

## Commentary

### Mycorrhizal phosphorus economies: a field test of the MANE framework

The conquest of the land by plants, *c.* 470 million years ago, was made possible by the arbuscular mycorrhizal symbiosis (Selosse *et al.*, 2015). In fact, the evolution of that symbiosis was so successful that plant roots have to fit into an arbuscular mycorrhizal world. But that conclusion at the same time hides a paradox. If the arbuscular mycorrhizal symbiosis was so successful, which empty niches (if any!) were left that could subsequently be filled by other mycorrhizal symbioses, particularly the ectomycorrhizal symbiosis? Explaining those unique niches has remained elusive. Several hypotheses have been forwarded, generally based on the idea that the arbuscular mycorrhizal symbiosis plays a larger role in inorganic nutrient (nitrogen (N), phosphorus (P)) cycling, while the ectomycorrhizal symbiosis is more important for organic nutrient cycling (Read & Perez-Moreno, 2003). Recently, Phillips *et al.* (2013) proposed a conceptual framework, MANE (mycorrhiza-associated nutrient economy), based on the same hypothesis that arbuscular mycorrhizal and ectomycorrhizal trees, not only across but also within biomes, have unique nutrient economies (primary forms of nutrient utilized by mycorrhizal plants and fungi), with ectomycorrhizal trees being characterized by an organic cycle of N and P, and arbuscular mycorrhizal trees by an inorganic cycle of N and P. In this issue of the *New Phytologist*, Rosling *et al.* (pp. 1184–1195) provide a first field test of the MANE framework for the P cycle, using temperate deciduous forest stands differing in the dominant type of mycorrhizal association.

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Rosling *et al.* observed that in these forests ectomycorrhizal and arbuscular mycorrhizal tree growth was equally limited by P. There were no differences in plant P uptake from, or plant P return to, the soil. Both mycorrhizal forests harboured a similar microbial biomass (of symbiotic and saprotrophic microbiota), a pool that contained almost three times as much P as the annual P uptake by the vegetation. It is this large microbial biomass that causes the severe P-limitation (which is notable from the very low litter P

contents), a finding confirming recent work that competition with microbes (often mycorrhizal fungi) can exacerbate nutrient limitation of plants. The mycorrhizal symbiosis then both constrains plant growth but also prevents non-mycorrhizal plants being able to invade such forests (Näsholm *et al.*, 2013; Franklin *et al.*, 2014). However, despite strong P limitation the forests described by Rosling *et al.* are surprisingly productive, to judge from data on annual litter fall.

At first sight the equal size of the microbial P-pool in forests dominated by ectomycorrhizal or arbuscular mycorrhizal trees is surprising. One would expect significantly larger microbial biomass in the ectomycorrhizal plots than in the arbuscular mycorrhizal plots – considering differences in hyphal biomass between ectomycorrhizal and arbuscular mycorrhizal systems; and consequently stronger nutrient limitation in the ectomycorrhizal plots as well. Rosling *et al.* explain the lack of differences in the microbial P pool by pointing out a major role for other soil microbes in P immobilization in the arbuscular mycorrhizal stands. This, of course, raises the question whether mycorrhizal types are the causal agents in the differential nutrient syndromes, or whether saprotrophic microbial activity plays a dominant role in nutrient cycling.

Rosling *et al.* did not observe differences in the various inorganic P pools between stands with different mycorrhizal types, a finding that does not seem to follow logically from the MANE framework. They noted large differences in the available organic P pool (which was higher under ectomycorrhizal trees) and the complex (= unavailable) organic P pool (which was higher under arbuscular mycorrhizal trees). These differences are consistent with (but not necessarily a test for) the hypothesis that ectomycorrhizal fungi can access complex organic P, transform it to available organic P and release orthophosphate due to enhanced phosphatase levels. But despite elevated phosphatase levels, the available organic P pool in the ectomycorrhizal stands was not reduced to similar levels as in the arbuscular mycorrhizal stands. There was possibly a larger total soil P pool in the arbuscular mycorrhizal plots. Fig. 3 in Rosling *et al.* suggests that the arbuscular mycorrhizal stands contain slightly over 20% more soil P than the ectomycorrhizal stands. Three potential explanations may account for this larger pool size. First, Rosling *et al.* suggest that the difference may be in the residual P pool, but they did not determine this pool in their sequential extraction. If so, we have to conclude that the ectomycorrhizal symbiosis not only acquired P from the unavailable organic pool, transforming it to available organic P, but also enhanced the residual P pool. The implication would then be that the ectomycorrhizal stands may gradually slow down the P cycle over larger temporal scales than could be observed from tree productivity. But two other explanations could also be envisaged. A second explanation is the thin soils in their research area that are derived from siltstone, shale and to a lesser extent limestone. As these rocks contain different amounts of P, it may be possible that differences

in geology over small spatial scales cause differences in soil P status impacting initial tree establishment (Porder & Ramachandran, 2013). The current composition of stands dominated by ectomycorrhizal and arbuscular mycorrhizal trees then reflects a soil geological legacy, rather than being the result of the MANE that affected P pools. A third explanation for the observed larger total soil P pool in arbuscular mycorrhizal stands could be the vertical distribution of P. Arbuscular mycorrhizal trees could root more deeply, transporting P from deeper layers to the surface. Phosphorus cycling in the ectomycorrhizal stands could be more superficial. Humus profiles in both stands apparently diverge, with the build-up of a more acidic, thicker and more N-limited organic layer under ectomycorrhizal trees (Table 1 in Rosling *et al.*). Litter decomposability could therefore be a major factor (which would fit with a somewhat larger role for saprotrophic microbes in driving stand differences): despite similar P content, litter decomposition could be different, slowing down (ectomycorrhiza) or enhancing (arbuscular mycorrhiza) P cycling rates. Rosling *et al.* assessed P pools during the growing season (May–November). Considering the large seasonal changes in microbial biomass carbon (C):P ratios (especially in the ectomycorrhizal stands) implying that microbes become strongly P-limited, it is an intriguing question to what extent the winter season would produce the mineral P to drive the annual cycle of plant and microbial uptake.

Both Phillips *et al.* (2013) and Rosling *et al.* make clear that their results may not (yet) be extrapolated beyond temperate forests. Studies in the tropics have cast doubts on a fundamental difference in N-cycling between both mycorrhizal forest types, as ectomycorrhizal forests in tropical Africa were characterized by an open inorganic N cycle (Tedersoo *et al.*, 2012). However, characterizing the P cycle, and especially the organic part of the P cycle, in such forests stands out as a clear research priority.

An even more intriguing question is whether ectomycorrhizal trees are able to invade arbuscular mycorrhizal stands (because ectomycorrhizal trees have access to complex organic P), whereas arbuscular mycorrhizal trees cannot invade the ectomycorrhizal stands (as they are competitively inferior in acquiring P from organic sources and in weathering capacity). Alternatively, strong geological legacies could make stable coexistence between both mycorrhizal guilds, rather than competitive exclusion by the ectomycorrhizal guild, likely. Targeted experiments in stands with comparable amounts of ectomycorrhizal and arbuscular mycorrhizal trees would be necessary to understand the outcome of competition between both guilds.

Rosling *et al.* show surprising and unanticipated similarities in P limitation, litter P and inorganic P cycling in both mycorrhizal forests. These results indicate that the MANE framework by

Phillips *et al.* (2013) needs further refinement, especially incorporation of geologically induced soil fertility and the role of other microbiota are needed. The work by Rosling *et al.* should serve as a major inspiration for important questions in mycorrhizal research, especially about the extent to which ectomycorrhizal and arbuscular mycorrhizal trees occupy different organic P niches, as hypothesized by Turner (2008), and whether any niche differentiation contributes to their coexistence.

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