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Review

Tipping the plant-microbe competition for nitrogen in agricultural soils

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SUMMARY

Nitrogen (N) is the most limiting nutrient in agroecosystems, and its indiscriminate application is at the center of the environmental challenges facing agriculture. To solve this dilemma, crops' nitrogen use efficiency (NUE) needs to increase – in other words, more of the applied nitrogen needs to reach humans. Microbes are the key to cracking this problem. Microbes use nitrogen as an energy source, an electron acceptor, or incorporate it in their biomass. These activities change the form and availability of nitrogen for crops' uptake, impacting its NUE, yields and produce quality. Plants (and microbes) have, however, evolved many mechanisms to compete for soil nitrogen. Understanding and harnessing these competitive mechanisms would enable us to tip the nitrogen balance to the advantage of crops. We will review these competitive mechanisms and highlight some approaches that were applied to reduce microbial competition for N in an agricultural context.

INTRODUCTION

Nitrogen is the most limiting nutrient for crops growth, and this is further intensified by microbial competition resulting in less than 15% of the N applied in the field ending up being consumed by humans.[1] About half of the losses occur when fertilizer is applied to the soil,[1] mostly because microbes use nitrogen as an energy source and electron acceptor (dissimilatory processes) or for their own growth (assimilatory processes) (Figure 1). Microbial dissimilatory processes – such as nitrification and denitrification – change the oxidation state of inorganic nitrogen and thereby its mobility and its state in soil, resulting in most of the applied N leaching into freshwater systems, where it can cause eutrophication, or being released back to the atmosphere, often in the form of the potent greenhouse gas (GHG) nitrous oxide. In addition to dissimilatory processes, microbes assimilate applied N for their own growth, immobilizing it in their biomass. As for the N already present in the soil – the soil organic nitrogen (SON) – which provides 50–90% of the N that reaches crops, microbes need to first depolymerize it – to release monomers such as amino acids – or mineralize it to ammonia so that plants can use it. Microbial activities, as influenced by their interactions with plants, other soil organisms, and their environment, will therefore determine the form and quantity of nitrogen that will reach plants. First, this will directly impact crops yields and quality, because depending on the form of nitrogen available plants will need to invest different amounts of energy to absorb it and transform it into nitrogen-containing polymers such as proteins and DNA. Second, it will also influence nitrogen use efficiency (NUE) – the amount of applied N fertilizer that reaches the crop – as some microbial activities result in losses from the soil or immobilization in microbial biomass. Plants have therefore evolved mechanisms to counter or tweak N-related microbial activities in their rhizosphere. Microbial competition is clearly an important ecological process for plant N nutrition, but more emphasis has been put on mutualistic interactions for increased N provision to plants.

Some microbes can increase plant N uptake through various strategies: fixing nitrogen,[2,3] transporting nitrogen to the roots, depolymerizing SON,[4] enhancing root length and density (by producing or degrading phytohormones),[5] and increasing the influx rates of the plant's nitrogen transporters.[6,7] While in theory these microbial strategies benefit plants, the outcome will depend on the biotic and abiotic environment in which they occur. For instance, under N-limiting conditions mycorrhizal fungi colonization can reduce plant N uptake because the fungi will compete for N.[8–10] Another limitation, is that even though N-fixing isolates have been shown to colonize the roots of maize (*Zea mays*)[11] and wheat (*Triticum aestivum*),[12] mutualistic N-fixation is not significant for these important cereal crops. In contrast, most crops have evolved mechanisms, such as nitrification inhibition and rhizosphere priming, to inhibit or steer microbial N-related activities. Could these competitive mechanisms be harnessed to improve crops yields, quality, and NUE?

Although developing new crop varieties with enhanced NUE and using slow-release nitrogen fertilizers has shown some promise, these solutions do not consider explicitly the microbial competition for N. We need to better understand the mechanisms behind this competition to increase crops' NUE, yields and nutritional quality while reducing fertilizer inputs and GHG emissions. In this short review, we will detail several examples of plant-microbe and microbe-microbe competition for nitrogen, namely amino acid uptake, rhizosphere priming, predation, fungal-bacterial competition, biological de/nitrification inhibition, and root architecture modification (Table 1). We will also

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https://doi.org/10.1016/j.isci.2024.110973

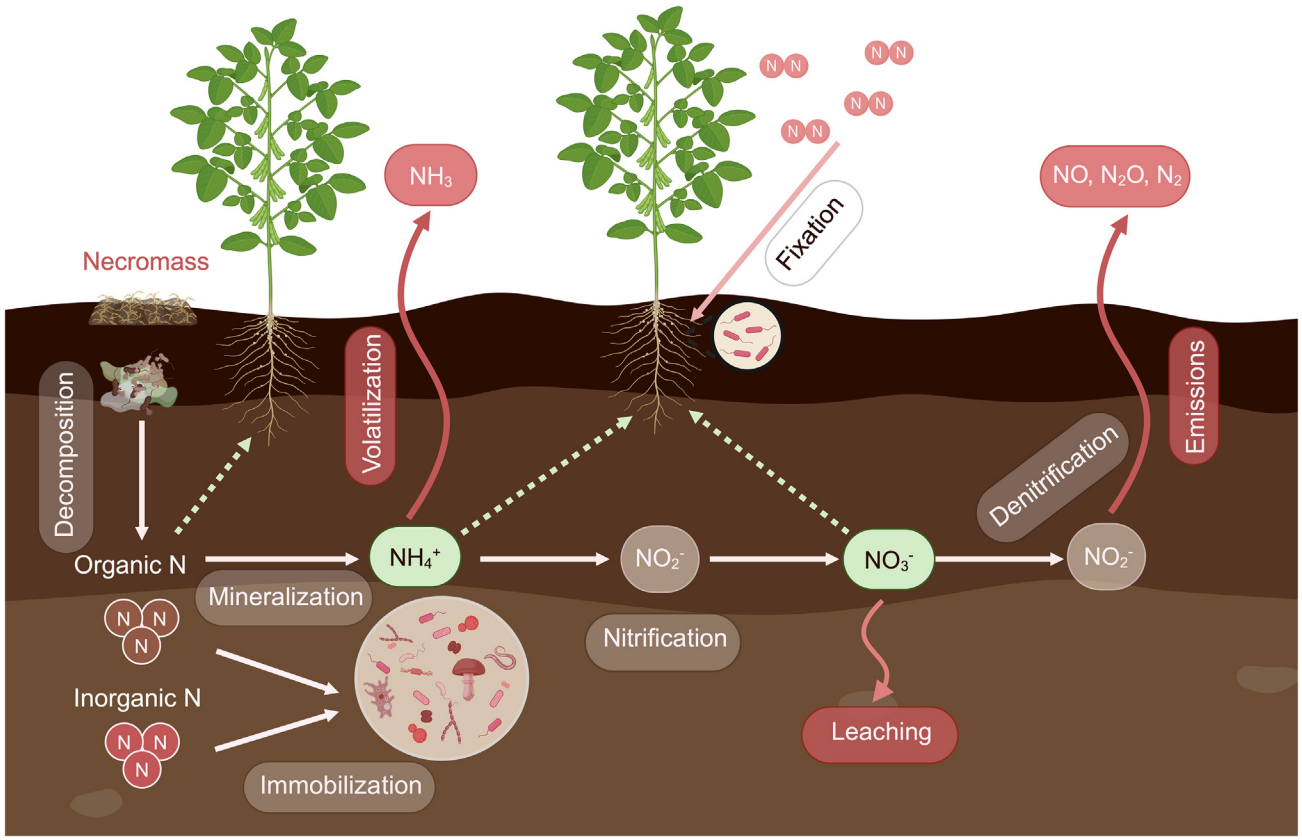

Figure 1. Overview of the nitrogen cycling in soils

Only key microbial steps mentioned in the text are shown for simplicity. Dotted arrows show plant uptake: ammonium, nitrate, and various organic nitrogen compounds. Created with BioRender.com.

discuss how these mechanisms could be harnessed to tip the competition for N in the favor of crops and increase their yields, quality, and NUE.

COMPETING FOR ORGANIC NITROGEN

Soil microbes secrete enzymes to degrade soil organic matter (SOM) and incorporate the resulting N in their biomass, stabilizing as microbial necromass after their death.[57–59] Microbial necromass refers to the different components of microbial cells, like peptidoglycan, chitin, and protein. More than 80% of the SON originates from microbial sources,[60] mostly in the form of protein.[61–63] Within SOM, we can distinguish different N-containing fractions: particulate organic matter (POM), and mineral-associated organic matter (MAOM). POM is the most studied SOM fraction because it contains nitrogen readily available for microbial depolymerization, whereas MAOM was long thought to be unavailable for microbial depolymerization[64,65]. MAOM contains a lot of nitrogen since it is characterized by a low C:N ratio of necromass by-products.[66–69] It is now widely accepted that this soil fraction represents a large organic N source for both plants and microbes. After depolymerization by their extracellular enzymes, microbes can further mineralize organic N to ammonium, which could be available for plants, if not immobilized in microbial biomass. But some organic N forms, such as amino acids can be taken up directly by plants and microbes.

Amino acids

Amino acids released by depolymerization are one of the least energy expensive N-source for plants and microbes since they can directly be used for protein synthesis.[70] Depending on the plant species and the SON concentration, plants can indeed directly absorb amino acids and small peptides[61,71,72]. It was first assumed that organic N uptake was higher in systems where the mineralization rate is low, like boreal forests, but it is now known that different plants from different ecosystems can bypass mineralization and directly take up organic N[73,74]. The concentration of amino acids in soil is typically low (around 20 μM), but it is very actively cycled, with half-lives of minutes to hours.[75,76] Amino acids are restocked >1,000 times per day,[77] which is orders of magnitude faster than the rates of ammonium and nitrate production in soils.[78,79] This suggests that amino acids are very actively taken up by plants and microorganisms and, indeed, microbial amino acid uptake exceeds

Table 1. Summary of the competitive processes adopted by plants, microbes and viruses for soil N

N forms	Processes	Involved organisms	Organismal interactions/strategy	Reference
Organic N	Amino acids uptake	Plants vs. bacteria and fungi	Competition for amino acids via different transporters.	Geisseler et al.,[13]; Fischer et al.,[14]; Jack et al.,[15]; Gournas et al.,[16]; Padan,[17]; Hosie et al.,[18]; Víglaš and Olejníková.[19]
	Rhizosphere priming	Plants vs. microbes	Plants and microbes compete for SON. Plants exude C-rich compounds to stimulate microbes to mineralize organic N to ammonia and nitrate.	Kuzyakov and Xu,[20]; Zhu et al.,[21]; Pausch et al.,[22]; Jiang et al.,[23]; Zhu et al.,[24]; Lu et al.,[25]; and Yin et al.[26]
	Predation	Predator protists vs. microbes	Predatory protists accelerate microbial turnover. Organic N fertilization increases protists abundance (such as nematodes) which could lead to shifts in microbial community composition and nutrient cycling.	Geisen et al.,[27]; Hu, and Qi.,[28]; and Qi et al.[29]
		Viruses vs. bacteria and archaea	Lytic viruses cause microbial lysis which releases bioavailable N, such as DNA and proteins into the soil.	Kuzyakov and Mason-Jones.,[30]; Jover et al.[31]
	SON depolymerization	Bacteria vs. fungi	Bacteria and fungi compete for organic N and nutrients by producing extracellular enzymes, adopting growth strategies (filamentous hyphae for fungi and biofilms for bacteria), and releasing various compounds, such as organic acids, volatile organic compounds, bactericides and fungicides.	Bahram and Netherway,[32]; Enggrob et al.,[33]; Jilling et al.,[34]; Hamlet and Plowright,[35]; Palmieri et al.,[36]; and Li et al.[37]
Inorganic N	Biological nitrification inhibition (BNI)	Plants vs. nitrifiers (AOA and AOB)	Plants produce and exude BNIs in the rhizosphere, which inhibit or suppress nitrification by targeting AMO and/or HAO enzymes, giving them time to assimilate N in ammoniacal form.	Li et al.,[38]; Subbarao et al.,[39]; and Subbarao et al.[40]
	Inorganic N immobilization	Heterotrophic microbes vs. nitrifiers (AOA and AOB)	Heterotrophic microbes immobilize inorganic N via intermembrane proteins and transform it into protein, creating microbial biomass.	Kleiner,[41]; Jansson and Persson[42]
	Biological denitrification inhibition (BDI)	Plants vs. denitrifiers	Plants root extracts can inhibit denitrifiers activity and reduce denitrification process in soil. BDI occurs by allosteric inhibition of the nitrate reductase through procyanidins modifications to the cell membrane.	Bardon et al.,[43]; Bardon et al.[44]

(*Continued on next page*)

Table 1. ***Continued***

N forms	Processes	Involved organisms	Organismal interactions/strategy	Reference
	Dissimilatory reduction of nitrate to ammonium (DNRA)	Denitrifiers vs. DNRA microorganisms	Denitrifiers compete with DNRA microorganisms which also use nitrate as an electron acceptor and can inhibit their activities.	Rütting et al.,[45]; Putz et al.[46]
Organic and inorganic N	Root traits modifications	Plants vs. microbes	Plants compete for N by modifying their root system architecture, which is regulated by many phytohormones. Root traits influence microbial diversity and certain microbes modify root traits.	Putz et al.,[47]; King et al.,[48]; Pervaiz et al.,[49]; López-Bucio et al.,[50]; Molina-Favero et al.,[51]; Schenkel et al.,[52]; Schroeder et al.,[53]; Kiba et al.,[54]; Sharma et al.,[55]; and Li et al.[56]

microbial ammonium and nitrate uptake by a factor >8.[80] Amino acids therefore appear to be a key organic N source in the plant-soil environment and an intense source of plant-microbe competition.

To compete for amino acids, bacteria, fungi, and plants have transporters with different characteristics.[13] Bacteria have many different transporters for specific amino acids, whereas fungi have fewer types of transporters with lower substrate specificity. Plants,[14] bacteria,[15] and fungi[16] actively utilize amino acid transporters found within the amino acid-polyamine-organocation (APC) superfamily. Fungi have well-characterized APC transporters,[16] while plants predominantly use transporters from the amino acid transporter superfamily (ATF).[14] ATF transporters expressed in roots include amino acid permeases (APP), proline transporters (ProT), and lysine, histidine transporters (LHT). Moreover, both fungi and bacteria benefit from amino acid transporters within the major facilitator superfamily (MFS). Another common amino acid transporter superfamily is the ATP binding cassette superfamily (ABC) which plays a crucial role in bacteria[17,18] and fungi,[19] although its involvement in amino acid transport in plants remains uncertain.[14]

Plants' high-affinity transporters create a steep concentration gradient across their membrane.[81] Amino acid exudation by plant roots is more likely a passive loss and a side effect of maintaining this steep concentration gradient.[82] The constitutive expression of organic N transporter genes by plant roots is therefore probably not geared toward the acquisition of new organic nitrogen, but more likely the re-uptake this unwillingly exuded organic N to limit microbial proliferation.[81,83,84] Microbes have evolved mechanisms to compete with plants high-affinity amino acid transporters. *Pseudomonas* produce 2,4-diacetylphloroglucinol and phenazine whereas *Fusarium* produce zearalenone, all of which increase amino acid net efflux from roots by blocking amino acid uptake or increasing efflux.[85] Bacteria can also stimulate roots to exude amino acids by releasing the phytohormone cytokinin.[86] This increased concentration of amino acids would increase the bacterial colonization of this niche, especially in N-limited soils where plants exude little amino acids.[86]

Soil protein depolymerization is partly constrained by the pool size of soil microbial extracellular enzymes,[80,87] making the cleavage of proteins a rate limiting step in the terrestrial N cycle.[75,80,87,88] Because of that, when N is applied as manure or crop residues in organically managed agroecosystems, N availability is the most important limiting factor.[89,90] Plant rhizosphere priming of microbial activities can partly alleviate this constraint.

Rhizosphere priming

Rhizosphere priming is a strategy that plants use to compete with the microbial community for the SON. In general, the higher surface-area-to-volume ratio and rapid growth rates of microbes should enable them to outcompete plants. To counter this, plants will exude C-rich compounds such as carbohydrates and organic acids to inflate the soil C:N ratio[84,91] that will stimulate microbes to cycle nitrogen compounds.[20] When stimulated by these exudates, microbes need to find available N to meet their elemental requirements and support their rapid growth. When the easily available N pool drops, microbes allocate their energy, provided by plant derived C, to produce extracellular enzymes and scavenge N contained in the SOM.[21] When the pool of available C-exudates declines, microbes begin to starve and mineralize N in excess, to balance their C:N ratio. Once organic N is mineralized, plants can effectively compete for ammonia and nitrate uptake. Since plants outlive microbes and maintain a strong net N flow from soil to roots, they are thought to outcompete microbes in the long run.[20]

Their competitiveness for SON-derived N varies depending on the plant type,[92–94] plant age,[95] soil nutritional status[96] and abiotic conditions. Wheat, barley (*Hordeum vulgare*), and sunflower (*Helianthus annuus*)[22] increase their N acquisition following rhizosphere priming. Rhizosphere priming has also increased microbial N-mining in the rhizosphere of maize,[23] sunflower[24] and soybean (*Glycine max*).[24] Among six grassland plant species, the plant with highest N priming had also the highest rhizosphere respiration,[25] suggesting that high root and microbial activity in the rhizosphere results in a stronger priming effect. Rhizosphere priming can also increase microbial turnover[22,26], potentially linked to increased predation.

Predation

Predatory protists act as microbial turnover accelerators because they prey on archaea, bacteria, and fungi.[27] A shift in the diversity or abundance of these predators can restructure the microbial network and change organic N availability.[97] Nitrogen fertilizers have been shown to affect protists more strongly than bacterial and fungal communities.[98] The abundance of predatory protists has also been shown to increase in sorghum (*Sorghum* spp.)[99] and banana (*Musa* spp.)[100] treated with organic fertilizers. In both these studies, the suppression of fungal pathogens caused by organic fertilization was explained by the predatory pressure exerted by protists.[99,100] Fertilization also alters the abundance of microbe-eating nematodes,[28,29] which play a vital role in microbial turnover. Prey preference could lead to shifts in microbial community composition and nutrient cycling. For instance, Gram-negative bacteria are preferentially grazed by nematodes.[101,102]

Limited by their size, nematodes and other animal predators can, however, only access 1/3 of the soil volume available to bacteria.[30] Although bacteria may find refuge in small soil pores (<10 μm of diameter), they are not protected from their most abundant threat: viruses.[30,103] The ecological relevance of soil viruses remains underexplored, but increased phage pressure can alter microbial community dynamics and microbial processes such as N-cycling.[104] The release of nutrients caused by virus-induced death is known as the viral shunt.[30,31] During that process, lytic phages cause bacterial lysis which release bioavailable N, such as DNA and proteins into the soil environment. Ammonia-oxidizing archaea (AOA) are also frequently infected by viruses,[105,106] which could interfere with nitrification. Phage pressure could also influence microbial diversity and other important community features, such as the fungal:bacterial ratio.

Fungal-bacterial competition

More than 90% of the soil microbial biomass consists of bacteria and fungi.[107] These two microbial groups compete for SON depolymerization. The outcome of this competition will likely determine the amount of N available to the plant. Fungi have a higher C:N ratio than bacteria and will require less N per unit of biomass. For an identical source of organic N, fungi are more likely than bacteria to mineralize part of the N.[108]

Fungi are the main decomposers in soil since they are highly diversified and produce a large variety of exoenzymes that decompose complex molecules.[32] *Basidiomycetes* depolymerize recalcitrant products from plant and microbial necromass, such as lignin, a main component of wood,[109] and chitin, the main component of fungal cell walls.[110] Bacteria also produce diverse extracellular enzymes to decompose necromass, but with some taxonomical variation: Gram–positive bacteria are more involved in the depolymerization of large protein compounds than Gram–negative bacteria.[33]

Another key difference between bacteria and fungi in their competition for organic N is their growth strategies. To scavenge nitrogen, fungi form filamentous hyphae, that enable them to access different soil micro-environments, and even penetrate soil aggregates and complex compounds.[111,112] In contrast, bacteria are less mobile traveling mostly with water movement, but have a larger contact surface with their environment, allowing them to absorb more soluble substrates than fungi.[113,114] Bacteria also form biofilms that enable them to maintain direct contact with soil minerals and organic matter, facilitating the depolymerization of organic N.[115] The biofilm exopolysaccharides matrix favors the release of bacterial exoenzymes, prevents them from drifting, and shields the community from predators.[116] Fungi also have an extracellular polymeric substance (EPS) matrix attached to their cell wall, which – like bacterial biofilms – enhances the stability of exoenzymes.[117]

Microorganisms also release diverse compounds, such as organic acids, volatile organic compounds, bactericides, and fungicides to compete for nutrients. For instance, some fungal species release oxalic acid to destabilize the chemical bond between the SOM and minerals,[34–36] which – coupled with their growth strategy – grants them an increased access to mineral-bound organic N. In contrast, to directly inhibit fungal growth and lower their access to organic N, bacteria produce volatile compounds that travel through air-filled soil pores.[37] Microbe-microbe competition accelerates the microbial loop and the release of organic N, as death resulting from competition will produce microbial necromass and SON that could eventually be accessible for plants.

COMPETING FOR INORGANIC NITROGEN

One key soil microbial activity is the cycling of inorganic nitrogen, which changes the quantity of ammonia and nitrate – the two main inorganic N sources available in soils for plant uptake.[118] The protonated form of ammonia, ammonium (NH_4^+; positively charged), is generally immobilized on negatively charged soil particles, and is therefore not very mobile and does not leach much. Plant ammonium uptake is passive and requires little energy (5 mol of ATP per mole,[119,120]) and it can be directly used for protein synthesis. Conversely, nitrate (NO_3^-; negatively charged) is mobile in soil and does leach,[118] and is also a substrate for denitrification. Plant nitrate uptake is an active process that requires energy (20 mol of ATP per mole[119,121]), and nitrate needs to be transformed back to ammonia before entering protein metabolism, resulting in supplementary energy expenses. Ammonia is therefore more energetically favorable than nitrate for plant protein synthesis, but this clashes with the needs of nitrifiers.

Nitrification

To uptake N in the ammoniacal form, plants need to compete with microorganisms that oxidize ammonia to nitrate (nitrifiers), using the energy thereby created to fix carbon dioxide (chemosynthesis). The first rate-limiting step of nitrification is due to two groups of chemosynthetic microorganisms, the ammonia-oxidizing bacteria (AOB) belonging to the Beta- and Gammaproteobacteria,[122] and the ammonia-oxidizing archaea (AOA) belonging to the *Thaumarcheota* phylum.[123] Nitrate is bioavailable for plant and microbes, but it can quickly be lost from the soil via two processes: (1) leaching, because nitrate is an anion and soils are generally negatively charged, (2) denitrification, which returns N to the atmosphere, possibly in the form of nitrous oxide,[124] a GHG ~300 times more potent than CO_2.[125] The addition of inorganic fertilizers containing ammonia promotes the growth of nitrifying microbes and N losses, decreasing plant NUE. Accordingly, recent models found negative relationships between ammonia oxidizer abundance and wheat grain baking quality.[126–128]

To counteract N losses due to nitrification, certain plant species, such as *Brachiaria humidicola*,[38,129–131] sorghum,[132–134] *Oryza sativa* (rice),[135–138] maize,[139] and wheat,[140] produce biological nitrification inhibitors (BNI).[38–40] Nitrification inhibition is thought to be a plant adaptation to N-poor environments.[40] BNIs inhibit or suppress nitrification, giving plants time to assimilate N in ammoniacal form. BNIs can be hydrophilic or hydrophobic compounds and may have complementary roles. Hydrophobic BNIs are more likely to remain in the rhizosphere zone, in contrast to hydrophilic BNIs, which can migrate and extend inhibitory activity outside the rhizosphere.[133,141]

Plants secrete BNIs based on inorganic N availability and form in the rhizosphere. The concentration of NH_4^+ near the roots promotes plant BNI production,[142–144] whereas plants in a NO_3-rich environments barely secrete BNIs.[38,134,138] BNI exudation is also closely linked to plant physiological state and development,[145] and stress could reduce BNI exudation rates. The reduction of net nitrification rates by *B. humidicola* depends on four interacting mechanisms: 1) heterotrophic N immobilization, 2) BNI exudation 3) plant facilitated inter-microbial competition (between bacterial heterotrophs and nitrifiers), and 4) efficient plant nitrate uptake.[146]

BNIs target the limiting step of nitrification which is the oxidation of NH_4^+ to NO_2^-, requiring two enzymes, ammonia monooxygenase (AMO) and hydroxylamine oxidoreductase (HAO) encoded by the *amo* and *hao* operons, respectively. There are two known mechanisms

of BNI action: inhibition of the nitrification AMO or HAO enzymes, or simultaneous inhibition of both. Some BNIs, including sakuranetin, sorgoleone (from sorghum roots), brachialactone (from *B. humidicola* roots), and certain fatty acids such as linolenic acid (LN) and linoleic acid (LA) (present in *B. humidicola* leaf tissue), can inhibit both enzymes,[147] whereas methyl 3-(4-hydroxyphenyl) propionate (MHPP, from sorghum roots) and 1,9-decanediol (from rice roots) can only inhibit the AMO enzyme.[40] To date, no studies have been carried out regarding the strategies or mechanisms that AOA and AOB might adopt as a direct defensive response to BNI, but different sensitivities among AOB and AOA species to different BNIs suggest potential resistance mechanisms that could have co-evolved with specific plant species.[148]

Heterotrophic microbes can also reduce nitrification-related N losses by immobilizing inorganic N in their biomass and competing with nitrifiers for NH_4^+.[149] Heterotrophic microbes immobilize inorganic N via intermembrane proteins and transform it into protein, creating microbial biomass.[41,42] When carbon is not limiting, N immobilization is favored because heterotrophs have a higher affinity for N.[150] Immobilization of inorganic N is also dependent on the soil C:N ratio. If the C:N ratio is high, immobilization will be favored to meet microbial demand. Nitrifiers will then be unable to use inorganic N, since it will not be available to them.[151]

Denitrification

In the absence of oxygen – either in the deeper anoxic layers of the soil or in anoxic microsites in the upper oxic layers – nitrate can be used as an electron acceptor by denitrifiers, resulting in its reduction to nitrite, nitric oxide, nitrous oxide, and dinitrogen. These last three forms are gaseous, leading to N losses to the atmosphere. Although it was less studied than nitrification inhibition, denitrification can also be inhibited by plants. *Fallopia* spp. root extracts inhibited the activity of two *Pseudomonas* denitrifiers and reduced denitrification activities in soil.[43] Biological denitrification inhibition (BDI) occurs by allosteric inhibition of the nitrate reductase through procyanidins modifications to the cell membrane.[44] BDI was further shown to be modulated by biotic factors (initial denitrifier abundance) across nine different soils,[152] and to modify root traits.[153] Exogenous application of procyanidins in the field decreased denitrification activities and denitrifiers abundance, increasing nitrate availability in soil and lettuce yields.[154,155] Exogenous application of procyanidins to three rice paddy soils resulted in lowered N_2O emissions through their effect on the nitrate reductase and the denitrifier populations.[156] Other than *Fallopia* spp., only two heathland plants were shown to have a direct BDI capacity.[157] Ideally, some crop genotypes would be able to directly inhibit denitrification, to reduce N_2O emissions and nitrogen losses from agricultural soils, without additional inputs of chemicals.

Denitrifiers compete with another microbial group that also uses nitrate as an electron acceptor and can inhibit its activities: dissimilatory reduction of nitrate to ammonium (DNRA) microorganisms. DNRA replenish soil ammonium and is a key process in the soil inorganic nitrogen cycle.[45] DNRA contributes largely to nitrate reduction in permanent grasslands[45] and in agro-ecosystems.[46] The relative abundance of denitrifying and DNRA bacteria and their activity was shown to determine nitrogen retention or loss in agricultural soils.[46] Soil management practices and cropping systems such as adding organic amendments and performing long rotations can help preserve SOM and increase the carbon-to-nitrate ratio in agricultural soils[158–161] to favor DNRA over denitrification.[46] Such approaches have stronger control on the DNRA community than N fertilizer application.[46]

ROOT TRAITS

The uptake of nutrients by plants depends on their root system architecture.[162] To compete against microbes for N, plants can modify their root system architecture.[47] Although root traits influence microbial diversity,[48,49,163] certain microbes[50–53] and even rhizobiomes[164] modify in turn root traits. Microorganisms can indeed change 1) root system architecture, 2) root growth, 3) the composition of root exudates and 4) microbe-microbe interactions,[165] which is often linked to microbial interactions with plant's phytohormones.

Plants root system architecture is regulated by many phytohormones.[54–56] For example, jasmonic acid inhibits the primary root's growth but stimulates lateral root growth, while cytokinins hinder overall root growth but can enhance the development of root hairs.[55,56,166,167] Rhizosphere microbes can break down or produce phytohormones such as auxin, cytokinin, ethylene, gibberellin and salicylic acid.[168] This enables them to alter the root system architecture and, consequently, impact plant NUE. For instance, 89% of the 391 Arabidopsis-associated bacterial strains tested modified one feature of the root system architecture, especially the lateral roots, through their influence on ethylene signaling.[169] This increase in lateral root branching, can negatively impact plant N acquisition in soils with low levels of N where the best performing maize lines were shown to have deeper and fewer lateral roots.[170] In contrast, some phytohormone producing bacteria, such as auxin-producing *Klebsiella*, have been found to improve the NUE in barley and *Cicer arietinum* (chickpea).[171] While many other plant growth promoting rhizobacteria (PGPR) are known to produce or degrade phytohormones, it is noteworthy that phytopathogens, including *Ralstonia solanacearum*,[172] *Xanthomonas oryzae*[173] and *Pseudomonas syringae*[174,175] also exhibit these properties. The ability of microbes to produce or break down phytohormones stands as an efficient mechanism through which they can manipulate the NUE of their host.

TIPPING THE BALANCE

Engineering or manipulating the soil microbiota to reduce plant-microbe competition for N could increase crop yields, quality, and NUE. Engineering the plant microbiota[176,177] can proceed through crop selection and amelioration, input selection and microbial inoculation (Figure 2). Most of these strategies are already available to farmers.

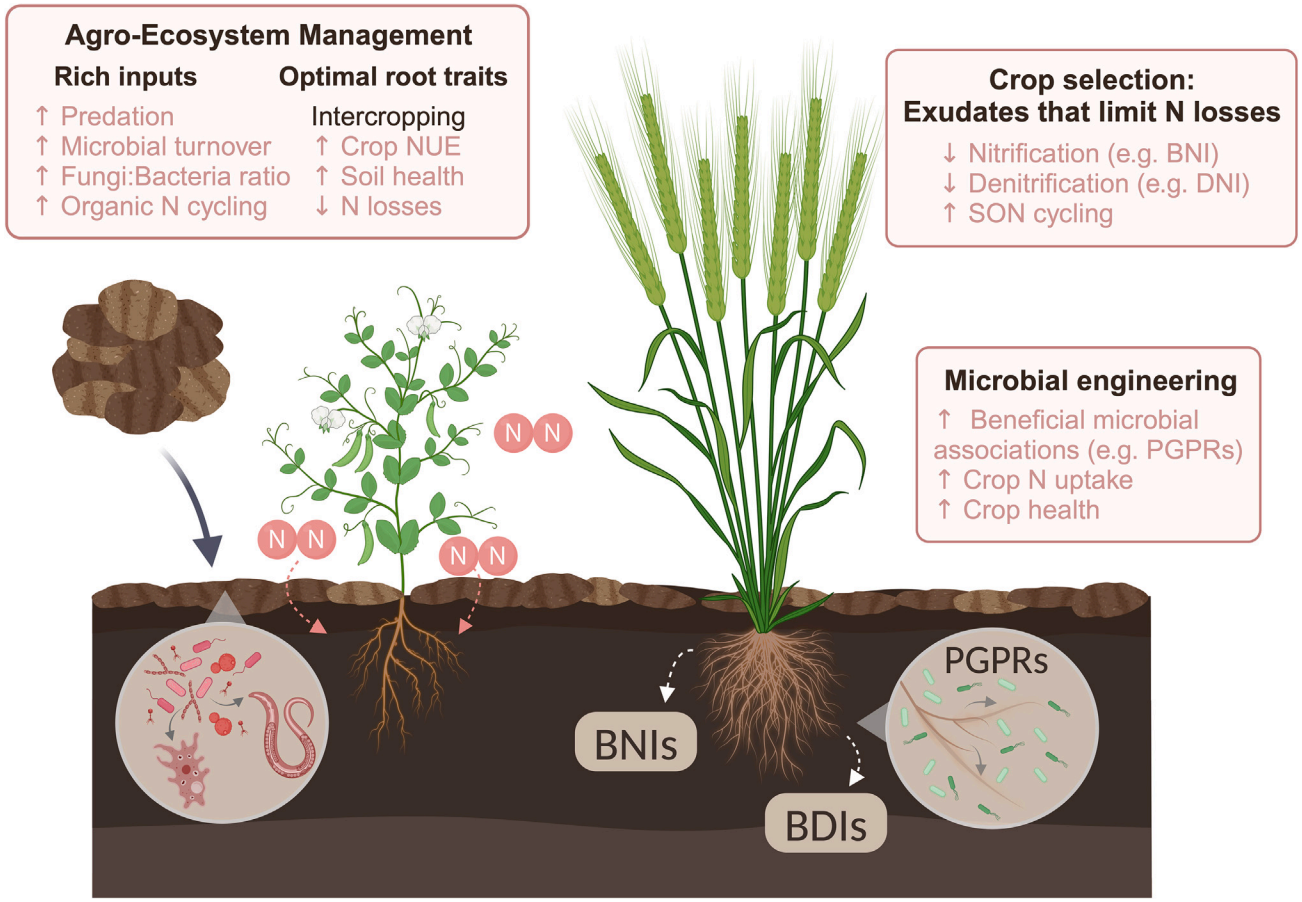

Figure 2. Approaches to modify plant-microbe interactions for nitrogen

Three main routes are highlighted: through the plant, through amendments, and through inoculations. Created with BioRender.com.

Crop selection and amelioration

BNI capacity of crops varies from one genotype to the other.[178,179] For example, the BNI capacity Australian wheat varieties varies from >75% inhibition to no inhibition[140]. Ideally, high-yielding elite varieties would also have high BNI capacity. This has been done in wheat by introducing genes from wild grass relatives.[180] Breeding cereal crops to increase their BNI capacity should also be possible,[178] and preferable to genetically modified organisms (GMOs).

Alternatively, incorporating plants with high BNI capacity such as *B. humidicola* or sorghum into crop rotations can significantly improve NUE and reduce N_2O emissions.[132,181–183] Sorghum inhibitory effect can persist from 60[184] to 140 days after harvest.[132] Intercropping is also an interesting avenue to increase BNI capacity, and intercropping maize with sorghum reduced nitrification, the abundance of ammonia-oxidizers, and N_2O emissions, while increasing soil ammonium concentration.[185] Another approach to intercropping is to grow two species with complementary N preferences and root spatiotemporal niche differentiation.[186] For instance, maize and wheat uptake N at a faster rate than legumes which are thereby required to fix atmospheric N to sustain their nutritional needs.[187] This type of intercropping increases crop NUE as compared to individual cereal monocultures[188,189], improves soil quality[190] and increases fertilizer NUE.[191]

Selection of inputs

Different types of amendments and fertilizers can also be used to modulate plant-microbe competition for N. BNI capacity varies with crop genotype, but also with organic C amendments such as biochar, with the addition of other inhibitors such as urease inhibitors or synthetic nitrification inhibitors (SNIs), and with the use of different inorganic N fertilizers.[132,135,192] For instance, fertilizing sorghum with urea resulted in higher N_2O emissions when compared to ammonium sulfate,[193] whereas fertilizing rice with urea increased NH_3 volatilization in the presence of the sorghum nitrification inhibitor MHPP.[135]

Another way to modify the microbial community is with specific organic amendments. For instance, amendments with high C:N ratios, like paper mill residue and sawdust,[194] favor fungi growth over bacteria, thereby increasing the fungal:bacterial ratio.[195–197] This can lead to an

increased release of N for plant use due to the lower N demand of fungi.[108] Amendments with high C:N ratios coupled with N fertilizer can also favor long term N retention in agricultural soils.[198]

Multitrophic interactions can also be modulated by organic inputs. Organic fertilizers such as chicken manure[100] and a combination of cow manure and straw[99] increased the abundance of Cercozoan predatory protists, a keystone group for SOM degradation in soil macroaggregates.[199] A 1:1 mixture of chicken manure compost and amino acid fertilizer increased the abundance of microbe-eating protists and decreased the abundance of phytopathogenic protists.[200] Organic fertilizer also decreased the abundance of plant-parasitic nematodes.[201]

Microbial inoculations

The use of inoculants in agriculture faces theoretical[176] and practical[202] barriers. Under some conditions, some microbes – including nitrogen fixers,[203] arbuscular mycorrhizal fungi (AMF),[204] and microbes that alter the root system architecture[168,205] – can, however, increase plant N and P uptake.[206] *Azospirillum* spp. fix nitrogen and promote root growth, increasing thereby maize grain yield.[207] The co-inoculation of both nitrogen fixers and AMF changed N allocation from soybean to maize in an intercropping system.[208]

CONCLUSION

Clearly, soil microbes have a disproportionate effect on the yield, quality, and NUE of crops. Here, we suggest refocusing the nitrogen fertilization paradigm on the competing soil microbes as they offer the potential to solve many of the issues related to low crop NUE. Using microbes to stimulate nitrogen release from soil organic matter while steering nitrogen transformations toward more advantageous forms for plants has the potential to drastically reduce the application of nitrogen fertilizers while increasing crop quality and yields, thereby increasing the profit margins for farmers and reducing the environmental footprint of agriculture.

ACKNOWLEDGMENTS

This review was supported by an NSERC discovery grant (RGPIN-2020-05723) and an FRQNT Programme de recherche en partenariat (322604).

AUTHOR CONTRIBUTIONS

Conceptualization, E.L.E., L.S.B., J.A.D., E.Y.; writing – original draft, E.L.E., L.S.B., J.A.D.; writing – review and editing, E.L.E., L.S.B., J.A.D., E.Y.; visualization, E.L.E., L.S.B., J.A.D.; supervision, E.Y.; funding acquisition, E.Y.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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