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Arbuscular mycorrhizal fungi associated with a single agronomic plant host across the landscape: Community differentiation along a soil textural gradient

Daniel J. Moebius-Clune [a], Bianca N. Moebius-Clune [b], Harold M. van Es [b], Teresa E. Pawlowska [a,*]

[a] Department of Plant Pathology & Plant–Microbe Biology, Cornell University, 334 Plant Sciences Building, Ithaca, NY 14853-5904, USA
[b] Department of Crop & Soil Sciences, Cornell University, Ithaca, NY 14853-1901, USA

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ABSTRACT

The arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are important for the functioning of terrestrial ecosystems because of their influence on plant nutrient relations and plant responses to stress. To assess the impact of dispersal limitation and identify niche-related environmental gradients affecting AM fungal community composition and structure, we studied AM fungal communities in an assemblage of maize fields across an eastern New York State landscape. We expressed AM fungal community differences in terms of abundance structure (Bray–Curtis dissimilarities), the presence of unique phylogenetic lineages (UniFrac), and mean phylogenetic relatedness between samples (mean patristic distance, MPD). We did not find strong evidence of dispersal limitation or isolation by distance within or between field sites. To identify environmental factors that may be related to community differentiation, we projected vectors of edaphic variables onto nonmetric multidimensional scaling (NMDS) ordinations of community dissimilarity measures. Of these factors, soil textural components appeared most strongly related to AM fungal community differences. We speculate that this pattern may be explained by the relationship between texture and soil moisture availability. In addition to soil textural components, phylogenetic measures of community differentiation suggested that AM fungal community structure was affected by nutrient concentrations, particularly Mg. Of the two phylogenetic indices of community differentiation, MPD was more consistent and stable with our data, whereas the UniFrac metric failed to be interpretable in several cases. Overall, our data suggest that, rather than phosphorus or pH, soil texture may have an influence on AM fungal community structure over large agroecological scales.

1. Introduction

Many of the key ecosystem functions provided by the arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) such as improved host plant nutrient relations (Smith and Read, 2008), improved plant pathogen resistance (Linderman, 2000), and contributions to soil structure (Tisdall, 1991) differ between AM fungal species, and, as such, will vary with the community composition of AM fungi. Realized functional differences between AM fungal communities in facilitation of plant growth, nutrient acquisition, and reproductive success have been documented in both natural (Ji et al., 2010) and managed systems (Johnson, 1993). Thus understanding of what factors influence AM fungal community composition and how these communities are distributed across large spatial scales can contribute to our knowledge of terrestrial ecosystem functioning.

AM fungal communities in natural ecosystems appear to be shaped by both niche-related factors and neutral processes (Dumbrell et al., 2010). AM fungal niche space is complex. As might be expected for obligate symbionts, the most noticeable niche-related influences are those of host plant community composition and diversity (Bever et al., 1996; Burrows and Pfleger, 2002). A primary mechanism for this influence is a negative feedback between host plants and their fungal symbionts' reproductive success (Bever, 2003). Other than host effects, mineral nutrient concentrations in soil seem to be important. The effects of P concentration on mycorrhization has been noted in several studies (Smith and Read, 2008), and it appears that in general, higher soluble P content in soil is associated with lower mycorrhizal root colonization rates and lower AM fungal diversity (Douds et al., 1993; Douds and Schenck, 1990). AM fungal communities also

* Corresponding author. Tel.: +1 607 254 8726; fax: +1 607 255 4471.
E-mail address: tep8@cornell.edu (T.E. Pawlowska).

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shift along environmental N deposition gradients (Egerton-Warburton and Allen, 2000), and N fertilization of soil leads to changes in AM fungal community with potentially broad functional significance (Egerton-Warburton et al., 2007). Finally, fungal communities respond to soil pH and moisture gradients (Porter et al., 1987), and to soil type (Oehl et al., 2010). Interactions between these host-related and edaphic factors influence the realized niche of the AM fungi.

In addition to the niche-related influences, recent work has highlighted the contribution of neutral processes, such as dispersal limitation, to AM fungal community composition and structure (Dumbrell et al., 2010; Lekberg et al., 2007). If species have similar traits related to their performance in the environment and to competitive ability, their distribution and thus community composition will be a product of stochastic processes governing arrival and local survival or extinction (Hubbell, 2001). According to the neutral theory, dispersal limitation is expected to result in greater compositional difference with increasing geographic distance, which is distinct from, but not mutually exclusive with, the patterns of spatial distribution controlled by biotic and abiotic factors.

Exploration of fungal communities in managed agroecosystems offers the opportunity to separate the effects of host plant community from fungal dispersal and the influence of soil characteristics. In an earlier paper describing a landscape-level study of agricultural fields with a common host plant species (maize, *Zea mays*) distributed across eastern New York State, we characterized an assemblage of AM fungal communities that exhibit substantial species level dissimilarities in taxonomic composition, and differences in dominance (Moebius-Clune et al., 2013). Specifically, multiple fields were dominated by *Claroideoglomus etunicatum* with richness ranging from 3 to 11 taxa and differences in the identity of subdominant taxa. Other fields had little or no *C. etunicatum* and were dominated variously by species from the genera *Paraglomus* and *Rhizophagus*. Dispersal limitation could be a simple explanation for the community differentiation observed between these agricultural fields. However, even fields in close proximity differed markedly in composition, which is not expected for communities shaped primarily by dispersal limitation. In addition, we found that the landscape assemblage, as well as the communities within individual fields, showed a lognormal species abundance distribution. This pattern suggested that multiple niche-related mechanisms influence the AM fungal community composition and structure in our study system.

The goal of the present study was to assess the impact of dispersal limitation, and elucidate the nature of the niche-related environmental factors that influence the composition and structure of AM fungal communities associated with maize in several fields across eastern New York State. We tested the hypothesis that AM fungal communities are shaped by dispersal limitation. This hypothesis would be supported by significant positive correlation between community dissimilarities and spatial distance between samples. To understand the impact of niche-related factors on AM fungal communities, we conducted indirect gradient analysis by fitting edaphic factor vectors into nonmetric multidimensional scaling (NMDS) ordinations of community dissimilarities. We further tested the significance of the relationships between key gradients in various soil characteristics identified by indirect gradient analysis, and community structural differences. In all our analyses, we expressed community differences in terms of abundance structure (Bray–Curtis dissimilarities), the presence of unique phylogenetic lineages (UniFrac), and mean phylogenetic relatedness between samples (mean patristic distance, MPD), and we compared performance of these metrics in terms of stability, interpretability in ordinations, and sensitivity to outliers.

2. Materials & methods

2.1. Sampling and identification of AM fungi

AM fungal community sampling is described in detail in Moebius-Clune et al. (2013). In brief, we sampled soil immediately surrounding roots of maize plants from eight active conventionally managed fields in eastern New York State in a spatially explicit manner. The fields were distributed with a range of distances from 200 m to 400 km. At field A, which was laid out physically in four blocks, 20 samples were taken, at regularly spaced intervals along a transect in each of the blocks. Fields B through H were sampled using a modification of the methods used by the Cornell Soil Health Team (Gugino et al., 2009; Moebius et al., 2007), keeping individual samples from within a field separate rather than compositing them. Ten samples from each field were taken in a "relaxed W" arrangement across the field, allowing for a series of distances from 2 m to 60 m to be represented between samples in a field, with each distance represented multiple times.

Greenhouse trap cultures with maize as a host were established for each individual sampling point. After spore extraction from each trap culture, ten random spores (fungal individuals) were selected from each sampling point and genotyped by sequencing PCR-amplified fragments of the 5′-end of the large subunit (LSU) rRNA gene (GenBank accession numbers JN937121–JN937574). AM fungal operational taxonomic units (OTUs) were defined based on a 95% sequence similarity level. Taxonomic affiliation of OTUs was assessed by reconstructing their phylogenetic histories relative to named reference taxa.

2.2. Soil properties

Soil data were obtained from the Cornell Soil Health Project (http://soilhealth.cals.cornell.edu/). These data include aggregate stability (AgSt), available water capacity (AWC), textural components (% sand, silt, clay), penetration resistance (PenRes), pH, extractable nutrients (P, K, Mg, Fe, Mn, Zn), organic matter (OM), active (permanganate oxidizable) carbon (ActC), potentially mineralizable N (PMN), and root health (RootH). AgSt was measured by rainfall simulation (Moebius et al., 2007). AWC was determined using pressure plates at field capacity and permanent wilting point equivalent pressures (Topp et al., 1993). PenRes (0–15 cm depth) was quantified using a compaction tester (Dickey-John, Auburn, WI); PenRes could not be measured accurately in Field H due to rockiness. The pH of each sample was measured in a 1:1 slurry with water, using a standard pH meter (Eckert and Sims, 1995). Plant available nutrients were extracted with Morgan's solution (Morgan, 1941) and measured on an ICP spectrometer (Jobin Yvon, Kyoto, Japan), except for PO_4–P, which was measured using an automated rapid flow analyzer (RFA/2, Alpkem), at the Cornell Nutrient Analysis Laboratory in Ithaca, NY. OM content was assessed by loss on ignition (Nelson and Sommers, 1996), and ActC by permanganate oxidation (Weil et al., 2003). PMN was measured by 7-day anaerobic incubation (Drinkwater et al., 1996). RootH values were determined visually using a *Phaseolus vulgaris* root pathogen pressure assay as described in Gugino et al. (2009). As organisms do not generally respond to edaphic factors linearly, Cornell Soil Health Test Report (CSHTR) scores were assigned to each measured soil property using nonlinear scoring functions, as described previously (Gugino et al., 2009; Idowu et al., 2009; Moebius et al., 2007; Moebius-Clune, 2010). The CSHTR scores interpret each soil property's measured value with respect to anticipated constraints for crop growth and environmental impact on a scale of 0 (very constrained) to 100 (optimal).