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Short communication

Arbuscular mycorrhizal modulation of diazotrophic and denitrifying microbial communities in the (mycor)rhizosphere of *Plantago lanceolata*

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A B S T R A C T

Impacts of divergent arbuscular mycorrhizal (AM) fungi, *Glomus intraradices* and *Gigaspora margarita*, on denitrifying and diazotrophic bacterial communities of *Plantago lanceolata* in nutrient-limited dune soil were assessed. We hypothesized AM species-related modifications that were confirmed in respective bacterial *nir*K and *nif*H sequence polymorphism -based community clustering and community variance allocation. The denitrifying community appeared more responsive to AM fungi than the nitrogen-fixing community. Nevertheless, the main explanatory variable, in both cases, was plant age. We conclude that AM fungi can modify N-cycling microbial rhizosphere communities and future work should aim to verify the functional significance and mechanistic basis.

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The rhizosphere is commonly defined as the volume of soil around living plant roots influenced by rhizodeposition. Rhizosphere organisms have a high dependence on root derived carbon (Jones et al., 2009) and, consequently, on the factors that modify patterns of rhizodeposition, such as plant species and age (Marschner and Timonen, 2005), nutrient and health status (Jones et al., 2004) and root architecture (Doussan et al., 2009). Additionally, the nature and extent of arbuscular mycorrhizal (AM) associations appears a crucial factor influencing rhizosphere microbial communities (e.g. Bonfante and Anca, 2009; Hartmann et al., 2009). Glomeromycotan fungi are ubiquitous symbionts of the roots of most terrestrial plants (Wang and Qui, 2006) and influence the rhizosphere through effects on root development (Hooker et al., 1992; Berta et al., 1995), rhizo- (Jones et al., 2004) and AM hypho- (Hooker et al., 2007) deposition. Marschner et al. (2001) were the first to demonstrate differential bacterial communities in mycorrhizal vs. non-mycorrhizal plants via 16S rDNA-DGGE profiling whilst studies, utilizing PLFA analysis or t-RFLP analysis of 16S rDNA amplicons, suggest that AM fungal identity may be a significant factor shaping total bacterial community composition in *in vitro* transformed root culture (Scheublin et al., 2010), pot experiments (Rillig et al., 2006) or under field conditions (Singh et al., 2008). Whilst delivering information on diversity and specificity of AM fungi–bacteria interactions, these markers do not address the likely functional importance of this specificity. It can be hypothesized that AM colonization, predominantly through effects on (mycor) rhizosphere carbon flow, will have an impact on the structure of soil N-cycling bacterial communities. Here we provide a first report on AM–species-specific modulation of diazotrophic and denitrifying bacterial communities under nutrient-limited soil conditions.

The experimental design comprised *P. lanceolata* plants that were either non-mycorrhizal (designated NM) or colonized by *G. intraradices* (GI; B.B/E (Biorize, France)) or *Gigaspora margarita* (GM; BEG 34, Biorize, France). These treatments were established in a pre-sterilized sandy loam (pH: 5.76, organic C: 2.06%) re-inoculated with a prokaryotic community extracted from the

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original soil. As an additional non-sterile (NS) treatment, *P. lanceolata* were grown in the original soil allowing root colonization by indigenous AM fungi. The experimental set-up has been described in detail in Veresoglou et al. (2011). Treatment replicates ($n = 4$) were harvested and rhizosphere soil (defined as that tightly adhering to roots) was extracted at the time of planting (non-sterilized (NS0) and sterilized re-inoculated (SR0) soil) and from the 2nd- (NS2, NM2, GI2, GM2) and 7th- (NS7, NM7, GI7, GM7) week harvests for DNA extraction (Griffiths et al., 2000). DNA was amplified using primers targeting fragments of genes encoding the nitrogenase reductase (of *Herbaspirillum* and other α- and β- Proteobacteria; *nif*H-b1; Burgmann et al., 2004) and copper-containing nitric oxide reductase (*nir*K; Hallin and Lindgren, 1999) enzymes involved in nitrogen fixation and denitrification, respectively. Microbial community fingerprints were obtained using denaturing gradient gel electrophoresis (DGGE) and the resulting gels were digitized and analyzed using clustering analysis (Shimodaira, 2002) and non-parametric analysis of variance (PERMANOVA) (Anderson, 2001). Further methodological information is provided in the Supplementary material.

Clustering community profiles of denitrifiers revealed time to be the main causal factor (Fig. 1a, Table 1). Two week-old sterilized re-inoculated soil samples (NM2, GI2, GM2; Fig. 1a) resembled those taken on the day of planting (both non-sterile (NS0) and sterilized re-inoculated (SR0)) whereas 7th week sterilized re-inoculated samples (NM7, GI7, GM7) resembled non-sterilized samples of the 2nd week (NS2). Although, non-mycorrhizal and mycorrhizal samples formed distinct clusters two weeks after initiation of the experiment, five weeks later *G. intraradices* inoculated samples resembled more those of the non-mycorrhizal treatment (Fig. 1a). In a corresponding PERMANOVA, the interaction terms of the mycorrhizal and *Gi. margarita* variables with time explained a high proportion of the variance (Table 1). By contrast, cluster analysis of diazotrophs revealed an increased level of divergence with time (Fig. 1b). This resulted in a chained clustering pattern, with the main group consisting of samples from the day of planting (NS0, SR0) and the samples of the 2nd week (NS2, NM2, GI2, GM2). Treatment effects were less pronounced and replicates rarely clustered together (Fig. 1b). PERMANOVA revealed that time explained most of the variability and treatment effects accounted for less variance than in the case of the denitrifying community. Interaction terms were of marginal importance (Table 1).

The ability of AM fungi to bring about a differential species-specific shift in (mycor)rhizosphere bacterial communities was in agreement with earlier studies (e.g. Marschner et al., 2001). Of particular note was the differential response of denitrifiers and

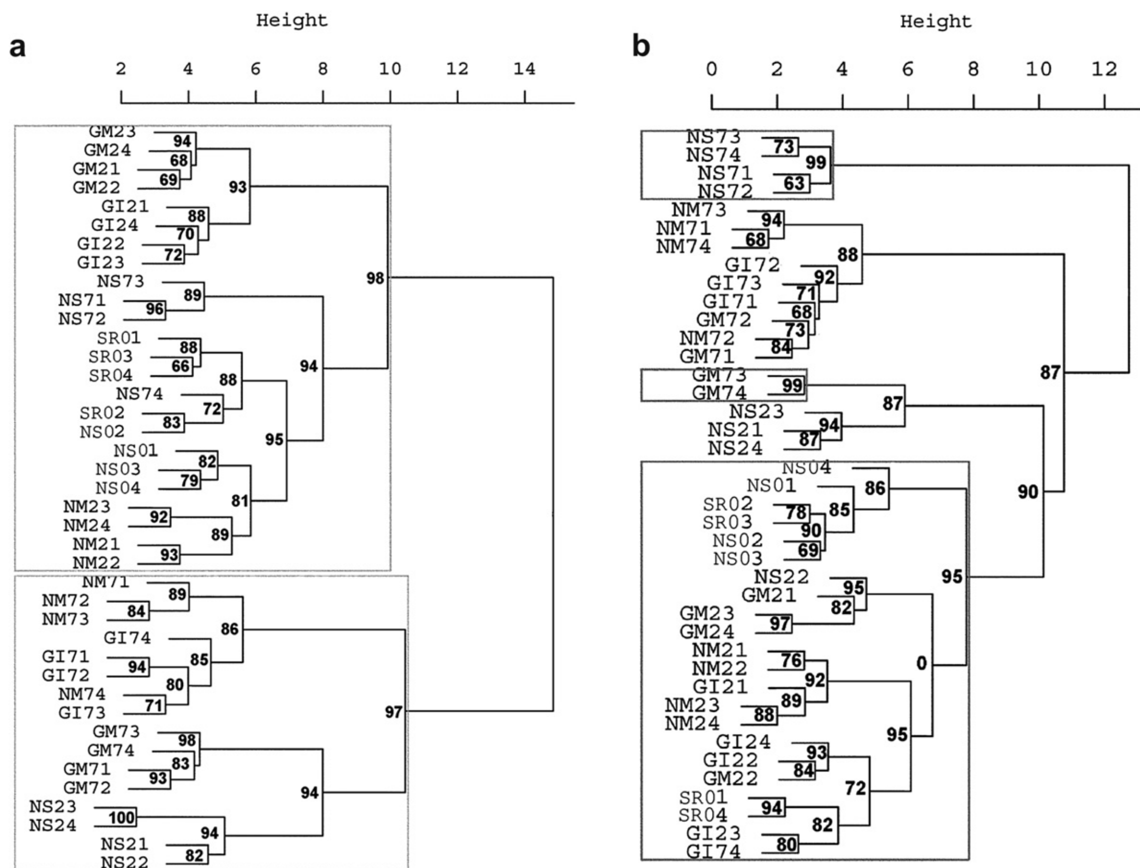

Fig. 1. Ward's minimum variance cluster analysis of band presence/absence DGGE patterns obtained from (a) *nir*K (denitrifiers) and (b) *nifH*-b1 (diazotrophs) gene fragments amplified from the rhizosphere of *Plantago lanceolata* plants that were either established in previously sterile, re-inoculated soil and were non-mycorrhizal (NM), colonized by *Glomus intraradices* (GI) or *Gigaspora margarita* (GM), or, established in non-sterile soil (NS) and colonized by indigenous AM fungi. Rhizosphere soil was taken at the time of planting (non-sterilized (NS0) and previously sterile re-inoculated (SR0) soil) and from the 2nd (NS2, NM2, GI2, GM2) and 7th (NS7, NM7, GI7, GM7) week harvests. The first and second numerical digits identify week of harvest and replicate number, respectively. The original DGGE gel images are included in the Supplementary material (Figures S1 & S2). *P* values (at the branch nodes) have been obtained according to the approximately unbiased (AU) test (Shimodaira, 2002). Rectangles are used to denote highly supported clustering alignments.

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