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Mini-review

Nutritional ecology of arbuscular mycorrhizal fungi

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ABSTRACT

Despite their large role in ecosystems and plant nutrition, our knowledge of the nutritional ecology of the fungi involved in the arbuscular mycorrhizal symbiosis, the Glomeromycota, is poor. We briefly describe the mechanisms that underlie the fluxes of the three major elements (C, N and P) and outline a model for the interchange of these between the partners. This model is consistent with data from physiological, ecological and taxonomic studies and allows a new and necessary focus on the nutritional requirements of the fungus itself, separately from its role in the symbiosis. There is an urgent need for new studies to identify the sources of nutrients such as N and P that AM fungi (AMF) use for their own growth and to elucidate the mechanisms that control the transfer of these to the plant in relation to fungal demand.

Introduction

Traditionally the arbuscular mycorrhizal (AM) symbiosis is viewed as a classic mutualism, an interaction in which both partners benefit. The fungi appear to acquire their entire carbon supply from the plant, and although colonisation of roots by AM fungi (AMF) can confer a wide range of benefits to the plant (Newsham *et al.* 1995), the most widely cited benefit is that of enhanced phosphorus (P) acquisition. The fungal hyphae can explore a large volume of soil and acquire P beyond the phosphate depletion zone that rapidly builds up around the root surface at a much smaller carbon cost than is possible by root growth (Harley 1989): this economy probably underlies the evolution of the symbiosis. The fossil record of the AM fungal phylum Glomeromycota goes back to the Devonian as a symbiosis (Remy *et al.* 1994) and to the Ordovician as spores (Redecker *et al.* 2000); they thus have a contemporaneous origin with the land flora. The first land plants had rhizomes and rhizoids, but no root systems. Acquisition of poorly mobile phosphate ions was therefore a major problem and fossil evidence reveals that these early plants had fungal structures strikingly similar to modern AM structures of the '*Arum*-type' in their rhizomes; it is not a big leap to the assumption that they performed the same function then as now, and were responsible for plant uptake of P (Helgason & Fitter 2009). That enhanced plant P nutrition is still a major outcome of the AM symbiosis demonstrates that while root systems have become larger and more complex, P acquisition is still a major challenge for most plants.

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The morphology of AMF colonisation can vary giving rise to the so-called 'Arum-' or 'Paris-type' mycorrhizas. In the Arum type inter-cellular AMF hyphae spread within the root cortex. Short side branches form which penetrate the root cortical cell walls and branch extensively to give the characteristic 'arbuscule' structure. In the Paris type there is little inter-cellular growth but, instead, extensive intracellular coiled hyphae which spread directly from cell to cell and from which arbuscules may develop. Much less is known about the Paris type than the Arum type and it is the latter that forms in the roots of most crop plant species (Smith & Read 2008). Around two-thirds of all plants form the AM symbiosis but, for a group with such ecological importance, our knowledge of the biology of the Glomeromycota is comparatively poor. Recent studies show that there is considerable genetic and phenotypic variation among AM fungal isolates (Koch et al. 2004; Croll et al. 2008), and although sexual stages have never been observed, genetic evidence suggests that recombination may occur (Gandolfi et al. 2003; Croll & Sanders 2009). These exciting new studies suggest that a greater understanding of AM fungal population structure, differentiation, dispersal and persistence is not far away; much nevertheless remains to be done. Critically for the purpose of this review we do not know why they are obligate symbionts and cannot be grown in the absence of live plant tissue, nor the most basic details of their physiology and especially what controls the fluxes of nutrients between plant and fungus in the symbiosis. This review examines the current knowledge of the nutritional ecology of AM fungi.

Nutrient fluxes in the AM symbiosis

Carbon

The major fluxes in the AM symbiosis appear to be of C from plant to fungus and of P, and possibly N, from fungus to plant. Reverse C movement – from fungus to plant – appears only to occur in special cases where the plant has an unusually restricted C supply, most notably in achlorophyllous plants (Bidartondo et al. 2002). In virtually all other cases, apparent plant-to-plant movement of C is best explained as the AM fungus moving C from the intra-radical mycelium in one root system to the same mycelium within another root; the carbon almost always remains in the roots and is retained in the intra-radical fungal structures (Robinson & Fitter 1999; Voets et al. 2008).

The mechanisms of these fluxes are not yet well understood. Even the location of the carbon flux is obscure, with the best evidence – from activity of ATPases – suggesting that it occurs in the Arum type at the inter-cellular hyphae (Gianinazzi-Pearson et al. 1991). A model for transport of C from intra- to extra-radical hyphae has been proposed (Bago et al. 2003) and a hexose transporter (GpMST1) has been identified in the fungus Geosiphon pyriforme, a non-mycorrhizal member of the Glomeromycota (Schüßler et al. 2006). The identity of the C transporters in mycorrhizal taxa will soon become apparent as genome information is published (Martin et al. 2008).

Phosphate

The phosphate flux is better characterised. Phosphate is taken up by high-affinity phosphate transporters in the extra-radical mycelium (Harrison & van Buuren 1995). Phosphate is probably transported within the fungus as polyphosphate (polyP), and once in the intra-radical hyphae the long chains are hydrolysed, facilitating transfer to the host plant (Harrison 1999; Bago et al. 2002; Ohtomo & Saito 2005). Fungus-to-plant transfer appears to occur principally at the arbuscule interface, although expression of P transporters around Paris type hyphal coils has also been demonstrated (Karandashov et al. 2004). Plant ATPase activity is strongly expressed at the peri-arbuscular membrane (Smith et al. 2009) and phosphate accumulation as polyP strongly correlated with AM colonisation (Ohtomo & Saito 2005). Most importantly, a subfamily (subfamily 1 under the family Pht1) of plant phosphate transporters is now known that is expressed only in colonised plants; the first of these was in Solanum tuberosum (StPT4; Rausch et al. 2001), and they have subsequently been identified in several other taxa (Javot et al. 2007). Acquisition of P *via* the symbiotic pathway downregulates direct P uptake by the plant (Smith et al. 2004, 2009).

Nitrogen

In contrast to P, fewer studies have considered a role for AMF in N acquisition, because the greater mobility of ammonium and especially nitrate ions in soil, compared to phosphate, led to the assumption that little benefit was likely to plants from enhanced N uptake. AMF can certainly transport N to roots: AM extra-radical mycelium (ERM) exposed to ^{15}N-labelled NO_3^- or NH_4^+ became highly labelled and this N was subsequently translocated to the roots (Govindarajulu et al. 2005), confirming earlier work (Tobar et al. 1994; Johansen et al. 1996; Mäder et al. 2000). N is translocated in the hyphae as arginine but probably broken down to urea and ultimately transferred to the plant as NH_4^+ with the resulting C skeletons from arginine breakdown being re-incorporated into the fungal C pools (Bago et al. 2001; Govindarajulu et al. 2005). A plant ammonium transporter (AMT) has recently been identified in Lotus japonicus which is mycorrhiza-specific and preferentially expressed in arbusculated cells (Guether et al. 2009a, b), and up-regulation of an ammonium transporter in Medicago truncatula has also been found (Gomez et al. 2009). Moreover, Leigh et al. (2009) demonstrated that a fifth of plant N could be derived from AM fungal transfer when only the fungus had access to a compartment containing an organic N source. However, the role played by AM fungi in N acquisition from organic N sources, the dominant form of N in most soils, remains controversial (but see Whiteside et al. 2009), especially when both roots and AM hyphae have access to the same N source (Hodge et al. 2000a; Hodge 2003a).

Plant–fungus reciprocity: who drives whom?

These fluxes underlie the operation of the symbiosis, but we do not know how the exchange is managed. Is there some reciprocity between the C supplied by the plant and the P (or N)