorpha* L. cv. Santiago. Specific objectives were to: (1) evaluate the contribution of AM fungal hyphae, relative to that of grapevine roots, to ^{15}N uptake from the decomposing cover crop, (2) quantify the response of the soil microbial community to the decomposing cover crop under the influence of mycorrhizal roots (mycorrhizosphere effects) or hyphae (hyphosphere effects), and (3) examine the effects of AM fungal hyphae, relative to that of grapevine roots, on decomposition of the cover crop tissue.

2. Materials and methods

2.1. Experimental design

Grapevines used in this study were *V. vinifera* L. cv. Cabernet Sauvignon (ENTAV clone 338), grafted onto 110 R rootstock (*V. berlandieri* Planch. X *V. rupestris* Scheele). We utilized the same container and mesh core design as in our previous labeling study with grapevines and cover crops (Cheng and Baumgartner, 2004a), but in this experiment no cover crops were grown inside the mesh core. Grapevines were grown in containers (20 cm diameter \times 25 cm depth) within which a polyvinyl chloride (PVC) mesh core was vertically inserted. Mesh cores, modified from a design by Johnson et al. (2001), were constructed by cutting four windows into a 25-cm-long section of PVC pipe (6.8 cm inner diameter, 7.2 cm outer diameter), which removed approximately 50% of its external surface. The inner and outer surfaces of each pipe were then wrapped with a layer of either 1 mm plastic mesh to allow grapevine roots to penetrate the mesh core, or 25- μm stainless-steel mesh to exclude roots. A piece of 2-mm-thick plastic mesh (8 \times 7 cm²) was inserted at each window between the two layers of 1-mm or 25- μm mesh, in order to create an air gap. Containers were randomly arranged on one greenhouse bench in a completely randomized design. The growth medium consisted of a 1:1 mixture of field soil (collected from a winegrape vineyard in Napa, CA, USA) and sterile sand. The soil and sand mixture contained 0.07% total N, 38 $\mu\text{g g}^{-1}$ of Olsen P, and 4 $\mu\text{mol g}^{-1}$ of exchangeable K with 102 $\mu\text{mol g}^{-1}$ of cation exchange capacity.

Dormant grapevines, obtained from a commercial grapevine nursery in California, were rooted in pots in the greenhouse. Dormant roots of field-propagated grapevines contain AM fungi that serve as inoculum for new roots (Cheng and Baumgartner, 2004b). To increase mycorrhizal colonization of the grapevines, chopped grapevine fine roots and rhizosphere soil, collected from the same vineyard we obtained field soil from, were added

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