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Arbuscular mycorrhiza and soil organic nitrogen: network of players and interactions

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Abstract

Arbuscular mycorrhizal (AM) symbiosis is heavily and positively implicated in phosphorus (P) acquisition from soil to plants, including many important agricultural crops. Its role in plant nitrogen (N) nutrition is generally not as prominent or beneficial, with exception of some situations when N is available predominantly in organic forms. Yet the AM fungi (AMF) are, due to their poor exo-enzymatic repertoire, unlikely to degrade organic compounds on their own, therefore they possibly depend on other microorganisms to liberate nutrients contained in those materials. Here, we review current knowledge on the roles played by the AMF in plant N nutrition in general and uptake of N from organic compounds in particular, with a specific reference to microbes and processes involved in liberation and AM fungal utilization of N from organic compounds. Future research needs and directions are outlined, as is the agronomic and societal context of such research.

Keywords: Arbuscular mycorrhizal fungi, Chitin, Exo-enzyme, Mineralization, *N*-Acetylglucosamine, Nitrogen, Organic nutrient recycling, Societal relevance, Soil microbial loop

Introduction—setting the scene

Nitrogen (N) is an integral part of a number of macromolecules supporting all life on Earth, including nucleic acids, proteins, some polysaccharides (e.g., chitin and chitosan) and a wide range of secondary metabolites. It is, thus, present in all living cells and is consequently regarded as one of the vitally important macronutrients (biogenic elements) for the life as we know it. The N-rich organic materials such as farmyard and green manures, composts and guano have been used for millennia to sustain sedentary agriculture [32]. Since about 100 years, large amounts of mineral N fertilizers have been manufactured through the Haber–Bosch ammonia synthesis with energy and hydrogen inputs from fossil fuels, mainly natural gas [17]. This single chemical invention, together with widespread use of potent pesticides and breeding for high-yielding crop cultivars, have together made what we refer to as Green Revolution, which allowed unprecedented yield increases and literally detonated the human population explosion, driving the world's population from 1.6 billion in 1900 to current approximately 8 billion [110]. Even though mineral N fertilizers did play a major role in the Green Revolution, their use poses a great risk of environmental pollution, degradation of soil quality, and great societal dependency on fossil energy. As the production of mineral N fertilizers is an energy intensive process, it will consequently be very difficult to maintain any close to the current production levels, shall the availability of fossil energy thin or vanish in the future [33, 129]. As the world population would only reach a maximum of about 4 billion without synthetic N fertilizers today, the other half of the world population is literally reliant on the Haber–Bosch process and, therefore, on fossil energy supplies [26].

Agriculture has always been a system out of (natural) balance, aiming at suppressing weeds and pathogens and maximizing yields of only a few or a single crop/product. Current agricultural practices reached much closer to the theoretical yield/production potential of many agricultural products than ever before, with further perspectives of closing the crop yield gap by fertilizers, supplementary irrigation, modern breeding and novel management options, e.g., precision agriculture [18, 121]. However,

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the humanity at the same time also achieved the lowest levels of global food reserves and the highest dependency on global reshuffling of resources than ever before. Therefore, the imminent danger of shortage of suppy of food, feed, and other agricultural commodities arises shall any of the current agricultural or linked resources be performing weakly under future stress scenarios. The scenarios include, among others: emergence of novel pathogens; drought or heat spells; lack of pollinators; low availability of mineral N and phosphorus (P) fertilizers, energy and/or pesticides; major soil losses due to erosion; and further degradation of soil and ground water quality [21, 36, 40].

Relying on mineral N fertilizers, conventional agricultural production literally feeds on finite fossil energy in large parts of the world today—and, at the same time, silently accepting rather low mineral N fertilizer use efficiency (with the maximum at around 50%) and immense environmental costs, particularly with respect to soil and water quality [98]. Fostering the transition of a significant portion of agricultural lands to more sustainable organic management is, thus, urgently required to improve both global ecosystem sustainability and resilience of the food production systems to current and future challenges [114]. This is because organic agriculture helps recycling organic waste, improves soil quality and organic food generally has a smaller environmental footprint than conventionally produced food (though it still requires judicious management of inputs), which all may be important with respect to mitigation of and adapting to climate changes [47, 70, 88]. Additionally, supporting personal modesty as a counterbalance to civilization of endless consumption must be encouraged; while at the same time, an increased level of agricultural productivity is required to feed the growing world population with rising demand for high quality food. As the altered needs of human civilization mutually interact with the Earth ecosystem, it could remain within habitable boundaries [115]. Therefore, future agricultural production systems will need to rely, more than ever, on healthy soil and its inhabitants, dedicating particular attention to maintaining and promoting soil quality. In this review, we summarize current knowledge on the roles played by the omnipresent yet still broadly under-appreciated arbuscular mycorrhizal fungi (AMF) in N cycling in soil–plant systems in general and recycling organic N from soil to plant in particular.

Arbuscular mycorrhizal symbiosis and nitrogen cycling

The AMF are establishing so-called arbuscular mycorrhizal (AM) symbiosis with majority (> 60%) of extant plant species [111]. This means that AMF can be regarded as an important biological soil resource. This is because the AM symbiosis, an intimate co-existence between the AMF and roots of their host plants, plays a substantial role in mineral nutrition, abiotic stress tolerance and pathogen resistance of the plants including many important agricultural crops such as wheat, maize, rice, banana, potato or sunflower [83, 95, 112]. Further, the AM symbiosis apparently plays a pivotal role in maintenance of diversity of plant communities through redistribution of symbiotic costs and benefits between individuals of the same or different plant species through so-called common mycorrhizal networks [7, 28, 131].

The AMF hyphae interconnect soil with the cortical cells of roots, establishing a unique and direct pathway to shuffling nutrients from the soil to plants and reduced carbon (C) in the other direction [82, 97, 132]. However, this connection is not very likely to facilitate any significant direct interplant nutrient and/or C transfers [30, 31], except when C is transferred from a green host to a neighboring mycotrophic, achlorophyllous plant [14, 23]. The AM symbiosis is particularly important for their host plant acquisition of P, zinc and copper from soil because those nutrients only have a limited mobility in most soils and AMF hyphae are well suited to reach those nutrients beyond the root depletion zone [1, 64, 92]. The AMF hyphae, however, have generally much lesser importance in directly improving N nutrition of their hosts from mineral N sources ([51] and reference therein). This may appear surprising because the AMF obviously possess the metabolic capacity to take up inorganic N forms from soil solution and transport the N to their host plants [27, 34, 39]. However, the mobility of inorganic N forms in soil is mostly not limiting the N uptake by the plants [86]—probably with the exception of N being present predominantly as NH_4^+ ions in clayey, highly organic, and/or calcareous, alkaline soils. Under such conditions, the mobility of ammonium ions in soil is low and, consequently, significant improvements of plant N acquisition are sometimes, though not always, recorded due to AM symbiosis establishment [4, 67, 85].

Yet, the AM symbiosis can have important indirect effects on plant N nutrition during which the mycorrhizal benefits and costs may vary according to the environmental context [22, 60, 69]. Particularly, under low mineral N availability in the soil, a competition for soil N between the plant and the AMF has been documented, resulting in less N being taken up from the N-deficient soil by mycorrhizal as compared to the non-mycorrhizal plants [99]. Only when the N demand of the fungus was satisfied, the mycorrhizal growth- and P-uptake responses became positive [54, 99]. This is mainly because the N demand of AMF hyphae can be substantial, as the N concentration in the AMF hyphae may (at least for some AMF taxa)

reach well over 5% [53]. On the other hand, in legumes supporting symbiotic dinitrogen fixation, AMF-mediated P supply could have significant positive feedback on the efficiency of atmospheric dinitrogen fixation [100]. Direct transfer of N from plant to plant via common mycorrhizal networks is remaining another intriguing yet largely unconfirmed hypothesis. It is namely difficult to separate processes like biotrophic (AMF hyphae-mediated) transfer of N from transfer via root exudates [61] or from recycling of nutrients contained in necromass—plant or fungal [29, 68]. Uptake of N from such different sources can only be unequivocally traced in very simplified ecosystems such as monoxenic cultures [74] or in reduced soil diversity experiments [130]. Using such simplified experimental systems, and benefitting from the use of isotopically labeled compounds, uptake of simple amino acids by AMF hyphae has previously been tested [46, 80]. Based on that research, there is thus far no experimental evidence for any substantial and quantitatively important acquisition of N by mycorrhizal roots via AMF hyphae from such simple organic sources, in the absence of other microbes. On the other hand, there is some limited and partly equivocal evidence from experiments employing quantum dot technology indicating that organic N fragments could potentially be taken up by AMF hyphae and that uptake of N in the form of certain amino acids is enhanced in mycorrhizal as compared to non-mycorrhizal roots [133, 134].

Nevertheless, there are specific situations where the AM symbiosis can indeed play a major and direct role in soil–plant N cycling—mainly, if the N is present in soil predominantly in organic forms (e.g., plant litter, manure, compost or organic wastes). This particular scenario will be handled in detail below.

Organic nitrogen in soil and AM symbiosis

The development of AMF in soil—both hyphal proliferation and spore formation—is often stimulated by organic amendments, particularly by those with a significant N content [16, 43, 101]. For example, farmyard manure, plant litter, yeast biomass, chitin, nucleic acids or proteins, when added to soil/growth substrate, have previously been shown to induce short-term increases in AMF hyphal and/or spore densities (Table 1 and references therein). Such effects have not been observed for compounds like cellulose or phytic acid, which contain no organically bound N, however [16, 44, 51]. Such a stimulation of AMF development could relate to release of nutrients (particularly of N in form of ammonium) from the soil amendments through mineralization, or to locally changed abiotic or biotic soil properties, or both [15, 43, 96]. Interestingly, addition of mineral nutrients does usually induce much weaker effects on AMF hyphal proliferation as compared to the organic amendments [15].

The AMF possess a particularly weak exo-enzymatic repertoire [124] as compared to other (ecto-, ericoid and orchid) mycorrhizal and saprotrophic fungi [76, 87, 118]. Thus, the AMF are very unlikely to mineralize soil organic nutrients effectively on their own, although some exo-phosphatase activity has previously been detected in the AMF hyphae [71, 72, 77]. Therefore, it is very likely that to effectively acquire mineral nutrients (be it P or N) bound either in the organic amendments or in the soil organic matter (SOM) itself, the AMF must rely on mineralization of such resources carried out by other saprotrophic or hypersymbiotic microbes [62, 96, 123]. The distinction between saprotrophic and hypersymbiotic microbes in this regards is the origin of C the microbes live on—either from the SOM or from the AMF hyphae, respectively. A nice example of a tight cooperation between the AMF hyphae and a soil bacterium *Rahnella aquatilis* with regards to organic P (phytate) mineralization has recently been described by Zhang et al. [136]. Although mineralization of organic N is at least equally important process as organic P mineralization, and microbial communities in AMF hyphosphere amended with organic N have been analyzed previously [16, 43, 96], there is as yet no specific information about the identity of primary organic N decomposers teaming directly with the AMF hyphae.

Besides the primary decomposers, which catalyze the liberation of small (organic or inorganic) molecules that could then be taken up by the microbial cells, it seems that for utilization by AMF hyphae of N supplied in organic forms, microbial grazers (protists and/or nematodes) play a particularly important role ([15] and references therein). This is because the grazers excrete, for stoichiometric reasons, large amounts of N they take in with their prey as free ammonium ions back to the soil solution [126]. From the soil solution, this N can then be readily taken up by the AMF hyphae to cover their own N demand or to transport it to the host plant [15, 68, 123]. The central role of free ammonium ions in the utilization of organic N by AMF hyphae has been postulated in several studies (e.g., [15, 117]). Further, ammonium is the preferred mineral form of N for uptake by the AMF hyphae [119]. And, interestingly enough, there is no unequivocal evidence as yet for the extraradical AMF hyphae to be able to directly and in significant amounts acquire small organic N molecules such as amino acids, peptides, chitin oligomers, or nucleotides from the soil solution ([46, 59, 80]; but see [134]).

Table 1 Responses of arbuscular mycorrhizal fungi (extraradical hyphal or spore densities) to various soil organic nitrogen (N) amendments, and the rates of transfer of N from the amendments to the mycorrhizal plants as recorded in previously published experiments (using different experimental set-ups, biological models, and lengths of exposure to the isotopes)

Identity (form) of N amendment	Quantitative response ratio of AMF hyphal or spore development[a]	Amount of N transferred[c]
Complex organic N sources (plant biomass, yeast biomass, dead mycelium)	919%[1], 292–519%[2], 756%[4], 55–138%[5], 72–341%[6], 611%[8], − 29 to 341%[9], 111–347%[18], 186–324%[19], 111–4179%[27]	28.3% (NM[d] 1.3%)[1], (7.9–16.7%)[4], 5.0–32% (NM 0.2%)[5], 6.0–6.2% (NM 0.2–0.3%[6], 26%[7], 5.4–9.0% (NM < 0.05%)[8], 2.1–3.9% (NM 3.5–6.5%)[11], 3.2–5.0% (NM 0.34–1.06%)[13], (0.8–7.5%)[14], 4.6–8.7%[15], 16–25% (NM 2%)[16], 15% (NM 5%)[19], 4–15%[27]
Polysaccharides (chitin[b], chitosan)	507–729%[1], 153–637%[2], 23–239%[9]	22.3% (NM 1.2%)[1]
Proteins (e.g., albumin)	485%[1], 244–760%[2]	
Nucleic acids (DNA)	602%[1], 233–644%[2]	
Amino acids (Gly, Arg)	439–1124%[3], 27–187%[20]	(72%)[3], 1.6–5.1%[17], 13%[28], 0.06–0.1%[29]
Humic substances (humic acids, fulvic acids)	5.2–158%[10], 0.3–203%[25]	
Mineral N (NH_4^+, NO_3^-)	323%[1], − 13% to 612%[21], − 1.3 to 25%[22], 5.5–59%[24], 828%[26]	0.35–4.67%[12], 1.9–8.2%[17], 2.0–5.8%[21], 6% (NM 0%)[22], 38.2–39.5% (NM 6.5–15.7%)[23], 27.4–49.2% (NM 0.1–0.7%)[24], (1–7%)[26], 34.5%[28], 0.58%[29], 12–17% (NM 6–8%)[30]

[a] Stimulation (positive values) or inhibition (negative values) of AMF mycelial growth and/or sporulation in contrast to control (non-mycorrhizal) treatment, of which the latter is arbitrarily set to 0%. The response of the most common AMF taxa was surveyed (e.g., *Glomus hoi*, *G. aggregatum, Rhizophagus irregularis/syn. G. intraradices/*, *R. clarus/syn. G. clarum/*, *Funelliformis mosseae/syn. G. mosseae/*, *Claroideoglomus claroideum/syn. G. claroideum/*)

[b] Crab-shell chitin or fungal chitin

[c] Amount of isotopically labeled nitrogen (N) added to the root-free patch and transferred to the plant in a mycorrhizal treatment; numbers in brackets indicate values recorded in the non-mycorrhizal (NM) treatment if preceded with "NM". Values in brackets without the prefix "NM" indicate values recorded in the mycorrhizal treatment without a significant difference from the NM control treatment, or absence of the NM control treatment from experimental design

[d] NM—figures for the nonmycorrhizal control treatments

[1] Bukovská et al. [15]

[2] Bukovská et al. [16]

[3] Hodge [48]

[4] Hodge [49]

[5] Leigh et al. [81]

[6] Hodge and Fitter [53]

[7] Hodge et al. [58]

[8] Barrett et al. [9]

[9] Gryndler et al. [43]

[10] Gryndler et al. [42]

[11] Saia et al. [105]

[12] Tanaka and Yano [119]

[13] Hodge et al. [56]

[14] Hodge et al. [55]

[15] Hodge et al. [57]

[16] Atul-Nayyar et al. [6]

[17] McFarland et al. [89]

[18] Tanwar et al. [120]

[19] Hodge et al. [52]

[20] Allen and Shachar-Hill [2]

[21] Fellbaum et al. [27]

[22] Johansen et al. [65]

[23] Johansen et al. [66]

[24] Johansen et al. [67]

[25] St. John et al. [116]

[26] Hawkins and George [45]

[27] Barrett et al. [10]

[28] Rains and Bledsoe [102]

[29] Cliquet et al. [20]

[30] Mäder et al. [85]

Chitin—a relevant organic N source for the AMF?

Chitin is the second (after cellulose) most abundant polymer in nature [122], and, unlike the cellulose, it is rich in N (it contains >6% N by weight). It is present in soil micro- and meso-fauna and in microorganisms, including many insects, crustaceans, and fungi, respectively. Large amounts of chitin are, thus, both produced and recycled in the soils [25, 29]. Addition of crab-shell chitin to plant cultivation substrate has earlier been shown to strongly promote sporulation of several AMF species [43], a trick that is now widely been used in commercial production of AMF inocula to enhance their quality. More recently, it has been shown by direct isotopic ^{15}N-labeling that a large fraction (>20%) of the organic N supplied as chitin into a pot zone accessible solely to AMF hyphae but not roots has been transferred to the plants within as little as 5 weeks [15]. Further examples of experimentally measured N transfer rates from organic N sources to plants via AMF hyphae are provided in Table 1. Such efficient release and transport of N as quoted above would require very fast chitin mineralization, for example, by specialized soil prokaryotes and/or fungi [12, 94] and further processing via the soil microbial loop involving microbial grazers [15]. It is noteworthy that chitinolytic microorganisms usually degrade chitin to oligomers that are directly taken to their cells via specialized transporters, referred to (at least in the prokaryotic world) as chitoporins ([12] and references therein). Specialized or more generic transmembrane transporters facilitate uptake of *N*-acetylglucosamine (a chitin monomer) to eukaryotic cells [3, 107]. Interestingly, genes responsible for *N*-acetylglucosamine transport across membrane and its further metabolism have also been described from AM fungus *Rhizophagus irregularis* [75], yet they have only been documented to be active in the intraradical mycelium, possibly recycling organic N from collapsing arbuscules. Regardless of the possible role of *N*-acetylglucosamine (or other soluble products of chitinolysis) in N nutrition of various microorganisms, chitin oligomers and their derivatives (such as lipo-chitooligosaccharides) also serve as signals to recognize pathogens or symbionts in the plant and microbial worlds [5, 93, 108]. To recognize such signals, specialized receptors and signaling cascades have developed in plants [5, 38], but these are unlikely to be involved in mass chito-oligomer uptake by cells for nutritional purposes.

Metabolic capacity to take up soluble organic N compounds derived from chitinolysis may give the microbes the priority of utilizing the N from chitin over other soil opportunists. Yet, regardless the priority in organic N uptake, once such microbes are digested by bacterial/fungal grazers, their N eventually returns to the soil ammonium pool. The AMF hyphal proliferation in chitin-enriched patches [15] could then be explained by locally elevated ammonium concentration or by the presence of specific microbiome in the chitin-amended patches, with countless of more or less specific interactions between individual microbes and the AMF hyphae [41, 63]. Among such interactions, we mention here just two examples: first, a competition for free ammonium ions in soil solution between AMF hyphae and soil ammonia oxidizers has recently been documented [15]. And second, stimulation of nosZ gene-carrying bacterial clades (e.g., Gemmatimonadetes and Deltaproteobacteria) by AMF hyphae has been suggested to explain overall reduction of soil N_2O emissions from AMF-colonized N_2O hotspots [13, 117].

There is also an interesting question remaining to be answered as to whether the AMF hyphae could directly be implicated in chitin mineralization and consequent N release from its polymeric structure. If we accept that the AMF have chitin in their cell walls [35], hyphal elongation (apical growth) requires a suite of membrane-bound and exo-cellular enzymes including chitin synthases and chitinases [37, 104, 109]. Having such enzymes in their repertoire, the AMF may (at least theoretically) be well capable of releasing N locked up in the exogenous chitin without involvement of other (chitinolytic) microorganisms. Whether the AMF generally utilize the N from exogenous chitin without involvement of other microorganisms and whether the rate of N release from chitin and its uptake into the hyphae is of any significance for the AMF is still remaining to be addressed experimentally, though.

Conclusions and future research directions

In spite of a significant progress in understanding of importance of organic N sources for AMF hyphal development and N acquisition [59], there are still a number of open questions to be answered by future research.

First, the effects should specifically be addressed of the chemical identity of model N compounds on AMF and the soil N cycling. There have namely been different organic N sources including complex substrates such as plant litter or yeast biomass tested in previous experiments ([16, 50, 52, 103]; see also Table 1), which might have stimulated different microbial groups and/or mineralization pathways [16]. Future experiments should, thus, concentrate on a few, chemically well-defined compounds to achieve deeper understanding of mechanisms and processes behind utilization of those model organic N sources by the AMF and their associated plants. Chitin may be a good candidate for such experimentation because of its chemical uniformity and simplicity, although, admittedly, complex plant litter [81] or even

entire roots [127] might well be even more relevant from a broader ecosystem-wise point of view.

Second, unambiguous identification should be achieved of the players involved in the release/uptake of N from the organic N sources, including their energy (and C) sources. Experimental approaches to achieve this include stable isotope labeling of the organic soil amendments coupled with density-gradient fractionation of nucleic acid and subsequent next generation sequencing (NGS) or with signature phospholipid fatty acid analyses, approaches known as stable isotope probing (SIP) experiments [24]. Studying soil meta-transcriptomes and genetic makeup of microorganisms identified in the SIP experiments, along with metabolic and co-occurrence network analyses, should allow reconstructing the entire organic N utilization pathway [8, 91]. Such experiments should carefully be designed to cover all relevant time points in the organic N mineralization and downstream N utilization within the complex microbial communities to seize their temporal dynamics aspect. The unprecedented depth of current NGS methods should be utilized, including less prominently studied, but functionally equally important, microbial groups such as soil protists and nematodes [79, 106, 135].

Third, fully quantitative insights should be provided into the fluxes of N and C in soil. The usage of stable isotopes allows addressing whether it was specifically the N that was cleaved off the organic moieties without further degrading/utilizing the C backbone structures of the organic soil amendments. Or, alternatively, whether mineralization of organic N sources such as chitin is only or preferentially happening upon strong microbial demand for C/energy. In the latter scenario, liberation of N contained in the organic molecules would effectively happen only as a by-product of mineralization of the organic N source primarily because of microbial C requirements. There is evidence for both pathways being operational in the microbial world—with deacetylation/deamination processes being more active if bacteria are N but not C limited, and full depolymerization/mineralization of chitin being predominant under conditions when chitin is the major C source [12]. Specific utilization of organic N but not C from the SOM (a process leading eventually to enhanced C sequestration) is also described for ectomycorrhizal fungi [11, 84] and also suggested by some earlier data from AMF systems [127]. When the entire organic N source including the C was taken up by the microbes, it would result in removal and not in stabilization/sequestration of the SOM, which is consistent with some other observations, showing co-incidental disappearance of both N and C added to the soil as organic amendment [19, 128]. Organic N mineralization in soil could also be catalyzed by different microbial groups, depending on resource stoichiometry such as relative C and N availabilities. This means that bulk processes such as organic N mineralization cannot always be unequivocally linked to the individual microbial groups—there obviously is a continuum in both [78].

Fourth, detailed and spatially explicit insight is needed into the microbial world, which would allow directly linking the players to individual processes in soil N cycling. Spatial arrangement of both the microbes and the stable isotopes could be visualized by advanced approaches such as fluorescence in situ hybridization (FISH) and by nanoscale secondary ion mass spectrometry (NanoSIMs), respectively [73, 90, 96, 125]. Further, the activity of the different enzymes potentially involved in chitin or other N sources mineralization (e.g., chitinases, deaminases, proteinases) can be visualized in a spatially discrete manner by zymography [113].

Fifth, the ultimate proof is required of the causal link between the functionality and the structure of processes. Reconstructing simple model ecosystems from individual microorganisms or from functional guilds [130] shall provide the direct experimental evidence for the processes suggested by observations of complex systems, e.g., involvement of protists in increasing N availability from the organic N sources for the AMF hyphae through so-called soil microbial loop (e.g., [15]).

Last but not least, in each and every stage of the research outlined above, it is always important to think about how the results relate to our ultimate goal—which is to utilize the new knowledge for the sake of global sustainability and human welfare. Applied research should translate the basic findings (for example, those related to efficiency of organic N recycling in soils) to improved and more environmentally sustainable agricultural practices. Improving efficiency and sustainability of agricultural production is urgently needed, while it is equally important not to accept any productivity decreases—an uneasy task to fulfill, yet vitally important to attain in order to ensure enough food for every human being on the planet—now and in the future.

Abbreviations

AM: arbuscular mycorrhizal; AMF: arbuscular mycorrhizal fungus/fungi; C: carbon; FISH: fluorescence in situ hybridization; N: nitrogen; NanoSIMs: nanoscale secondary ion mass spectrometry; NGS: next generation sequencing; P: phosphorus; SIP: stable isotope probing; SOM: soil organic matter.

Authors' contributions

JJ and PB devised the structure of the article and both substantially contributed to defining the content and conclusions of the paper. SF reviewed literature on hyphal responses to soil organic amendments, and on nitrogen transfer rates from organic amendments to plants via mycorrhizal hyphae. MR specifically contributed to discussion on interaction of AMF hyphae with bacteria. DP provided insights into plant–mycorrhiza–nitrogen interactions. HH helped defining future goals with respect to molecular analyses of

the microbial communities. JJ wrote the first draft of the paper, all authors contributed to subsequent revisions. All authors read and approved the final manuscript.

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