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The role of arbuscular mycorrhizas in reducing soil nutrient loss

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Substantial amounts of nutrients are lost from soils via leaching and as gaseous emissions. These losses can be environmentally damaging and expensive in terms of lost agricultural production. Plants have evolved many traits to optimize nutrient acquisition, including the formation of arbuscular mycorrhizas (AM), associations of plant roots with fungi that acquire soil nutrients. There is emerging evidence that AM have the ability to reduce nutrient loss from soils by enlarging the nutrient interception zone and preventing nutrient loss after rain-induced leaching events. Until recently, this important ecosystem service of AM had been largely overlooked. Here we review the role of AM in reducing nutrient loss and conclude that this role cannot be ignored if we are to increase global food production in an environmentally sustainable manner.

Nutrient loss from soil

Crops take up approximately only half of the nutrients in applied chemical fertilizers, with the remainder therefore at risk of being lost to production [1]. Nutrients that are mobile in soil, such as nitrate (NO_3^-) and sulfate (SO_4^{2-}), can be readily leached below the root zone of plants. Relatively immobile nutrients, such as phosphorus (P), potassium (K), and zinc (Zn), can also be lost via leaching or erosive processes, when bound to organic matter or colloids, or precipitated with organomineral complexes and chelates (see [2]). Nutrient losses via leaching can be substantial, with up to 160 kg of nitrogen (N) and up to 30 kg of P per hectare lost annually due to leaching and surface run off in some areas [3,4]. Leached nutrients can contaminate ground water and waterways, leading to eutrophication, algal blooms, and the loss of terrestrial and aquatic biodiversity [5]. In addition to losses via leaching, N can also be lost from soil as the potent greenhouse gas nitrous oxide (N_2O) (see Glossary) and as dinitrogen gas (N_2) [6–9] with losses of up to 143 kg of N per hectare [10], although rates vary among studies [11]. An estimated 150 Tg of N are exported from soil each year, with plant uptake, leaching, soil erosion, and gaseous N losses accounting for 55%, 16%, 15%, and 14% of losses, respectively [12]. Together, these nutrient loss pathways can be expensive in terms of lost potential crop production and environmentally damaging.

Plants have an important role in reducing soil nutrient loss. In addition to direct root uptake of nutrients, most terrestrial plant species can also acquire nutrients by forming associations with arbuscular mycorrhizal fungi (AMF) [13]. Hyphae of AMF can extend beyond the root surface by more than 10 cm [14,15], with common hyphal densities of >10 meters of hyphae per gram of soil [14,16,17]. This extensive absorbing network, which extends beyond the rhizosphere nutrient-depletion zones that form around roots, allows AM to access a larger volume of soil than roots not colonized by AMF. There is clear evidence that AMF can help plants acquire nutrients including P, Zn, ammonium (NH_4^+), nitrate (NO_3^-), copper (Cu), and potassium (K) [18–20]; for example, up to 90% of plant P and 20% of plant N can be provided by AMF, although estimates vary among studies and study systems. Uptake and transfer of nutrients from organic sources to plants has also been reported [21–23].

In addition to improving plant nutrient acquisition, there is emerging evidence that AM have the ability to reduce nutrient loss from soils by enlarging the nutrient interception zone and preventing nutrient loss after rain-induced leaching events. Until recently, this important

Glossary

Arbuscular mycorrhiza (AM): the association formed between the roots of most terrestrial plant species and AMF.
Arbuscular mycorrhizal fungi (AMF): fungi belonging to the Glomeromycota that form AM with the roots of most terrestrial plant species.
Biogeochemical cycling: the chemical, physical, geological, and biological processes and reactions that govern the cycling of nutrients and C in the environment.
Denitrification: the microbial transformation of NO_3^- to N_2O and ultimately N_2.
Leaching: the drainage of water containing solutes away from soil by the action of percolation.
Nitrification: the microbial transformation of NH_4^+ to NO_3^-.
Nitrous oxide (N_2O): a potent greenhouse gas.

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ecosystem service of AM had been largely overlooked. Here we review recent evidence on the role of AM in reducing soil nutrient loss. We discuss the mechanisms and present a conceptual framework showing under which conditions the reduction of nutrient loss by AM is expected to be most prevalent.

The premise of this review is that AM can reduce the risk of nutrient loss by enhanced nutrient immobilization (compared with non-mycorrhizal plants) or by altering soil nutrient and water cycling processes in ways that favor the retention of nutrients in the soil (Figure 1). We focus on inorganic and organic N and P compounds. Specifically, we review the role of AM in reducing: (i) N loss via leaching of inorganic and organic N-containing compounds and as the potent greenhouse gas N_2O; and (ii) P loss via leaching of inorganic and organic P-containing compounds.

We use the term 'non-mycorrhizal' when referring to plants that have the capacity to form AM but have not done so. Further, we define nutrient loss as nutrients moving beyond root zones.

The role of AM in reducing N loss from the soil

AMF can take up N as NH_4^+ [24,25], NO_3^- [7], and amino acids [21,22]. There is also evidence to suggest that AMF may be able to acquire nutrients from organic matter patches [26,27], although it is likely that this is due to uptake of inorganic N following organic matter mineralization (see [13] for a recent discussion). While the molecular basis of N uptake by AMF has not been fully elucidated, the identification of fungal glutamine synthase and nitrate reductase genes in AMF [28,29] further supports the role of AMF in assimilating mineral forms of N [30]. AM may also impact soil N transformations and cycling (see below and [30] for a recent review). Although the contribution of AM to plant N acquisition can be variable, with some studies showing little or none (e.g., [31–33]), it is clear that AM can

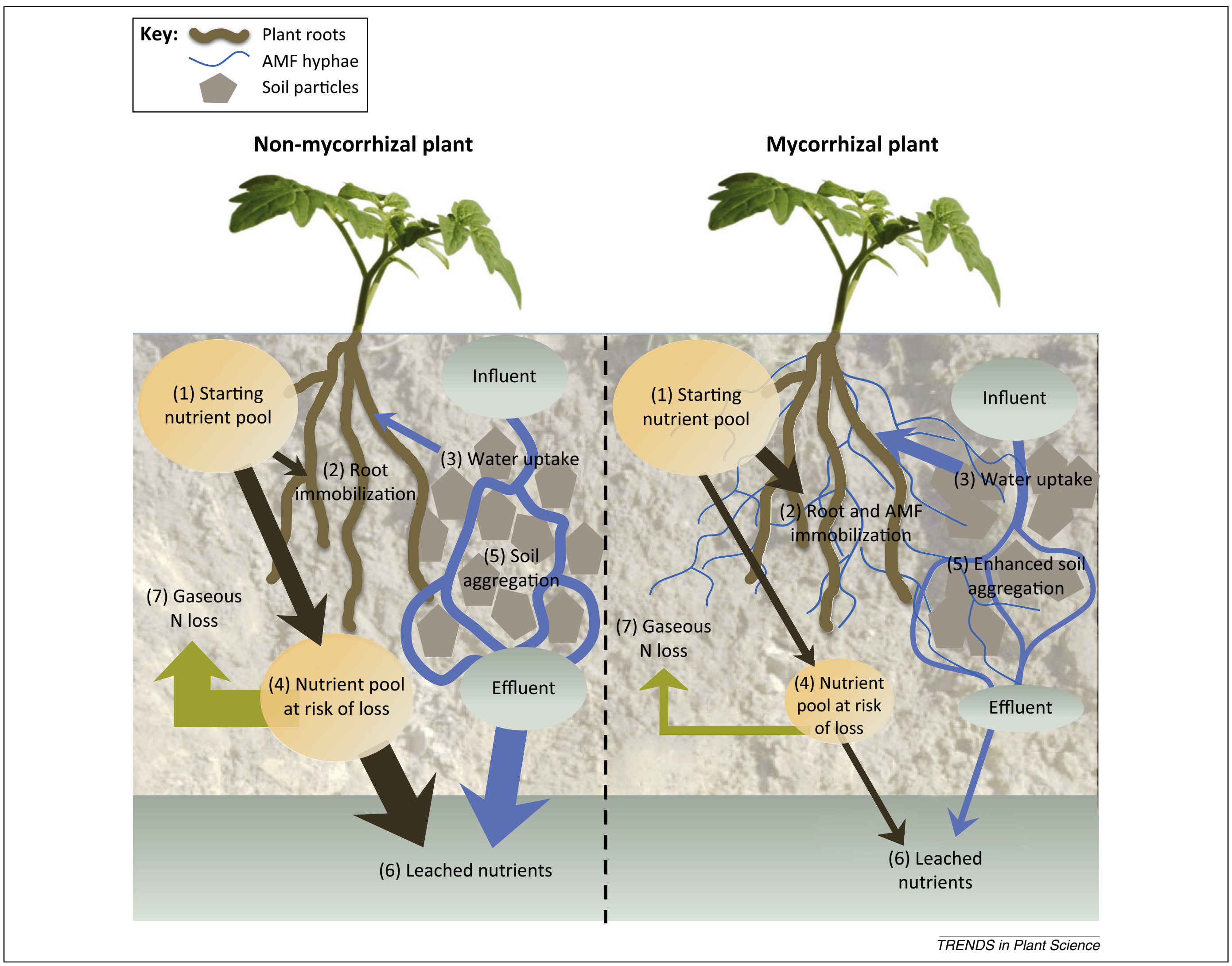

Figure 1. Overview of potential impacts of mycorrhizal versus non-mycorrhizal plants on soil nutrient loss pathways. The starting nutrient pool (1) may comprise inorganic and/or organic nitrogen (N)- and phosphorus (P)-containing compounds. Immobilization of nutrients (2) and water uptake (3) are enhanced when plants are colonized by arbuscular mycorrhizal fungi (AMF). As a consequence, the pool of nutrients at risk of being leached (4) will be reduced with mycorrhizal plants. Simultaneously, AMF can improve soil structure (5). As a consequence of all of these factors, we anticipate more nutrients to be leached (6) where plants are non-mycorrhizal. Similarly, we expect gaseous N loss (7) to be enhanced when plants are non-mycorrhizal due to reduced plant N assimilation. Although not represented in this figure, the effects of forming AM on plant biomass may also be important (see text). The sizes of the arrows indicate the direction of change (i.e., increased, decreased, or similar), but they are not drawn to scale.