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# The role of arbuscular mycorrhizas in reducing soil nutrient losses

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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). There is emerging evidence that AM have the ability to reduce nutrient loss from soils by enlarging the nutrient interception zone and preventing nutrient losses 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 losses and conclude, that this role cannot be ignored if we are to increase global food production in an environmentally sustainable manner.**

## Nutrient losses 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 sulphate ($SO_4^{2-}$), 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 organo-mineral complexes and chelates (see [2]). Nutrient losses via leaching can be substantial, with up to 160 kg 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 also as di-nitrogen 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 annually, 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 to play in reducing soil nutrient losses. In addition to direct root uptake of nutrients, the vast majority of 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 centimeters [14, 15], with common hyphal densities of >10 m 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 arbuscular mycorrhizas (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), potassium (K), and others [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. The 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 to prevent nutrient losses after rain induced leaching events. Until recently, this important ecosystem service of AM had been largely overlooked. Here we review recent evidence on the role of AM in reducing soil nutrient losses. We discuss the mechanisms and present a conceptual framework showing under which conditions the reduction of nutrient losses 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 to 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

Arbuscular mycorrhizal fungi can take up N as $NH_4^+$ [24, 25], $NO_3^-$ [7] and as amino acids [21, 22]. There is also some 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 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 support the role of AMF in assimilating mineral forms of N [30]. Arbuscular mycorrhizas may also impact upon soil N transformations and cycling (see below, and [30], for recent review). Although the contribution of AM to plant N acquisition can be variable, with some studies showing little or no contribution of AM to plant N acquisition [e.g. 31, 32, 33], it is clear that AM can enhance plant N acquisition in many situations [30], which in turn may help reduce N loss from the soil (see below and Table 1).

AM can reduce N loss via leaching (Table 2), with reductions in leaching of $NH_4^+$ and/or $NO_3^-$ having been reported [e.g. 34, 35]. These reductions in N loss via leaching have been accompanied by enhanced plant N assimilation, and sometimes, but not always, a reduction in leachate volume [34-36]. Reductions in N loss via leaching associated with the formation of AM, do however vary with plant species; for example, one study found that the formation of AM resulted in an increase in the growth and nutrient uptake of two fast growing ornamental perennial plants, but that there was a reduction in the concentration of $NO_3^-$, $NH_4^+$ with only one of the species [36]. In another study using large outdoor-lysimeters, the presence of AM together with other soil biota contributed strongly to increased N and P contents of maize, whereas the leaching of total N was strongly reduced by up to a half [37]. In this study a significant reduction (45 %) in the leaching dissolved organic N compounds was also found.

The impact of AM on N leaching can also be influenced by soil type. For example, in a study [6] investigating the effect of AM on nutrient leaching in two different soil types and under $NH_4^+$ or $NO_3^-$ dominated conditions, it was found that while $NH_4^+$ leaching was constantly reduced, the leaching of dissolved organic N compounds was reduced in one soil type only. Further, $NO_3^-$ leaching was not affected by AMF in this study. The importance of AM in reducing N loss via leaching has also been explored at larger scales. For example, a large scale correlative field study showed that AMF abundance was a strong predictor of total N leached (reduced N loss) in agricultural land-use systems [38]. However, apart from this example, field evidence for the potential for AM to reduce N loss via leaching is scarce. While there are clear examples of AM reducing the loss of N via leaching, , at least one study showed the opposite effect [39]. Interestingly, in this study red clover was much more abundant in mycorrhizal grassland microcosms and the amount of $NO_3^-$ leaching may be related to the fact that the clover was fixing N (which could subsequently be lost by leaching). Finally, no association was found between the presence of AMF and N leaching in another microcosm-based model grassland system [40].

The cycling of N in soils is rapid and dominated by a series of microbially-mediated N transformations [41]. This presents a challenge in the study of the role of AMF in soil N cycling. This is because the establishment of non-mycorrhizal treatments in experiments usually involves the sterilization of the soil and back inoculation with bacterial filtrates. While such an approach does provide a soil microbial community similar to that of non-sterlised soils (i.e. AM treatments), some time is required for microbial communities to equilibrate [34, 35, 42]. To overcome this issue, the authors of [43] compared N loss via leaching from cores containing either a mycorrhizal defective tomato (*Solanum lycopersicum*) mutant, or its mycorrhizal wild-type progenitor. It was found that mycorrhizal tomato root systems dramatically reduced $NO_3^-$ loss via leaching. This large reduction in N loss may have been due to either an inherently high efficiency of AM formed by tomato to intercept N, or the impact of AMF on soil microbes involved in N cycling. The potential to use mutants in field studies of AM functioning (see also [7, 44, 45]) is one area that is open to further investigation.

Although N losses from soil due to denitrification can be substantial [11, 46, 47], only a few studies have investigated AM effects on soil $N_2O$ and/or $N_2$ emissions, and results are variable. For example, in a field experiment, using a mutant based approach to control for the formation of AM, the formation of AM enhanced the capacity of plants to immobilize a recently applied pulse of $^{15}NO_3^-$, but had no impact on soil $N_2O$ emissions [7]. By contrast, in another study comprising two independent greenhouse experiments using either a mutant/wild-type pair of tomatoes (different from those used by [7]) or sterilized and re-inoculated soil to manipulate the presence of AMF [44], fluxes of $N_2O$ were 33% and 42% higher where plants had formed a reduced or no association with AMF, in the two experiments respectively. Finally, in a recent glasshouse study using the same tomato genotypes used in [7], AM reduced soil $N_2O$ emissions at high soil moisture [9]. This study suggests that control over $N_2O$ emissions by AM plants is related to higher use of soil water (which will affect rates of dentrification and thence, $N_2O$ emissions), rather than increased N uptake. Given the importance of $N_2O$ as a greenhouse gas, this is an area ripe for further investigation.

While it is clear that AM can impact upon N loss from soils, the underlying mechanisms are less clear. Enhanced rates of N immobilization by AM will reduce the size of the mineral N pools in the soil, thereby reducing the risk of N loss via leaching, or the amount of N available to be denitrified (Figure 1). In the case of leaching, the preferential uptake of $NH_4^+$ by AMF [24] is likely to be especially important in this regard as it not only reduces the pool of $NH_4^+$ that can be leached, but it also reduces the pool of $NH_4^+$ available to be transformed into $NO_3^-$ (via nitrification) which is much more mobile in soil. However, preferential uptake of $NH_4^-$ over $NO_3^-$ may not always be the case [see 6], and AM can also assimilate N in organic forms

[21, 22]. For gaseous N losses, reducing the pool of $NO_3^-$ in the soil will decrease the risk of N loss as $N_2O$ (or $N_2$) generated via denitrification. Similarly, reducing the soil $NH_4^+$ pool may also be important as some $N_2O$ is generated in the process of nitrification.

Arbuscular mycorrhizas can improve soil structure and soil water retention [45, 48]. In doing so, AM could help reduce N losses by reducing the volume of soil leachate (Figure 1). Conversely, improvements in soil structure associated with formation of AM may help to retain water in the root zone, which is not taken up by plants and/or AMF and may promote the $N_2O$ producing process of denitrification under some circumstances, as rates of denitrification are strongly moisture dependent. Some studies show an AM-mediated reduction in leachate volume [35, 49], whereas others do not [34, 43]. Arbuscular mycorrhizas may also affect soil $N_2O$ emissions via enhanced water use by AM plants [9]. Arbuscular mycorrhizas may also reduce N loss by competing with organisms involved in the soil N cycle (e.g. nitrifiers and denitrifiers) for both $NH_4^+$ and $NO_3^-$ [see 30]. The abundance of microbes involved in N mineralization may also be impacted by AMF [50, 51], and so also need to be taken into consideration. Finally, whereas carbon (C) exudation from plant roots can be reduced in presence of AMF [52], AMF exude C from their extraradical hyphae [53]. This C may help to improve soil structure as well as providing an energy source for N cycling microorganisms, including denitrifiers. This, however, is yet to be specifically tested. Finally, the presence of AMF in soil can induce shifts in soil microbial communities, including organisms involved in N cycling processes, e.g. denitrification [54], which could also affect N losses from soil through denitrification and leaching.

Irrespective of the underlying mechanisms, AM can impact upon soil N loss. Although the mechanisms that underpin AM impacts on soil N losses are likely to be multifarious and complex, it will be important to understand them if we are to make predictions about AM impacts on N losses, be it in the context of leaching or $N_2O$ (and $N_2$) emissions.

## The role of AM in reducing P loss from the soil

Phosphorus, is relatively immobile in soil compared to N. Usually only a small percentage of soil P is available to plants, while up to 90% of P can be effectively rendered unavailable via precipitation reactions in the soil or sorption to mineral soil particles and/or organic matter [55-57]. Therefore, P fertilizers are often applied in excess and soils are accumulating P [58, 59]. Although loss of P via leaching is low compared to that of N, it can be especially important in soils with a low P sorption capacity [60, 61]. Furthermore, small amounts of P leached may have a strong environmental impact, with P entering freshwater bodies considered the main cause of eutrophication [62-64].

Arbuscular mycorrhizas are best known for their capacity to enhance plant P acquisition. The molecular and physiological basis of the role of AM in enhancing plant P acquisition is very well understood, with P transporter genes in AMF, and genes involved in plant P transport whose expression can be affected by the formation of AM (in a number of plant species), having been identified (see [13]). Given that P loss can be significant in some soils, and that AMF can acquire large amounts of P, it follows that AM are likely to play a significant role in reducing P loss via leaching in soils susceptible to P leaching. Recent studies are beginning to show that AM have an important role to play in reducing P loss via leaching (see below and Table 1)

Arbuscular mycorrhizas can improve plant P acquisition and reduce inorganic P loss via leaching (Table 2) [6, 34-36, 49]. These effects are generally most pronounced where soil P is low and levels of AM colonization are generally higher [34, 35], although this is not always the case [36]. In one study [65], no effects of AM on P leaching in three soils were found, but substantial reductions in three other soils were. Importantly, the amount of P leached was negatively correlated with the amount of fungal hyphae in soil. AMF are capable of reducing not only leaching of reactive, plant-available P compounds, but also of unreactive P compounds (e.g. organic P, polyphosphates and P bound to particulate inorganic material) [6].

It is important to note that AM do not always reduce P loss via leaching. For example, in a lysimeter study [37], P losses were slightly higher in the ‘enhanced soil-life treatment’, which included AMF, compared to where AMF were not present. Interestingly, this was despite the fact colonization of roots by AMF (measured as percent colonization) was strongly positively related to plant biomass and P contents and that the mobilization of soil P resources was strongly increased in the ‘enhanced soil-life treatment’ treatment. Compared to the strong increase in plant P contents, the amount of P leached was very small and the authors concluded that the enhanced losses might be a by-product of the massively increased mobilization of soil P by AMF. While total P leaching was higher in presence of AMF, again leaching of non-reactive P compounds was reduced. This example highlights the importance of considering nutrient losses in different chemical forms, as is also the case for N (see above).

We consider the ‘scavenging’ for inorganic P beyond rhizosphere depletion zones, to be the primary mechanism by which AM reduce the risk of P loss via leaching [14, 66] (Figure 1). AM may also indirectly influence P surface runoff by stimulating plant P acquisition and by reducing soil P availability. While acquisition of P from organic sources and from insoluble inorganic P compounds may explain the reductions in the leaching of unreactive P compounds [6], more needs to be known about the role of AMF in acquiring P from organic and other soil sources before firm conclusions can be drawn. Reduced leaching of organic P compounds could also be due to enhanced uptake of inorganic P by AMF, thereby reducing the amount of P available to be transformed into organic forms by other soil biota. While AM effects on leaching of dissolved organic P, and P associated with colloids and other particulate matter are not well understood, their contribution to leaching is captured in measures of leached total P. We also note that effects of AMF on soil structure and water retention may also be important in reducing soil P loss via leaching, as with N leaching (see above). A reduction in the magnitude of AM effects on P leaching, with increasing soil P supply, are consistent with prior studies showing that the formation and functioning (at least in terms of P acquisition) of

AM is reduced as soil P is increased.

## Arbuscular mycorrhizas and nutrient losses: the way forward

Arbuscular mycorrhizas can have a significant role in reducing the loss of N and P from soil. This is an important but largely overlooked ecosystem service provided by AM. We anticipate that these processes could be especially relevant in sandy soils, irrigated farming systems, high input farming systems, nutrient rich natural systems, and points in the landscape where water and nutrient fluxes are high (e.g. riparian zones). Maintaining high levels of AMF in soils will be important, especially in agroecosystems where the use of fungicides, fumigants, inclusion of non-mycorrhizal crops such as oilseed rape or sugar beet, prolonged fallow periods, and soil cultivation can reduce the inoculum potential of the soil. Furthermore, excess application of P fertilizers may be especially problematic in this context, as in addition to the higher levels of nutrients being applied, AM colonization of roots is reduced with increased P supply [67-69]. To this end, a reduction in the formation of AM is likely to be one of the reasons for greater levels of P loss from fertilized ecosystems [35]. In Fig. 2, the relationships between soil management intensity and nutrient levels, AM abundance and total nutrient losses are integrated into a conceptual framework to identify the situation where AM-mediated reduction in nutrient losses is maximized. With higher management intensity and nutrient additions, total nutrient losses increase, while AM abundance is reduced. We expect the relative contribution of AM to the reduction of nutrient losses to be highest at low nutrient availability when effects of AM are expected to be highest. However, in terms of total amounts, the contribution of AM to the reduction of nutrient losses will be highest at intermediate management intensity and soil fertility, where nutrient losses would be expected to occur in significant amounts but AM abundance is still sufficient to reduce nutrient losses (Fig. 2). A further increase in management intensity may on one hand lead to higher nutrient losses because of excess nutrients in soil, and on the other hand, because AM abundance is further reduced. Ultimately, the goal should be to "push" the system in such a way that the stimulation of AMF will reduce the total amount of nutrient losses.

It has been proposed, that nutrient stoichiometry, especially the N/P ratio, can have a significant impact on AM functioning (see [70], for review). In these studies, the functioning of AM is evaluated by looking at effects on plant growth and nutrition. It is suggested that AM benefits for plant growth and nutrition are highest under P limiting conditions, but with sufficient availability of N. However, the effects of nutrient stoichiometry on nutrient leaching may be more complex and may, in addition to effects on plant nutrition, also be influenced by the ability of AM to directly or indirectly immobilize nutrients (e.g. in AM fungal hyphae or through effects on soil microbial communities) and to reduce soil nutrient availability. Nevertheless, it seems reasonable to suggest that improved AM functioning through adequate nutrient stoichiometry could also maximize AM effects on nutrient losses from soil; however, this remains to be tested.

Further research efforts should be directed towards the identification of conditions and measures suitable to maximize AM benefits in agroecosystems. Equally, it will also be important to consider the impact of other management practices that help to reduce nutrient losses, such as the use of cover crops and optimizing the timing of fertilizer application. In addition to focusing on the fate of inorganic N and P losses in mineral N forms, it is clear that there is also a need to consider losses in organic forms. The processes underlying the involvement of AM in the reduction of losses of organic nutrients require further investigation as very little is known about the utilization of organic compounds by AM and whether these effects are direct or indirect via associated microorganisms.

At several points in the review we noted the paucity of field-based studies of the role of AM in reducing nutrient loss. Field based studies, however, present a number of challenges. For example, for measurement of nutrient loss via leaching in the field it will be necessary to use techniques that allow collection of leachate with a minimum of disturbance to the soil, such as the use of anion- and cation-exchange resins, lysimeters or soil water samplers. Establishing non-mycorrhizal treatments in the field is also a challenge, although it can be overcome using a genotypic approach to controlling for the formation of AM [42, 45]. Further, we suggest that all of these experimental approaches will be particularly valuable when used in conjunction with isotope labeling techniques (e.g. [7]). Although not considered here, temporal asynchrony may be an important factor in field-based studies. For example, in deciduous systems most nutrient losses occur in autumn, when plant and mycorrhizal activity is low. However, if AM efficiently scavenge soil nutrients in times of high activity, this should enhance the nutrient uptake capacity of soils as more nutrient exchange sites are available. Hence, AM effects on nutrient losses in times of low mycorrhizal and plant activity could still be expected through indirect mechanisms. Moreover, there is compelling evidence that AM interact with a wide range of other soil organisms involved in nutrient cycling processes. Due to the reductionist nature of many experiments studying AM effects on nutrient cycling (e.g. using sterilized soils), there is a strong need to further investigate interactions of AMF with other soil biota, and test how they jointly influence nutrient losses from soil. Taken together, we consider the potential for AM to reduce nutrient loss from soils an important ecosystem service that is ripe for further detailed mechanistic investigation.

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## Glossary

**AM**: arbuscular mycorrhiza; association formed between the roots of most terrestrial plant species and AMF.

**AMF:** Arbuscular mycorrhizal fungi; 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 carbon in the environment.

**Leaching:** The drainage of water containing solutes away from soil by the action of percolation.

**$N_2O$:** Nitrous oxide; a potent greenhouse gas.

**Denitrification:** the microbial transformation of $NO_3^-$ to $N_2O$ and ultimately $N_2$.

**Nitrification:** the microbial transformation of $NH_4^+$ to $NO_3^-$.

## Figure Legends

**Figure 1.** Overview of potential impacts of mycorrhizal versus non-mycorrhizal plants on soil nutrient loss pathways.

Starting nutrient pool[1] may be comprised of inorganic and/or organic N and P containing compounds. Immobilization of nutrients[2] and water uptake[3] is enhanced when plants are colonized by AMF. As a consequence, the pool of nutrients at risk of being leached[4] will be reduced with mycorrhizal plants. At the same time, AMF can improve soil structure[5], resulting in a reduction in leachate volume. 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, effects of forming AM on plant biomass may also be important (see text). N.B. Size of arrows indicate direction of change (i.e. increased, decreased or similar), but are not drawn to scale.

**Figure 2.** Hypothesized relationship between soil nutrient levels, and total nutrient loss, AM colonization, and AM-mediated reduction in nutrient loss.

The lag in the first panel represents the situation where nutrient binding sites are unsaturated. In the second panel the small increase in colonization is consistent with studies suggesting that when soil P is low, low levels of P supply can stimulate colonization. The third panel suggests that AM-mediated reductions in nutrient loss will be quantitatively greatest at intermediate levels of management intensity and nutrient addition, and where levels of AM colonization are not minimized. The relative contribution of AM to reducing nutrient losses is expected to be highest at the low end of soil nutrient availability (not shown).

## Tables

**Table 1. Soil N and P compounds and their mobility, sources, transformations and potential impacts of arbuscular mycorrhizas (AM) upon their loss from soil**

| Nutrient compound | Soil Mobility | Nutrient cycling processes | | Involvement of AM fungi |
|---|---|---|---|---|
| | | Sources/inputs | Transformations/losses | |
| $NH_4^+$ | Low | Organic matter mineralization/ ammonification; Dissimilatory nitrate reduction; fertilizer addition | Plant and microbial immobilization; bound to soil particles or formation of precipitates/complexes, which may be leached; Nitrification yielding $NO_3^-$ | Immobilized by AMF. Impacts of AMF on soil water relations |
| $NO_3^-$ | High | Nitrification; fertilizer addition | Plant and microbial immobilization; leaching; denitrification giving rise to gaseous forms of N; Dissimilatory nitrate reduction. | Immobilized by AMF, but less so than $NH_4^+$. Impacts of AMF on soil water relations |
| Dissolved organic N | Variable | Organic matter decomposition; extracellular enzyme production; root exudation, manure application, animal and microbial excretion | Mineralization; Plant and microbial immobilization; Leaching | AMF may promote mineralization and can immobilize the product ($NH_4^+$). Direct uptake |
| $PO_4^-$ | Very low | Organic matter mineralization; fertilizer addition<br>Desorption from soil particles<br>Solubilisation of Phosphate-minerals | Plant and microbial immobilization; bound to soil particles or formation of precipitates/complexes, which may be leached | Is often strongly immobilized by AMF. Impacts of AMF on soil water relations |
| Dissolved organic P,<br>Complex-bound P.<br>Sorbed P | Variable | Organic matter decomposition; mineral weathering, extracellular enzyme production; root exudation, manure application, animal and microbial excretion | Mineralization; Plant and microbial immobilization; Leaching | AMF promote mineralization and can immobilize the product. Involvement in solubilisation of non-plant available compounds. Impacts of AMF on soil water relations |

**Table 2. Overview of studies investigating effects of arbuscular mycorrhizas (AM) on soil N and P losses via leaching**

| Experimental system | AM effects on N and P loss via leaching | Refs |
|---|---|---|
| Clover in microcosms | Experiment 1. Approx 2.7 times reduction in content of P leached with AM under low P conditions. No difference where soil P was high. Experiment 2. Approx 2.4 times reduction in content of P leached with AM under low P conditions. No difference where soil P was high. | [49] |
| Grassland microcosm | 7.5% and 60% reductions in loss of $NH_4^+$ and inorganic P respectively, from AM microcosms. No change in $NO_3^-$ with AM. | [35] |
| Pasture grass microcosm | Approx. 7.5, 3 and 1.4 times reductions in $NH_4^+$, $NO_3^-$ and P concentrations in leachate, respectively. | [34] |
| Ornamental perennial plants and *Rhus integrifolia,* in pots | Up to a 65-80% reduction in $NH_4^+$, $NO_3^-$ and inorganic P content of leachates with mycorrhizal *Encelia californica*, but not *Rhus integrifolia.* | [36] |
| Mycorrhiza defective and mycorrhizal tomato genotypes. | 40 times reduction in N loss via leaching of $NO_3^-$. No change in $NH_4^+$ loss via leaching with AM. | [43] |
| Pots with maize | No effects of AM on P leaching in three soils. 40% to two-fold reduction of P leaching in three other soils. P leaching negatively correlated to AMF hyphal length in soil. | [65] |
| Agricultural crop rotation grown in outdoor-lysimeters | 24.3% reduction in total N leached with AM during two growing seasons. Increase in P leached with AM. | [37] |
| Grassland microcosms with two different soil types | Reduction by 31 and 24 % of total and unreactive P leaching, respectively, with AM. Up to 90% of P leached in unreactive form. $NH_4^+$ leaching reduced by 69% with AM, reduction of DON leaching by 24 % with AM in one soil type only. No effect on NO3 leaching. | [6] |
| Grassland microcosm with red clover | 40% increase and decrease in $NO_3^-$ and $NH_4^+$ leaching respectively, with AM. 20% increase of unreactive P leaching with AM, and no effect on dissolved inorganic P. | [39] |

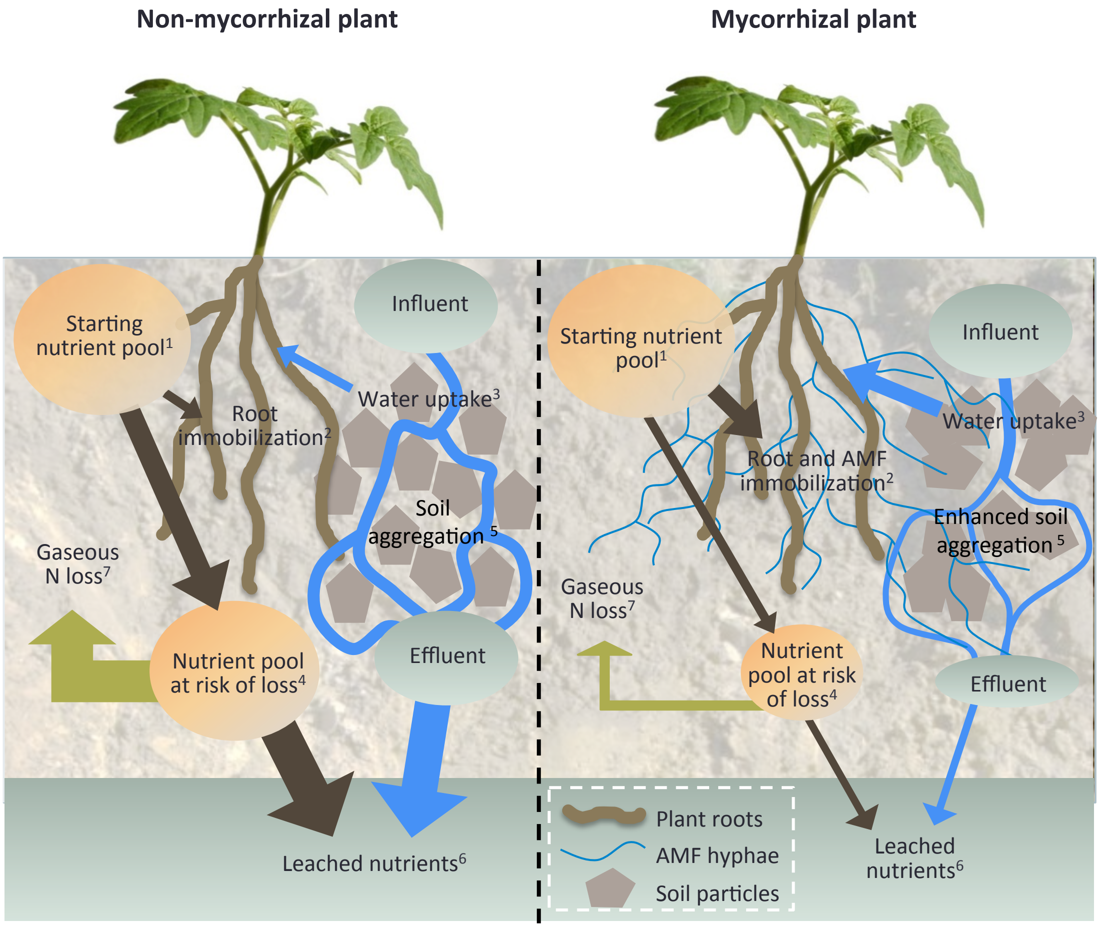
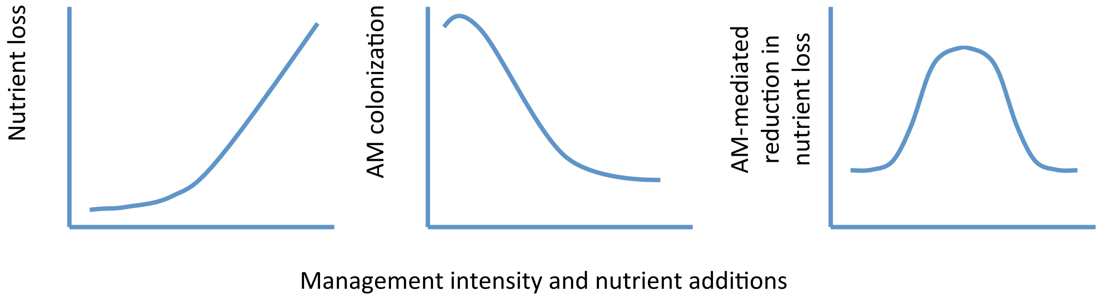

Non-mycorrhizal plant
Mycorrhizal plant
Starting nutrient pool[1]
Root immobilization[2]
Influent
Water uptake[3]
Soil aggregation [5]
Gaseous N loss[7]
Nutrient pool at risk of loss[4]
Effluent
Leached nutrients[6]
Starting nutrient pool[1]
Influent
Water uptake[3]
Root and AMF immobilization[2]
Enhanced soil aggregation [5]
Gaseous N loss[7]
Nutrient pool at risk of loss[4]
Effluent
Plant roots
AMF hyphae
Soil particles
Leached nutrients[6]

**Figure 1.**



Nutrient loss
AM colonization
AM-mediated reduction in nutrient loss
Management intensity and nutrient additions

**Figure 2.**