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journal or publication title	Journal of Integrated Field Science
volume	15
page range	2-7
year	2018-10
URL	http://hdl.handle.net/10097/00123995



Symposium paper

Utilization of Organic Nitrogen by Arbuscular Mycorrhizal Hyphae in Soil - Zooming into the Hyphosphere Microbiome

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Keywords

chitin, protist, nitrification,
soil microbial loop, review

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Abstract

Nitrogen (N) availability often limits growth and yields of crop plants. Utilization of synthetic N fertilizers resulted in great yield improvements but also brought with it negative consequences such as soil degradation and environmental pollution. Organic N sources are thus likely to play a greater role in future agriculture, as they did before the Green Revolution. Arbuscular mycorrhizal (AM) fungi form symbiosis with majority of world crops, providing their host plants with a multitude of nutritional and other benefits. Development of AM fungal hyphae is usually stimulated by organic N inputs into soil and the fungi can gain a significant share of N from the organic soil amendments and eventually transport the N to their host plants, in spite of the fact that they are unable to mineralize the organic materials themselves. It has been postulated that the AM fungi depend on activity of soil saprotrophs to gain access to organic N. Recent studies indicated that not only the primary degraders, but also their grazers such as soil protists, most likely play an important role in making the N once released from organic materials and then immobilized in microbial cells, available for uptake by the AM fungi. On the other hand, AM fungi are likely competing for free ammonium ions released by the protists with ammonia oxidizers, suppressing nitrification in consequence. In this short paper we provide new insights into organic N recycling from soil to plant and identify knowledge gaps to be filled by future research.

Nitrogen – importance, synthetic fertilizers, and future challenges

Nitrogen (N) availability is one of the most prevalent resource limitations of plant productivity in both natural and anthropogenic (e.g., agricultural) ecosystems (Gill and Finzi 2016; Hallin *et al.* 2009; Sochorová *et al.* 2016). High crop yields in current agriculture are, since the beginning of Green Revolution, maintained mainly due to massive inputs of synthetic N fertilizers, and this has led to global rearrangements of N cycling, reducing soil organic matter content and thus soil quality, increasing soil erosion, eutrophication of water bodies, and great societal dependency on fossil energy, above all the natural gas (Canfield *et al.* 2010; Lal *et al.* 2007; Pimentel and Pimentel 2008; Rockström *et al.* 2009; Steffen *et al.* 2015). With steadily increasing global human population and rocketing requirements for their food quality (e.g., meat or other products with large ecological footprint), largely stagnating crop yields also pose a serious

uncertainty to global food security as well as political stability (Jansa *et al.* 2010; Lal 2009). This means that the synthetic N fertilizers that are important components of modern production agriculture for several decades, sustaining yields an order of magnitude higher than ever before, may bring along (particularly if used excessively) very dramatic negative consequences for soil quality and long-term ecosystem productivity, which may be difficult or impossible to reverse at decent temporal scales (Jones *et al.* 2013). Unwise and excessive applications of synthetic N fertilizers can also undermine other (unrelated) ecosystem services such as clean water supply even at distant places from agricultural fields – mainly because about half of the N applied to the fields is not taken up by the crops but is lost to the environment (Lassaletta *et al.* 2014; Somers and Savard 2015). If the fossil energy once becomes scarce, it is likely that organic N sources such as farmyard or green manure, compost or sewage sludge become as important as they were before the Green Revolution – yet it remains unclear if such organic agriculture could ever feed

human population inhabiting the world today or projected to be there in the future (Cui *et al.* 2014; Muller *et al.* 2017; Razon 2015; Seufert *et al.* 2012)

Roots and mycorrhizas

Most plants take up N from soil with their underground organs, the roots. Legumes and few other plant taxa are a notable exception in this regards, because they derive a significant part or all of their N requirements from the biological dinitrogen fixation through tight association with diazotrophic prokaryotes (Sprenst *et al.* 2017, and references therein). Plants take the N from the soil solution either as nitrate (NO₃⁻), ammonium (NH₄⁺) ions or small organic molecules such as aminoacids (Ganeteg *et al.* 2017; Klement *et al.* 2009; Miller and Cramer 2005; Warren 2013). Most plants, strictly speaking, do not have roots, however. They develop symbiotic relationship with specialized soil fungi called mycorrhizas, where some of the root functions (e.g., uptake of phosphorus) are taken over to smaller or larger extent (or almost completely) by the fungi (Smith *et al.* 2004). Since most herbaceous plants and particularly all mycotrophic (i.e., mycorrhiza-forming) crop species such as wheat, maize, rice, bean, potato and cassava develop only one, the primordial type of mycorrhizal association called arbuscular mycorrhizal (AM) symbiosis (Parniske 2008), we dedicate further text exclusively to this type of mycorrhizal symbiosis, intentionally leaving out the ecto-, ericoid- and other types of mycorrhizal symbioses (Smith and Read 2008) that do not play such an important role in production agriculture as the AM symbiosis.

The AM symbiosis is globally widespread, evolutionarily ancient and quantitatively important component of microbial communities in virtually all soils on Earth inhabited by suitable host plants - which is more than a half of extant plant species, actually (Brundrett 2002; Davison *et al.* 2015; Fitter 1990; Remy *et al.* 1994). Hyphae of AM fungi connect the soil environment with inner layer of root cortex, as well as they are providing functional interconnection between plant individuals of the same and/or of different species in a plant community (so called common mycorrhizal networks, CMN), transporting mineral nutrients towards plants while gaining carbon from their plant hosts, and also providing a highway for transport of signalling molecules and/or secondary metabolites (Babikova *et al.* 2013; Duhamel *et al.* 2013; Jakobsen *et al.* 1992; Lendenmann *et al.* 2011; Robinson and Fitter 1999; Simard and Durall 2004). This symbiosis plays important roles in plant acquisition from the soil of phosphate, micronutrients such as zinc and copper, in soil aggregate stabilization and conditioning soil hydraulic properties, shaping mycorrhizosphere microbiome, and interactions between plants themselves as well as interactions between plants and their pathogens (Bitterlich *et al.* 2018; Leifheit *et al.* 2015; Newsham *et al.* 1995; Philippot *et al.* 2013; Smith and Read 2008). Trading of resources in mycorrhizal symbiosis based on reciprocal reward concept such as phosphate for plant carbon has been documented between the plants and their fungal symbionts (Kiers *et al.* 2011), although patterns deviating from this concept such as asymmetric redistribution of symbiotic costs and benefits in multispecies plant communities interconnected by CMN have also been observed (Walder *et*

al. 2012; Weremijewicz *et al.* 2016).

Arbuscular mycorrhiza and nitrogen

As every other living organism on Earth, known to science, the AM fungi also contain nucleic acids and proteins, compounds that require N for construction of the molecules. Therefore, the AM fungi require N for building up their biomass and maintaining their metabolic activity. Further on, as the cell walls of AM fungi contain N-rich biopolymer chitin (Bago *et al.* 1996; Balestrini and Bonfante 2014; Lanfranco *et al.* 1999; Shinya *et al.* 2015; Tisserant *et al.* 2012), this structural biomolecule represents another significant sink for N in AM fungal biomass. The AM fungi thus need lots of N for building up their biomass (see Kaschuk *et al.* (2009) and references therein) and thus it is not surprising that competition for N occurs between plants and the AM fungi at low N availabilities (Püschel *et al.* 2016). When the fungal needs are satisfied, additional N could be moved to plants and traded for plant carbon in a similar way as phosphorus, although the contribution of AM fungi to N uptake of plants is considered to be generally lower than the contribution to phosphorus uptake (Fellbaum *et al.* 2012; George *et al.* 1995; Hodge *et al.* 2010; Johansen *et al.* 1992; Mäder *et al.* 2000). The N could be taken up from the soil solution both as nitrate or ammonium ions, because ion channels for transport of both these ions have been characterized for the AM fungi (Garcia *et al.* 2016, and references therein). Interestingly, earlier research indicated that AM fungal hyphae can also take up and assimilate amino acids such as glycine and glutamate from the soil solution (Hawkins *et al.* 2000). Long-distance transport of N through the AM fungal hyphae occurs most likely in a form of arginine, possibly coupled with the polyphosphate granules (Cruz *et al.* 2007; Govindarajulu *et al.* 2005; Kikuchi *et al.* 2014). Release of N from the AM fungus to the plant is most likely in form of ammonium (Guether *et al.* 2009).

Organic N and mycorrhizas

Proliferation of AM fungal hyphae in soil is stimulated by organic N amendments – a phenomenon that has been described for several AM fungal species since a couple of decades ago. Originally, the research has been carried out with complex organic materials such as plant litter or baker's yeasts applied in root-free zones (Gavito and Olsson 2003; Hodge *et al.* 2001; Hodge *et al.* 2000) and those results were confirmed recently for a range of pure N-containing polymers such as chitin, DNA and proteins (Bukovská *et al.* 2016, and references therein). The AM fungi were reported to speed up the decomposition of organic N, probably in concert with other (saprotrophic) microorganisms, acquire the N originally bound in the organic materials, and transport it towards the plant, where it could be (but not always was) transferred to the host plant (Bukovská *et al.* 2018; Hodge 2014; Hodge and Fitter 2010; Hodge *et al.* 2000; Thirkell *et al.* 2016). Although microbial communities in organic N patches accessible only to AM fungal hyphae differed between mycorrhizal and non-mycorrhizal pots (Herman *et al.* 2012; Nuccio *et al.* 2013), with Firmicutes responding positively to AM fungal presence and Actinobacteria and Comamonadaceae

responding negatively to the same, it remains unclear which of the microbes were directly involved in the decomposition of the organic N, which of them could have been primed by AM hyphal exudates (Jansa *et al.* 2013, Kaiser *et al.* 2015) and which were just back-seat riders.

Several of the above studies have indicated that the AM fungal hyphae could transfer not less than 20% of the N supplied as soil organic amendment to the plants within just a few weeks (Bukovská *et al.* 2018; Hodge *et al.* 2001; Thirkell *et al.* 2016). This efficient “mining” of organic N has consequences for the soil microbes, too: recently, we showed that just a few weeks after placing the organic N in the AM fungal hyphosphere, both bacterial and fungal communities diminished in size due to presence of the AM fungal hyphae (Bukovská *et al.* 2018), a phenomenon strongly resembling so called Gadgil’s effect (Gadgil and Gadgil 1971; Verbruggen *et al.* 2016). The strongest reduction was recorded for ammonia-oxidizing bacteria, indicating that the AM fungi actually outcompeted ammonia oxidizers, responsible for the first step of nitrification (see Fig. 1), most likely through reducing NH_4^+ concentration in the soil solution (Bukovská *et al.* 2018; Veresoglou *et al.* 2012).

Another important phenomenon that we observed in our organic N patches was higher abundance of soil protists (Bukovská *et al.* 2018; Bukovská *et al.* 2016). Although the diversity of this heterogeneous group of organisms is still not easy to capture (Geisen 2016; Geisen *et al.* 2017), they seem to play a very important role in releasing N from the primary decomposers, via so called soil microbial loop (see also Fig. 1). This is because, for stoichiometric reasons, the protists release up to one third of N they ingest back to the soil solution as free ammonium ions (Bonkowski 2004; Trap *et al.* 2016). This is also why soil protists likely play a key role in increasing availability of the N supplied to soil originally as organic amendment to AM fungi, which virtually

lack any potent exoenzymes and may not be able to compete successfully with the primary decomposers (Bukovská *et al.* 2018; Ekelund *et al.* 2009; Raynaud *et al.* 2006; Tisserant *et al.* 2012).

Open questions to be addressed in future

Above all, the “smoking gun” of the primary decomposition of soil organic N shall be carefully described in the subsequent studies, and linked to AM fungal activity, if any (e.g., priming of activity of the decomposers by AM hyphal exudates or cross-talking via signaling compounds, Kaiser *et al.* 2015). Ecological significance of soil protists (and soil microbial loop more generally) in making the organic N available to plant and AM fungi needs to be further studied, as this is an exciting and novel subject of soil ecology (Geisen *et al.* 2018). Consequences of AM fungal uptake and transport of N from the organic patches to their host plants should also be scrutinized as to the effects on other N transformation pathways (e.g., nitrification and denitrification). Previous research carried with just a handful of model plants and AM fungal genotypes should also be replicated for a broader selection of model organisms and soil properties to allow generalization of the observed effects. Particular care should then be dedicated to establishing realistic microbial communities in the model experiments, particularly with respect to including sufficient populations of slow-growing members such as ammonia oxidizers (Veresoglou *et al.* 2012, Bukovská *et al.* 2018).

Acknowledgments

Funding is gratefully acknowledged by the Czech Science Foundation (18-04892S) and by the long-term development program RVO61388971.

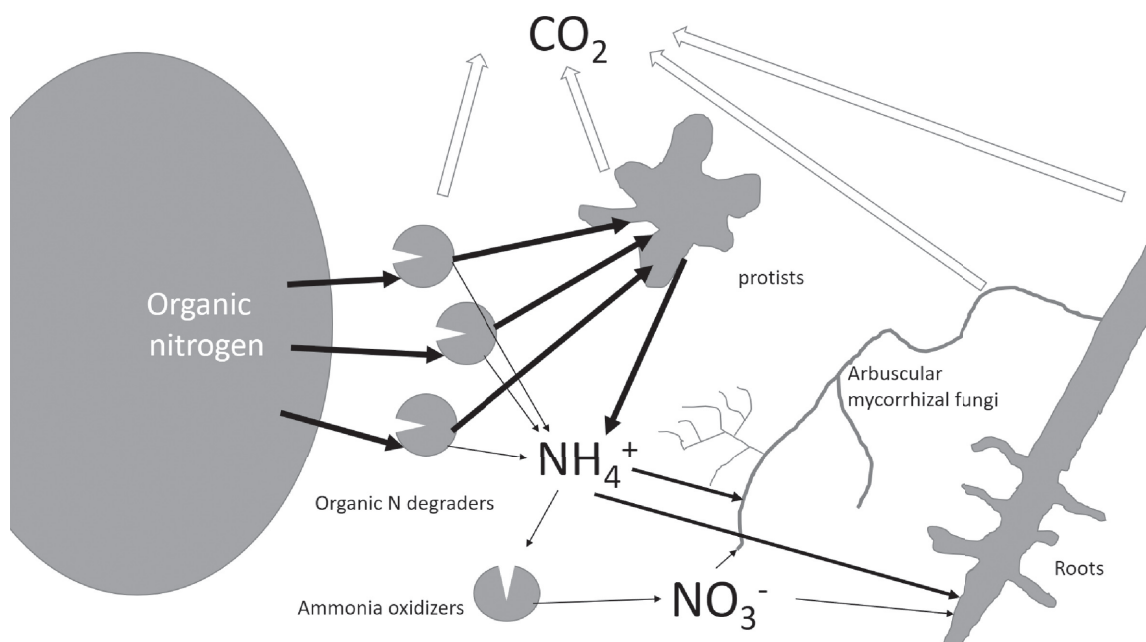


Fig. 1. A scheme showing trophic dependencies between and N transformations carried by different members of soil microbial community involved in decomposition of organic N and transport of the released N towards the plants. Thickness of black lines indicates assumed relative importance of the different pathways of recycling organic N to the plants in mycorrhizal systems.

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