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OPINION PAPER

How to get to the N – a call for interdisciplinary research on organic N utilization pathways by plants

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Abstract
Background and aims While nitrogen (N) derived from soil organic matter significantly sustains agricultural plants, the complexities of organic N utilization pathways remain poorly understood. Knowledge gaps persist regarding diverse organic N pools, the microbial processes in N mineralization, and how plants shape the N-mineralizing microbial community through root exudation.
Results To address these gaps, we propose an integrated conceptual framework that explores the intricate interplay of soil, plant, and microbiome dynamics within the context of soil carbon (C) cycling. Emphasizing plant effects on gross depolymerization and deamination of organic N—a crucial yet often overlooked aspect—we aim to enhance our understanding of plant N utilization pathways. In this context, we suggest considering the linkages between root and hyphal exudation, followed by rhizosphere priming effects which in turn control N mobilization. Based on the relation between exudation and N turnover, we identify microbial necromass as a potentially important organic N source for plants. Furthermore, we propose applying root economic theory to gain insights into the diverse strategies employed by plants in accessing soil organic N. Stable isotope tracers and functional microbiome analytics provide tools to decipher the complex network of the pathways of organic N utilization.
Conclusions The envisioned holistic framework for organic N utilization pathways, intricately connects plants, soil, and microorganisms. This lays the groundwork for sustainable agricultural practices, potentially reducing N losses.

Keywords Organic N · Necromass recycling · Rhizosphere priming · Root economic space · Root exudation

Introduction

In agricultural systems, only about 50% of the nitrogen (N) taken up by annual crops is current-year fertilizer derived (Gardner and Drinkwater 2009; Yan et al. 2020), indicating that plants are supplied with N derived from soil organic matter (SOM) to a large extent. Up to now, the contribution of different SOM pools to N nutrition and the processes by which these compounds are made available to the plant are not well understood (Leinweber et al. 2013; Yan et al.

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2020), although a greater uptake of organic N sources might improve the efficient use of N resources (Drinkwater et al. 2017) and mitigate the environmental impacts of agriculture.

Our incomplete knowledge of organic N utilization pathways, i.e. organic N conversion to plant-available N, can be explained in part by the historical focus on the inorganic N pool (Daly et al. 2021) but is certainly also caused by the complexity of the soil N cycle. This complexity arises because of the strong functional link between microorganisms, plants and the soil matrix which shape the N cycle and N bioavailability. Moreover, the conversion of N within the soil is closely linked to the quality of soil organic matter input. This is because the ratio of C to N in organic matter (C/N ratio) determines the balance between microbial net N mineralization and immobilization (Manzoni et al. 2012).

We see a strong need to determine plant-microbe interactive effects on SOM cycling. Hence, we propose an integrated conceptual framework that addresses the interplay of soil, plant and microbiome functioning, all within the context of soil C cycling. Such a holistic framework has the potential to significantly advance our understanding of the contribution of organic N utilization pathways to the N nutrition of plants. Specifically, we propose an increased focus on plant effects on depolymerization and deamination of organic N, a crucial yet often overlooked aspect in understanding plant N use efficiency. We will suggest potential organic N sources for plants and elucidate the processes through which plants can influence the availability of these organic N sources. Additionally, we advocate for the application of root economic theory to gain insights into the diverse strategies employed by plants in accessing and mobilizing soil organic N.

Soil N cycling and sources of organic N

More than 90% of N in soil is present in organic form (Amelung 2001). Organic N primarily originates from plant litter decomposition, fire or animal residues and enters the soil from the surface as particulate organic matter (POM) or dissolved organic N (DON) (Knicker 2011). However, organic N is also introduced belowground in significant amounts through root litter and rhizodeposits (McNeill et al. 1997; Wichern et al. 2008; Arcand et al. 2013). Plant derived organic N is mostly present as particulate organic matter (POM) (Fig. 1) (Baldock and Skjemstad, 2000; Lavallee et al. 2020) and, unless protected

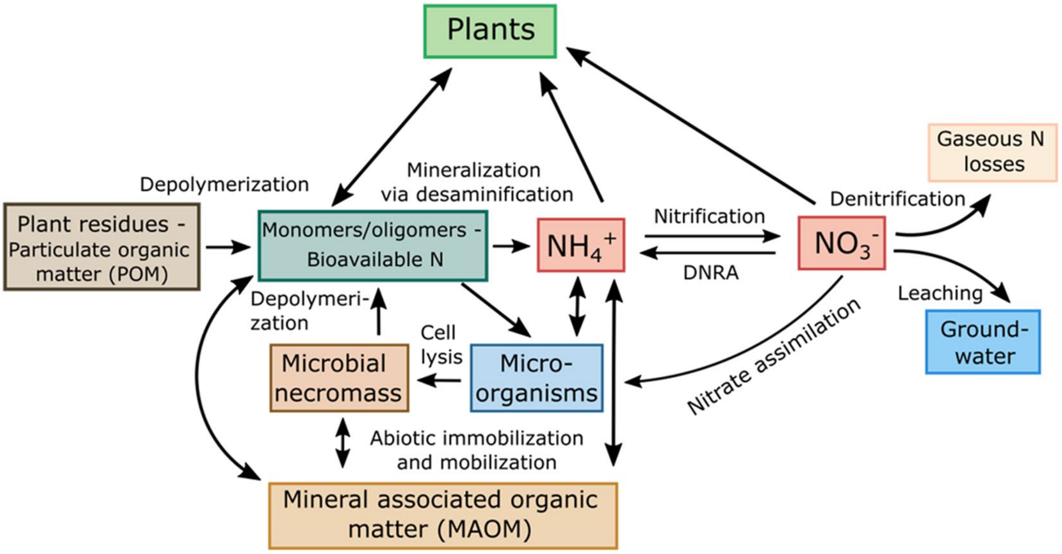

Fig. 1 Pools of nitrogen and pathways of N cycling between these pools. Considered as N pool are plant residues/POM, monomers as bioavailable N, mineral N as NH_4^+ and NO_3^- as well as microbial biomass N and microbial necromass N. Some of these pools are in exchange with MAOM via adsorption and desorption. DNRA = dissimilatory nitrate reduction to ammonium. Figure adapted from Schimel and Bennett (2004) and Daly et al. (2021)

within aggregates, susceptible to rapid decomposition by microbes (Cotrufo et al. 2019; Mueller and Koegel-Knabner, 2009; von Lützow et al. 2007). The products of microbial decomposition can contribute significantly (15–80%) to SOM (Liang et al. 2019; Angst et al. 2021; Camenzind et al. 2023). They have usually a lower C/N ratio than plant derived organic N (Khan et al. 2016; Wang et al. 2020b) and are to a large extent incorporated into mineral associated organic matter (MAOM) (Kopittke et al. 2018, 2020) which is more stable in soil compared to POM (Cotrufo et al. 2019).

About 30–60% of soil organic N consists of proteinaceous materials (e.g. proteins, peptides, and amino acids; plant or microbial derived), while amino sugars (e.g. muramic acid, glucosamine; microbial derived) make up 5–8% and heterocyclic N compounds (e.g. pyrroles, pyridines, pyrazoles; plant or microbial derived) account for 5–35%, although there are some uncertainties in quantification of heterocyclic N (Schulten and Schnitzer 1997; Nannipieri and Eldor 2009; Leinweber et al. 2013). Therefore, overall proteinaceous materials contribute significantly to soil organic N (Geisseler et al. 2010). Amino sugars also play an important role as they are the building blocks of microbial cell walls and they are used as biomarkers for microbial residues (i.e. microbial necromass). A major component of fungal cell walls is chitin, an unbranched polymer of N-acetylglucosamine (Rinaudo 2006). Bacterial cell walls are constructed of peptidoglycan consisting of glycan strands, repeating units of N-acetylglucosamine and N-acetylmuramic acid, crosslinked by short peptide stems (Steen et al. 2003; Vollmer et al. 2008).

To become plant available, complex organic N needs to be microbially depolymerized into its monomers (e.g. amino acids, amino sugars) before it is subsequently transformed into mineral forms such as NH_4^+ or NO_3^- (Schimel and Bennett 2004; Daly et al. 2021) (Fig. 1). Extracellular depolymerases are involved in the first step of soil organic N decomposition (Schimel and Bennett 2004). The most important extracellular depolymerases vary depending on the chemical composition of soil organic N. Proteases, chitinases, and peptidoglycan hydrolases are all prevalent among soil microorganisms, reflecting their widespread ability to degrade protein, chitin, and peptidoglycan (Geisseler et al. 2010 and references theirin). The small organic molecules released by extracellular depolymerases (e.g. free amino acids, free amino sugars) are available for microbial uptake, and their pool is therefore very small (less than 1% of the total pool) and highly dynamic (Wanek et al. 2010; Warren 2014; Hu et al. 2017). While there is evidence that crops can also take up dissolved organic N molecules (such as small peptides or amino acids), the ecological significance of this N acquisition pathway, particularly in agricultural systems remains controversial (Näsholm et al. 2009; Moreau et al. 2019). Specifically its relevance under field conditions and at realistic concentrations of organic N molecules in solution remains questionable (Jones et al. 2005). Therefore, NH_4^+ or NO_3^- can be considered the most important N forms for crop uptake (Schimel and Bennett 2004; Britto and Kronzucker 2013). NH_4^+ and NO_3^- are provided by the mineralization of N-containing monomers into its mineral forms (Fig. 1) and involves the deamination of amino acids and the hydrolysis of urea by ureases (Schimel and Bennett 2004; Daly et al. 2021). N mineralization is counteracted by N immobilization. This includes biotic N immobilization, the transformation of inorganic N by microorganisms and plants into organic N (Hart et al. 1994) and its subsequent incorporation into soil organic matter (Denk et al. 2017; Zhang et al. 2018) as well as plant N uptake (Van Groenigen et al. 2015). Additionally, N can be immobilized chemically by sorption to mineral surfaces (Bingham and Cotrufo 2016). This process is referred to as abiotic N immobilization.

In general, N turnover rates are controlled by temperature, latitude, ecosystem type, soil clay content, soil microbial biomass, the soil C/N ratio and soil pH (Li et al. 2020). In particular, the soil C/N ratio has long been recognized as an important control over decomposition processes as it governs the nutrient demand and the structure of soil microbial communities, thereby affecting the production of extracellular enzymes and finally N turnover (Mooshammer et al. 2014). On the one hand, organic N compounds with relatively low C/N ratios are likely to be immobilized by sorption on minerals and within the mineral associated organic matter (MAOM) (Kopittke et al. 2018, 2020; Wang et al. 2020a; Buckeridge et al. 2022). This preferential sorption of N rich compounds can be explained by the onion layer model, according to which N-rich compounds sorb directly and more strongly on mineral surfaces compared to other organic matter compounds and form a stable organic layer (Kleber et al. 2007). On the other hand, compounds with low C/N ratios might be an attractive source of N for microbes. For example, narrow C/N legume residues were shown to be preferentially incorporated into microbial biomass and resulted in higher net N mineralization compared to wide C: N wheat residues (Luce et al. 2016). Also, under low N availability, microbial necromass was shown to be preferentially decomposed and metabolized by microorganisms compared to other SOM fractions, leading to a rapid turnover of microbial residues (Zeglin and Myrold 2013). The direct quantification of microbial necromass cycling rates in soil has just recently been established based on isotope pool dilution (Hu et al. 2018). The authors found that microbial cell wall residues rapidly turn over in soil and that products of this microbial cell wall decomposition (e.g. free amino sugars, amino acids) add significantly to the bioavailable soil organic N pool, indicating that necromass-derived N could significantly contribute to plant nutrition (Hu et al. 2018). Although the cycling of necromass N and its contribution to plant N nutrition has not been directly quantified in the presence of plants so far, two studies have attempted to indirectly assess its potential significance (Cui et al. 2020; Pausch et al. 2024).

First, Cui et al. (2020) conducted an incubation experiment with addition of high amounts of ^{13}C-labeled glucose in order to study priming, i.e. the short-term change in the turnover of SOM caused by addition of easily available C (Kuzyakov 2002). Particularly the addition of excessive amounts of glucose resulted in distinctive peaks of glucose-derived CO_2, deviating from the typical exponential decay pattern normally observed after glucose decomposition. These peaks were interpreted as indicative of the recycling and mineralization of ^{13}C-enriched microbial necromass stimulated by glucose addition. Building on this observation, the authors hypothesized that N recycling from microbial necromass after root exudation could serve as a significant mechanism, mitigating microbial N deficiency and possibly enhancing plant N availability. Second, Pausch et al. (2024) observed an increase in ^{15}N natural abundance in plants with increases in rhizosphere priming. Considering that microbial necromass is enriched in ^{15}N compared to total soil N (Dijkstra et al. 2006; Craine et al. 2015) the authors concluded that rhizosphere priming likely promotes the recycling of necromass-N cycling and the acquisition of necromass-derived N by plants. Notably, as of our current knowledge, no other efforts have been made to quantify the importance of microbial necromass as an N source for plants, though, recent advancements in methodology offer promising tools to quantify turnover rates of microbial necromass (Hu et al. 2018; Warren 2021). Therefore, unraveling the significance of microbial necromass as a potential N source for plants is critical. We strongly advocate to explore its contribution to plant N nutrition in future studies.

Plant control on soil N cycling and mineralization

Although soil and rhizosphere microorganisms shape N cycling most strongly as they transfer N between different pools, plants also exert control over N mineralization and availability by the following processes: (1) Plants remove mineral N from the soil solution with their root N uptake and immobilize this N in their biomass, whereby they compete with microorganisms such as nitrifiers or denitrifies for N (Schimel and Bennett 2004; Kuzyakov and Xu 2013; Thion et al. 2016). (2) Part of the N that plants immobilize is returned as litter to the soil after plant death or organ senescence. The amount and quality of the plant litter has a distinct effect on its decomposition and mineralization by oligotrophs and copiotrophs in succession (Myrold and Bottomley 2008; Geisseler et al. 2010; Pascault et al. 2013). (3) Moreover, some of the C that is assimilated by plants is allocated to roots, mycorrhizal hyphae and finally released into soil via root and hyphal exudation (Dilkes et al. 2004; Jones et al. 2004). Some of those compounds can directly affect N turnover, such as biological nitrification inhibitors that reduce the microbial process of nitrification (Coskun et al. 2017; Nardi et al. 2020; Sun et al. 2016). Moreover, plants may release proteases from their roots into the soil, potentially elevating the concentration of free amino acids in the soil solution as a source of N (Godlewski and Adamczyk 2007; Adamczyk 2021). However, research aimed at comprehending the impact of plant-released proteases on increased proteolysis has yielded conflicting results and interpretations (Greenfield et al. 2020; Adamczyk 2021). The vast majority of C released by plants into soil is likely to affect N turnover rather indirectly, through elevation of microbial activity and turnover. Although it is not yet clear, to which extent plants can control the exudation of C into soil (Jones et al. 2009; Carvalhais et al. 2011) it is clear that this exudation, enhances microbial activity and shapes the rhizosphere microbial community (Huang et al. 2014; Zhalnina et al. 2018; Iannucci et al. 2021; Lewin et al. 2024). Soil microorganisms are largely C limited and easily available plant derived C (e.g. simple sugars such as glucose) shapes a rhizosphere microbial community, predominated by r strategists capable of resource competitive traits such as antibiotic production and biofilm formation. Competitive microbial communities profit from elevated C availability due to their high yield energy metabolism (i.e. ATP gain per substrate used) (Wood et al. 2023) accelerating N assimilation and possibly subsequent microbial N mineralization. However, the disparate range in metabolism of soil microbes hinders efficient classification into resource use strategies (Wood et al. 2023). Thus, up to now only a fragmented understanding of the effect of root and hyphal exudation on microbial N depolymerization of complex organic N and deamination of organic N monomers such as amino acids along the root soil continuum exists. A multitude of functional genetic traits of microbes needs to be assessed to better understand how changes in belowground plant activity shape microbial community assembly and affects microbial community members capable to perform N mineralization or denitrification (Legay et al. 2020). To better understand the overall process of gross N mineralization (GNM) and the involved functional microbial groups, we propose using ‘omic’ approaches, such as metagenomics and -transciptomics, to decipher active microbial N processes in the root-associated microbial community. This would follow the recently suggested approach of holo-omics (Xu et al. 2021; Rai et al. 2022) which is considered as a simultaneous assessment of the plant metabolism including root exudate synthesis and metabolic activity based on specific metabolic pathways of plant-root associated microbial communities. If such approaches are also combined with compound occurrence by metabolomics, this would allow for mapping the connections between root exudates and the microbial communities responsible for key steps like dissimilation of inorganic N, depolymerization of complex organic N, and deamination of monomers such as amino acids.

Plant strategies to access organic N

Plant species differentially influence the N cycle (Wang et al. 2020c), primarily through variations in their rates of C exudation and N uptake (Moreau et al. 2015). These variations reflect phylogenetically conserved plant resource utilization strategies. Plant ecologists have described these strategies to explain plant trait diversity from a resource acquisition point of view (root economic theory) (Wright et al. 2004; Freschet et al. 2010; Reich 2014; Díaz et al. 2016). Different strategies thereby evolved to serve the same function in different ways while resulting in a continuous functional trade-off between the opposing strategies with consequences for plant fitness under specific conditions (Laughlin et al. 2021). Resource acquisitive plant species are characterized by a fast strategy with short root longevity, low root tissue density (RTD) and narrow C/N ratios while resource conservative plants exhibit opposite root traits (Eissenstat 1992; Ostonen et al. 2007; Freschet et al. 2010; Luke McCormack et al. 2012; Reich 2014). These traits distribute along the fast-slow resource conservation gradient. Recently, this framework of resource acquisition was expanded for the collaboration gradient to include the symbiosis with mycorrhiza (Bergmann et al. 2020) and later on for root exudation (Wen et al. 2021). The “outsourcing” strategy within the collaboration gradient is characterized by high root diameter (D), low specific root length (SRL) and strong mycorrhizal symbiosis. In contrast, plants following the “do it yourself” strategy exhibit a fine-root system with high SRL and have lower mycorrhizal colonization rates (Bergmann et al. 2020). Root exudation, particularly concerning root exudates associated with the mobilization of soil N is typically linked with the fast side of the resource conservation gradient (Wen et al. 2021). As such, it is expected to be independent of the collaboration gradient (Wen et al. 2021) (Fig. 2). As both, root exudation and mycorrhizal collaboration, require C investment for the plant, a tradeoff between root exudation and investment into mycorrhizal symbiosis can be expected (Jones et al. 2004; Kaiser et al. 2015). The diverse root economic

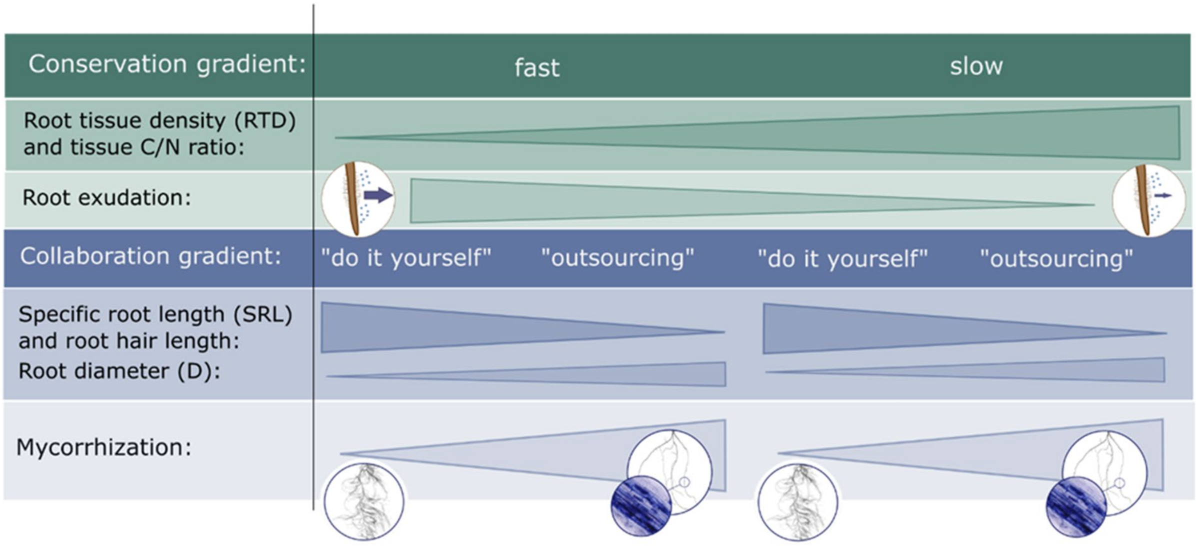

Fig. 2 Root economic strategies that are expected for plants based on the work of Bergmann et al. (2020) and Wen et al. (2021). While the "Conservation gradient", refers to nutrient acquisition, the "Collaboration gradient" refers to collaboration with mycorrhizae. Root exudation, particularly concerning root exudates associated with the mobilization of soil N is typically linked with the fast side of the resource conservation gradient. As such, it is expected to be independent of the collaboration gradient (Wen et al. 2021). Root hair length is suggested to be negatively associated to mycorrhization as proposed in Kothari et al. (1990)

strategies illustrated in Fig. 2 embody the aforementioned processes, through which plants regulate soil N cycling and N availability. This regulation involves: (a) the uptake of N and its uptake rates, (b) the quality (chemical composition, structure, C/N ratio) and quantity of litter input, (c) the C input to the soil via roots and hyphae. Consequently, we propose that a thorough examination of these diverse root economic strategies will substantially enhance our comprehension of the organic N utilization pathways employed by annual crop plants. As the majority of annual crops, such as cereals, mostly align with the fast side of the resource conservation gradient (Roumet et al. 2006; Cornwell and Cornelissen 2013; García-Palacios et al. 2013) our focus in this context predominantly centers on the fast side of the resource conservation gradient.

Strategies related to root exudation

Based on the root economic strategies summarized in Fig. 2, fast type plants that focus on root exudation are expected to grow a fine-root system with a narrow C/N ratio and a high exudation rate. Their high-quality litter (i.e. narrow C/N ratio) together with high exudation rates and fast fine-root turnover probably favors a high activity and abundance of microorganisms and fast N turnover in the soil.

High root exudation rates of 'fast' type plants can induce rhizosphere priming, i.e. a short term increase in soil organic matter (SOM) decomposition caused by addition of easily available C from the root to the soil (Kuzyakov 2002). Rhizosphere priming is positively related to gross N mineralization (Holz et al. 2023; Fig. 3) and is therefore likely an important mechanism for plant N nutrition (Henneron et al. 2020). However, the quantification of priming-derived N to plant N as well as the underlying mechanisms remain largely unknown and warrant further investigation. We suggest that root exudation initiates a cascade of processes along the developing root that finally results in increased plant access to SOM derived N (Fig. 4 left). In principle these processes will also occur in 'slow' type plants that invest in root exudates, but to a less intense degree.

High exudation from the root tip and root hair zone (Dennis et al. 2010; Holz et al. 2017) will result in short lived regions of high C availability. In this area a high abundance and activity of bacterial

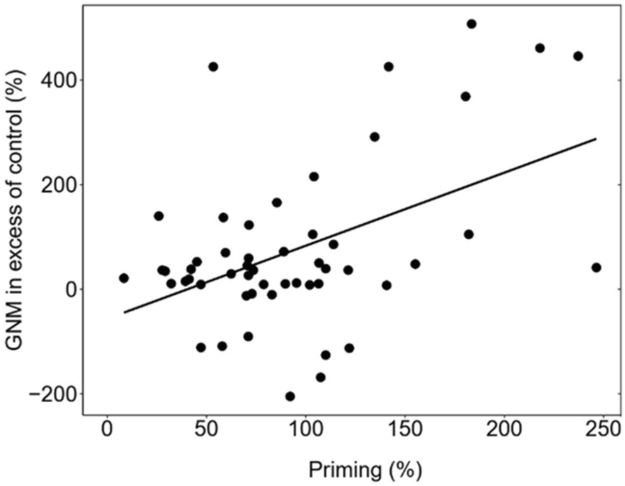

Fig. 3 Summarized literature data for the relationship between soil priming (a short term increase in SOM decomposition caused by addition of easily available C to the soil) and gross N mineralization in excess of the control treatment. The correlation was significant at R²=0.21 (Holz et al. 2023)

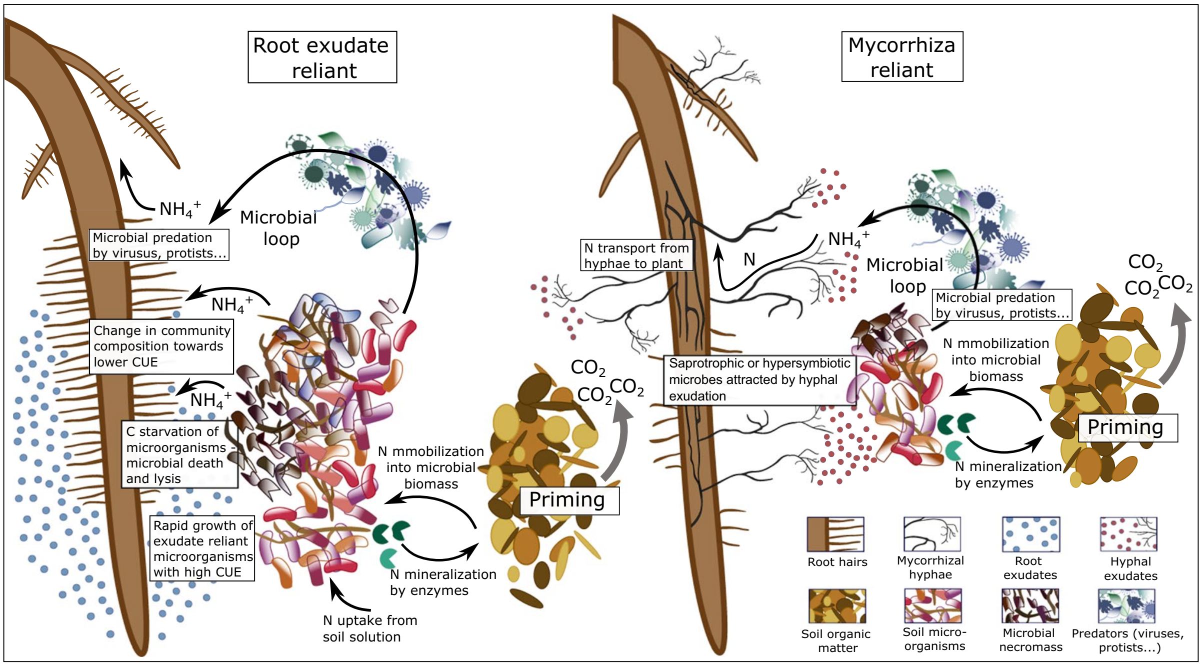

Fig. 4 Hypothesized organic N utilization pathways for strategies focusing on root exudates (left) and those in combination with mycorrhiza (right). Both scenarios are not exclusive and that a specific plant likely relies on both mechanisms but to different degrees. Though both strategies described rely on exudation, we suggest that they may exhibit certain differences as outlined in the section "Differences in root exudate and AM fungi induced N cycling". Although, plants might take up N in the form of either NH_4^+ or, if nitrified, as NO_3^- but for simplicity, only NH_4^+, as the direct product of N mineralization is indicated here. Note that apart from the processes outlined here, plants also take up N directly from the soil solution. CUE: carbon use efficiency

dominated copiotrophs characterized by high N uptake is expected (Folman et al. 2001; Kuzyakov and Xu 2013; de Vries and Bardgett 2016). The high C input through root exudates will likely cause microbial N limitation and result in organic N mining through exo-enzymes (Dijkstra et al. 2013).

These two factors, N limitation and enzyme activity can then cause increased rhizosphere priming, gross N mineralization and immobilization into the microbial biomass (Geisseler et al. 2010; Farrell et al. 2014).

In the region behind the root tip root exudation decreases and easily available C becomes exhausted. This depletion may lead to a shift in microbial communities towards low C use efficiency (oligotrophic/stress tolerant microorganisms) (Bernard et al. 2022). This resource constrained microbial community may recycle nutrients from “old” communities, i.e. from microbial necromass (Kaiser et al. 2014; Cui et al. 2020; Pausch et al. 2024). Due to the narrow C/N ratio of the necromass, net N mineralization will occur, enhancing plant N availability (Eshel and Beeckman 2013). Additionally, microbial grazers (nematodes, protists, phages) will be attracted by the high microbial abundance. If microbial grazers consume microorganisms, mineral N is released into the soil caused by small differences in C/N ratios between predators and prey and a low assimilation efficiency of predators (microbial loop) (Bonkowski 2004; Kuzyakov and Mason-Jones 2018). The mineral N released via the microbial loop is then potentially available to the plant (Fig. 4). Based on the sequence of processes described, we expect a tight link between exudation, fast microbial build up, priming and subsequent N mineralization from the microbial necromass. These processes are likely triggered by rapid changes in root exudation and microbial activity and composition along the root.

In comparison to ‘fast’ economic crops, ‘slow’ type plants that invest in root exudates produce long living dense fine roots. These roots have a wider C/N ratios and higher chemical recalcitrance which means that they exhibit an elemental composition, presence of functional groups, and molecular conformation that restrict their microbial decomposition (Freschet et al. 2010; Reich 2014) resulting in a low microbial activity and abundance and slower N cycling compared to ‘fast” type plants (Chapman et al. 2006; Henneron et al. 2020). Due to the wide litter C/N ratio and the slower N cycling, a larger share of organic N is likely to be present as POM compared to MAOM (Averill and Waring 2018). In these plant-soil systems, slow root turnover, together with lower exudation (Fig. 2) will likely result in low priming effects. In light of the higher occurrence of POM-N in comparison to ‘fast’ type plants, we propose that POM-N serves as a significant N source for these plants, leading to a reduction in microbial necromass recycling compared to the scenario with ‘fast’ type plants.

Strategies in combination with arbuscular mycorrhizal (AM) fungal colonization

We propose that fast plants that invest in collaboration with mycorrhiza grow a fine-root system with each root having a comparably short life span, a narrow C/N ratio and a high C investment in AM fungi, the mycorrhizal form most relevant for annual agricultural crops.

AM fungi possess a very weak exo-enzymatic repertoire (Tisserant et al. 2013) and it is therefore unlikely that they directly acquire mineral N from organic matter (Hodge and Storer 2014; Jansa et al. 2019). Therefore AM fungi must rely on mineralization by either saprotrophic or hypersymbiotic microbes, i.e. microbes that rely on mycorrhiza derived C as an energy source (Quilliam et al. 2010; Jansa et al. 2013). We propose that the symbiotic relationship with mycorrhizal fungi and the exudation of readily available C through their hyphae initiate a series of processes, ultimately leading to enhanced availability of N derived from organic matter for the plant. These processes are summarized in Fig. 4 (right) and described below. In principle these processes are also expected for slow mycorrhizal plants, but to a less intense degree.

The AM fungi hyphal exudation of labile C is likely to stimulate the activity and abundance of saprotrophic or hypersymbiotic microbes (Toljander et al. 2007; Herman et al. 2012) and induce priming of SOM (Talbot et al. 2008; Paterson et al. 2016). Moreover, the mycorrhizal fungi’s effective assimilation of NH_4^+ from the soil solution significantly diminishes soil NH_4^+ concentrations. This intensifies microbial N limitation, extracellular enzyme production by saprotrophic or hypersymbiotic microbes and rhizosphere priming (Hodge et al. 2001; Atul-Nayyar et al. 2009). As described above, the high C availability likely results in microbial N immobilization (Geisseler et al. 2010; Farrell et al. 2014). At the same time, the high microbial abundance is expected to attract microbial grazers, such as nematodes or protists and phages resulting in the ‘microbial loop’ with a net release of mineral N into soil

(Bonkowski 2004; Kuzyakov and Mason-Jones 2018) and finally an increased N availability for the plant. It has been shown that in the presence of AM fungi a large fraction organic N supplied as chitin is relatively fast transferred plants (Bukovská et al. 2018; Jansa et al. 2019). This transfer is probably governed by prokaryotes and fungi specialized on chitin mineralization, while the N will likely be made available to plant uptake via the soil microbial loop (Jansa et al. 2019). There is good evidence that AM fungi hyphal development is positively correlated to soil protist abundance (Amora-Lazcano et al. 1998; Bukovská et al. 2016). Hence, we suggest that the 'microbial loop' plays an important role in AMF-induced N cycling. Additionally, the very efficient uptake of NH_4^+ by AM fungi (Herdler et al. 2008; Koller et al. 2013) reduces plant-denitrifier competition while it increases competition with nitrifiers (Legay et al. 2020) and results in a high immobilization rate of NH_4^+ into AM fungi biomass.

However, as of now, there is no established direct correlation between AM fungi induced priming, which triggers NH_4^+ release via the 'microbial loop,' and the subsequent NH_4^+ uptake by AM fungi. Additionally, it remains unclear, whether a portion of this N taken up by hyphae is allocated to the plant. Hence, we recommend that future research endeavors focus on elucidating the relationship between AM fungi-induced priming and the uptake of priming-derived N.

'Slow' type plants that invest in collaboration with mycorrhiza produce denser plant tissue with wide C/N ratios and thus reduced decomposability to soil microorganisms as compared to plants following fast strategies. The low-quality litter (i.e. wider C/N ratio) input together with the slow root growth results in slow N cycling in the surrounding soil as compared to plants following fast strategies. Additionally, the transfer of N derived from SOM from the fungus to the plant, as well as the mutualistic benefits of the mycorrhizal symbiosis, will be reduced compared to fast-type plants (Ingraffia et al. 2020).

Differences in root exudate and AM fungi induced N cycling

Although both strategies described rely on exudation, we suggest that they may exhibit certain differences. While root exudation is strongest at the root tip and root elongation zone (Dennis et al. 2010; Holz et al. 2017) the symbiosis with AM fungi is present along the whole root axis (Guo et al. 2008; Long et al. 2013) and consequently, hyphal exudation might therefore differ in its spatial distrbution from root exudation. Therefore, priming induced N cycling is expected in different soil locations for plants with contrasting belowground strategies. Additionally, the very efficient uptake of NH_4^+ by AM fungi (Herdler et al. 2008; Koller et al. 2013) and the fact that their small diameter hyphae can reach soil pores that plants cannot reach, likely leads to a very efficient N uptake by mycorrhiza. This could lead to a high immobilization rate of NH_4^+ into AM fungi which has also been shown to reduce N losses from soil (Asghari and Cavagnaro 2012; Storer et al. 2018; Veresoglou et al. 2019). Finally there are some indications that AM fungi might react more plasticly to reduced soil N availability compared to root exudation. Low N availability increased AM fungal abundance (Treseder 2004; van Diepen et al. 2010; Zhang et al. 2020) and the percentage of plant derived N from fertilizers (Azcón et al. 2008). Therefore, plants focusing on AM fungi might be particularly successful in low N conditions.

Conclusions and a perspective for future research

In order to gain conclusive insights into the influence of plants with diverse root economic strategies on their organic N utilization, we advocate for a comprehensive research approach that integrates various scientific disciplines.

Screening for root strategies Major information can be gained by investigation of plant root and rhizosphere traits. Conducting comparative screenings of root traits and root exudation pattern of plant species spanning a spectrum of resource acquisition strategies will serve as a critical foundation for subsequent studies. In the context of root exudation, sampling technique and the chosen analysis of root exudates is relevant. In terms of sampling technique soil-based sampling approaches should be chosen for example by the hydroponic-hybrid approach (Oburger and Jones 2018; Santangeli et al. 2024) in order to account for the effect that soil conditions have on exudate composition and quantity (Oburger and Schmidt 2015). With regard to the analysis, it is important to quantify the total C released by plant roots and to combine this for example with non-targeted metabolomic fingerprinting of exudates (Fuhrer and Zamboni 2015; Oburger and Jones 2018); which provides information on the exudate compound composition in its entire complexity that controls microbial community composition and activity (van Dam and Bouwmeester 2016).

Linking root strategy to C exudation and N turnover Understanding how plant species with different root economic strategies modulate their organic N utilization pathways requires linking rhizosphere priming with gross N transformation rates, for instance, through ^{15}N tracing (Rütting et al. 2011; Holz et al. 2016). Innovative methods now enable quantification of turnover rates of microbial necromass (Hu et al. 2018; Warren 2021) which could potentially be coupled with measurement of rhizosphere priming. Additionally, analyzing total N and ^{15}N isotopes (natural abundance) of different N pools, particularly mineral N and microbial biomass, along with amino sugars as indicators of microbial necromass can link rhizosphere priming to the turnover of specifc organic N pools (Pausch et al. 2024).

Quantification of accessible organic N While linking rhizosphere priming to N turnover rates aids in understanding the extent to which root strategies influence N cycling and availability, it is crucial to quantify the amount of organic N accessible to plants. This involves understanding which organic N pools contribute to plant nutrition, including fresh root and shoot litter, microbial necromass or MAOM and POM. Incorporating ^{15}N-labelled organic N pools, such as necromass (Schmitt et al. 2022), and quantifying their turover and plant uptake presents an opportunity to assess the contribution of organic N pools to plant nutrition.

Resolve microbial functionality in rhizosphere N cycling Unraveling the dynamics of microbial-mediated organic N depolymerization and microbial assimilation of N is crucial for understanding plant-microbiota interactions and synergism for N nutrition (Sieradzki et al. 2023a, b). The use of stable isotope probing, in combination with metagenomic and metatranscriptomic approaches, allows for linking the quantification of N transformations to microbial community structure and changes in microbial gene expression. By combining the analysis of plant metabolism including root exudate synthesis and metabolic activity with stable isotope probing, in combination with metagenomic and metatranscriptomic approaches (holo-omics; Rai et al. 2022; Xu et al. 2021) would allow for mapping the connections between root exudates and the microbial communities responsible for key steps in organic N mobilization while also quantifying organic N mobilization. However, further bioinformatic developments are needed to assess gene expression related to the degradation of macromolecular N (Sieradzki et al. 2023a). Additionally, a future challenge lies in predicting extracellular protease activities based on gene expression.

In summary, an interdisciplinary approach, combining methods and concepts from plant functional ecology, metagenomics in combination with isotope approaches holds significant potential to unravel the complex interactions between plants with varying root strategies and soil microbiota in regard to organic N utilization pathways.

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Declarations

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