Ecosystems (2019) 22: 1561–1572
https://doi.org/10.1007/s10021-019-00356-y

ECOSYSTEMS

Ectomycorrhiza, Friend or Foe?

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Abstract

Many ecology textbooks present the interaction between mycorrhizal fungi and their host plants as the archetype of symbiosis or mutualism. However, mycorrhiza drains carbon directly from the plant and also competes with the plant for soil inorganic nitrogen. We developed hypotheses based on a simple model to qualitatively investigate when, in a nitrogen-limited system, the fungal partner returns sufficient extra nitrogen to compensate for the amount of carbon allocated to it by the plant. We showed when the mycorrhizal association can be beneficial to the plant, but also when mycorrhizal immobilization of soil inorganic nitrogen can be a limitation. The amount of carbon and nitrogen that the mycorrhizal fungus can obtain from soil organic matter, by producing extracellular enzymes, is also important. Saprotrophic capability decreases the value of the fungus to the plant, as fungal uptake of soil carbon augments the use of the plant-supplied carbon and increases the fungal requirement for N. The stoichiometric mismatch between low-N soil organic matter and high-N fungal biochemistry turned out to be a bottleneck in making the fungus a net provider of additional N to the plant. The most important properties determining the usefulness to a plant of a mycorrhizal symbiont are plant nitrogen use efficiency and the amount of inorganic N taken up per unit extra fungal growth. The fraction of carbon the fungus allocates to its own growth, relative to its investment in exocellular enzymes, is also a critical property. Our results show that plants could benefit from the association with the fungus, which could explain the ubiquitous nature of this association between fungi and plants.

Key words: allocation; mycorrhiza; nitrogen; parasitism; plant growth; symbiosis.

Highlights

- Mycorrhiza can, depending on environment, be a benefit or a cost to the host plant
- Saprotrophic capabilities of mycorrhiza is an important aspect
- Supply of inorganic nitrogen by the fungi to the host plant may be the major benefit.

Received 8 October 2018; accepted 24 January 2019;
published online 18 March 2019

Author Contributions GIÅ designed the study and performed the calculations. GIÅ, RH and PB wrote the paper.

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Introduction

Many ecology textbooks present the interaction between mycorrhizal fungi and their host plants as the archetype of symbiosis or mutualism (for example, Odum 1971; Ricklef 1993). However, some studies show that mycorrhizal plants grow less well than non-mycorrhizal plants (for example, Corrêa and others 2006; Hoeksema and others 2010) and that mycorrhizal fungi can immobilize large quantities of nutrients, causing nutrient deficiency in the host plant (Näsholm and others 2013). These processes might not be mutually exclusive, as there is likely a gradient between mycorrhiza being beneficial to the plant and acting as a parasite (Hoeksema and others 2010). This gradient is likely to depend on availability of nutrients in the environment and on specific plant,

soil, and fungal properties. A key aspect should be the stoichiometric imbalance between low-N soil organic matter and high-N fungal biochemistry, which could mean a high-N cost for the fungus to extract N in a low-N environment.

Several models have been developed in recent years to account for mycorrhizal processes, with regard to their importance for both plant nutrition and soil carbon (C) stocks. These models pay explicit attention to microbial mechanisms, describing decomposition as a product of microbial activity and extracellular enzymes (Schimel and Weintraub 2003; Allison and others 2010; Wieder and others 2013). In some models, mycorrhizal symbiosis is included by considering the C and nitrogen (N) flows between the plant and the mycorrhizal fungus, while accounting for mycorrhizal mobilization of organic N (Meyer and others 2010; Orwin and others 2011). Baskaran and others (2017) developed a model that includes feedback from total plant N uptake to C supply to the fungus and, using this model, identified an optimal C supply to the fungus by the plant at around 10% of net primary production. However, all these models are quite complex, with many processes and parameters, and aim at quantitative predictions, making it difficult to identify the properties and conditions that are most critical. Bever (1999) and Bever and others (2001) address another important aspect of the plant–mycorrhizal interaction, it can be an important vehicle for maintaining the diversity of both the plant and the fungal community. The models by Bever explore the complexity of a host plant interacting with a community of fungi, whereas we want to focus on how one fungal species can use soil C in addition to plant-supplied C to provide the host plant with N from a mixture of soil inorganic and organic sources. In both cases there will be a continuum of relations from parasitism to symbiosis.

Therefore, we set up a simple model (for improving understanding rather than generating numbers, sensu Rastetter (2017)) for qualitative investigation of the transition between symbiosis and parasitism. For simplicity, we focused on delivery of N by the mycorrhizal fungus to the plant, although other key nutrients such as phosphorus (P) could have been used. A detailed analysis based on stoichiometric requirements of C, N, and P in both the host plant and the fungus in a mycorrhizal association is provided by (Johnson 2010). We concentrated on two aspects of the mycorrhizal interaction: (1) the mycorrhizal fungus delivers N in return for plant C and (2) the fungus immobilizes N, making it unavailable to the plant. In these two roles, the mycorrhizal fungus can act as a parasite and/or competitor. At the same time, the fungus takes up inorganic and organic N, part of which is delivered to the plant. It is the balance between supply to the plant and immobilization that determines whether the fungus is a parasite or a mutualist. For simplicity, in our model we excluded the quantitative aspects of such mycorrhizal models. Instead, we focused more on qualitative analysis, that is, the environmental circumstances and the key features of plant and fungus that make the association with the mycorrhizal fungus beneficial to the plant, with particular emphasis on the availability of inorganic N in the soil and the ability of the fungus to use soil C as an additional C source. The ability of mycorrhizal fungi to decompose soil organic C saprotrophically is a contested issue (Lindahl and Tunlid 2015). However, according to Koide and others (2008), ''Evidence for the existence of facultative ectomycorrhizal fungi is now abundant'' and ''…ectomycorrhizal fungi can occur along a large portion of the biotrophy–saprotrophy continuum.'' The key aspect we want to investigate is, therefore, how the fungus uses plant carbon, that is, whether it is used solely for growing fungal mycelia or whether it also can be used for producing exoenzymes to degrade soil organic matter, making both organic N and organic C available for uptake. Another aspect to be studied is how the fungal use of plant C benefits both the fungus and the plant. Because the ability to decompose soil organic matter seems to be restricted to ectomycorrhizal fungi, the present analysis is mainly applicable to this group of mycorrhiza. The plant–fungus symbioses includes also a cost to the fungal partner (Bever 1999, 2015), which could shift the balance along the mutualism–parasitism continuum but we leave this aspect out for simplicity.

Model Description

The basic concept is that an N-limited plant allocates a fixed amount, ΔC_a (gm^{-2}), of its C to the fungus and in return receives a quantity ΔN_p (gm^{-2}) of nitrogen (Figure 1). We will only consider the marginal N uptake and loss of uptake as a result of the plant's interaction with the fungus and not the total N uptake; the latter is studied by Baskaran and others (2017). The plant can use this amount of N to assimilate a certain amount of carbon, ΔC_p (gm^{-2}):

$$\Delta C_p = P_N \, \Delta N_p / \mu_P \qquad (1)$$

where μ_P (y^{-1}) is the turnover rate of plant biomass and P_N ($gC\ (gN)^{-1}y^{-1}$)is plant nitrogen productiv-

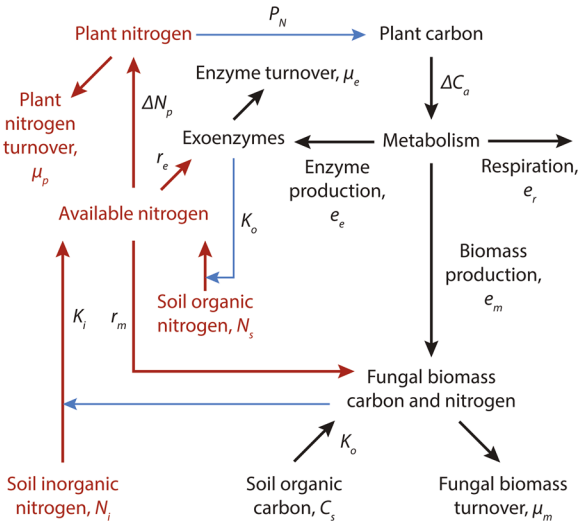

Figure 1. Schematic diagram of the model. Black, solid, arrows show carbon flows, red, dashed, arrows show nitrogen flows, and blue, dotted, arrows show important controls. Symbols next to arrows show the key parameters controlling a flux. Arrows ending in nothing indicate losses that are not considered in the model. The plant can also take up soil inorganic N but that is not consider in the model (Color figure online).

ity [rate of plant biomass production per unit N in the plant (Ågren 1985)]. Note that P_N/μ_P is the plant N use efficiency (NUE, gC $(gN)^{-1}$) (Vitousek 1982). ΔC_p is not equal to GPP but the marginal increase in production from the extra N received from the fungi; the plant has also an uptake of N through its roots. This investment of ΔN_p in plant biomass can be a short-term investment when the mortality rate, μ_p, is high or a long-term investment when μ_p is small. We were not interested in the absolute magnitude of plant and fungal C and N stores, but only in how the C allocated from the plant to the fungus increases fungal degradation of soil organic matter and whether this is matched by increased plant growth resulting from increased N uptake. An immediate observation is that plants with higher NUE should benefit more from mycorrhizal associations, because with the same return of N from the fungus they assimilate more carbon. To keep the model simple, we are also neglecting the probable increase in plant C available for allocation to the fungus as a result of increased plant N.

For mycorrhizae to be beneficial to the plant, ΔC_p should be larger than the amount ΔC_a allocated to the fungus, as otherwise the plant is acquiring less C than a non-mycorrhizal plant and the mycorrhizal fungus is a parasite to the plant:

$$\Delta C_p > \Delta C_a \tag{2}$$

The amount ΔN_p received from the fungus is thus critical to whether it is parasitic or not to the plant. The problem then is how to calculate ΔN_p. For this purpose, Eqs. (1) and (2) can be rewritten as:

$$\frac{\Delta C_p}{\Delta C_a} = \frac{P_N}{\mu_P}\frac{\Delta N_p}{\Delta C_a} > 1, \text{ or } \frac{\Delta N_p}{\Delta C_a} > \frac{\mu_P}{P_N} \tag{3}$$

The fungus can use the ΔC_a received from the plant in three different ways: (1) it can be respired, letting the fraction going to respiration be e_r, (2) it can be used to build new biomass, represented by a fraction e_m and (3) it can be used to produce exoenzymes, represented by a fraction e_e, where $e_r + e_m + e_e = 1$. We calculate these parameters as follows. For each unit of C invested in fungal biomass, γ_m units of C are respired as construction costs. The remaining C is invested in enzyme production, where each unit of C requires γ_e units of C in construction costs. This gives

$$e_e = \frac{1 - e_m(1 + \gamma_m)}{1 + \gamma_e} \tag{4}$$

and $e_r = \gamma_m e_m + \gamma_e e_e$.

The transfer of C from the fungus to the plant that accompanies transfers of N (Franklin and others 2016) has been omitted from the model for simplicity.

The fungus has two sources of carbon, C obtained from the plant and C liberated from SOM by the action of its enzymes (the second term on the right-hand side of Eq. (5) below). We considered this extra C uptake an 'augmentation factor' and compared situations where it was included or not (in the latter case the fungus lives only on C obtained from the host plant, that is, it is exclusively biotrophic). We introduced a parameter s (degree of saprotrophy, $0 \le s \le 1$) to describe that a variable fraction of C released from SOM is taken up by the fungus, where $s = 0$ (only biotrophic) gives no uptake and $s = 1$ means all C released is taken up (augmentation or fully saprotrophic). We focus our analysis only on the C obtained directly from the plant plus the soil-derived C obtained as a result of enzymes produced with the C obtained from the plant. Total fungal uptake of C can then be written as:

$$\Delta C_f = \Delta C_a + sK_o e_e \Delta C_a C_s/\mu_e \tag{5}$$

where the parameter μ_e (y^{-1}) is the turnover rate of the enzyme and K_o combines the rate of depolymerization of SOM carbon (C_s) and rate of enzyme production per unit C allocated to enzyme production.

Because plant-derived plus soil-derived C contribute to enzyme production, and ΔC_a in the last term in Eq. (5) has to be replaced by ΔC_f. Solving for ΔC_f then gives the total C uptake by the fungus

$$\Delta C_f = \frac{\Delta C_a}{1 - sK_o e_e C_s \mu_e} \quad (6)$$

This result can also be derived by summing the infinite geometric series of uptakes, where each uptake of SOC by the fungus contributes to an additional uptake of sK_oC_s/μ_e times the previous contribution to the uptake. Both ways of deriving Eq. (6) assumes that the amounts of SOC released by the fungal enzymes are small such that soil C (C_s) can be considered constant. With the default parameters, see below, Eq. (6) predicts that for each unit of C the plant provides, the fungus will get an extra 0.376 units of C from SOC (the second term in Eq. (5). Eq. (6) also sets restrictions on parameter values to ensure a positive ΔC_f, The enzymes may not be too efficient (setting an upper limit on K_o) and investments in enzymes have also to be limited (there is an upper limit to e_e or a lower limit to e_m). The increase in fungal biomass (ΔC_m) resulting from the plant-supplied C is then a combination of the directly supplied plant C and the extra soil C derived with the aid of the plant C

$$\Delta C_m = e_m \Delta C_f = \frac{e_m \Delta C_a}{1 - sK_o e_e C_s \mu_e} \quad (7)$$

The plant also has two sources of N passing through the fungus, an inorganic (ΔN_i) and an organic (ΔN_o) source; plant uptake not mediated by the fungus is not explicitly included in the model because our analysis is on the effect of the fungus on N uptake. However, we do account for the decrease in plant inorganic N uptake resulting from competition with the fungus (see Eq. (8) below).

We assumed that the increases in fungal biomass, ΔC_m, also increase fungal uptake of inorganic nitrogen at a similar rate [Eq. (8)], whereas uptake of organic N is controlled by the rate at which N is made available by depolymerization by exoenzymes [Eq. (9)]. We further assumed that fungal uptake of inorganic N is proportional to the level of N_i in the environment (remember, we are considering N-limited conditions only and saturation of the N uptake capacity should not be an issue):

$$\Delta N_i = K_i \Delta C_m N_i/\mu_m = K_i e_m \Delta C_f N_i/\mu_m \quad (8)$$

where K_i is the rate of uptake of inorganic N per unit fungal biomass and μ_m the turnover rate of fungal biomass. We combined the parameters K_i and μ_m into what we refer to as 'biomass use efficiency' (BUE = K_i/μ_m), that is, the amount of inorganic N uptake per unit C invested in fungal growth.

Fungal uptake of N from SOM depolymerized by enzymes produced by the fungus occurs in parallel to uptake of C, but in proportion to soil organic N:

$$\Delta N_o = K_o e_e \Delta C_f N_s/\mu_e \quad (9)$$

where N_s is the soil organic N store and we define the soil N:C ratio as r_s. It is also convenient to combine μ_e with K_o to obtain 'enzyme use efficiency' (EUE = K_o/μ_e,), that is, the efficiency with which enzymes are used or the amount of organic N uptake per unit C invested in enzyme production. This uptake of organic N does not require augmentation. Augmentation increases the organic N uptake by the fungus because the fungus obtains more C (ΔC_f) that can be invested in enzymes. The organic N released could also be taken up by the plant but, for reasons of geometry, we assumed the fungus to have priority and that all organic N uptake by the plant occurs via the fungus. We used the same description of depolymerization for both C and N, based on the assumption that exoenzymes are primarily produced to release N, which corresponds to the 'coincidental decomposer' hypothesis (Talbot and others 2008).

The increase in fungal biomass requires the fungus to immobilize some nitrogen, r_m ΔC_m, where r_m is the N:C ratio of the fungal mycelium. We also had to consider the N consumed in enzyme production (r_e, that is, N:C ratio of enzymes). The excess N (ΔN_p) that the fungus can deliver to the plant is then:

$$\Delta N_p = \Delta N_i + \Delta N_o - r_m \Delta C_m - r_e e_e \Delta C_f \quad (10)$$

Combining Eqs. (7), (8), (9) and (10) gives the N gain of the plant per unit C invested:

$$\frac{\Delta N_p}{\Delta C_a} = [e_m K_i N_i/\mu_m + K_o e_e r_s C_s/\mu_e - e_m r_m - r_e e_e] \; [1 + sK_o e_e C_s/\mu_e] \quad (11)$$

Increasing the allocation to fungal biomass growth (increasing e_m) means that less C is available for enzyme production (e_e) and hence release of C and N from SOM. Thus, although more of the C from the plant builds fungal biomass, less C is assimilated from SOM. However, despite these counteracting forces in the fungal use of C, the change in C uptake from SOC responds so slowly to changes in e_m that there is no optimal allocation giving a maximal increase in fungal biomass C. We will, therefore, use as default parameters equal

allocation to biomass and enzymes $e_m = e_e = 0.26$. For similar reasons, there is no allocation that maximizes the transfer of N to the plant.

We defined transfer efficiency (TE), similarly to Näsholm and others (2013), as the fraction of the total nitrogen uptake by the mycorrhizal fungus that is transferred to the plant:

$$TE = \frac{\Delta N_p}{\Delta N_i + \Delta N_o} \quad (12)$$

To assess the effect of competition between the plant and the fungus for inorganic N, we calculate the associated reduction in plant growth. We calculated this N deduction from plant uptake as the fraction of N_i uptake in total N uptake incorporated in the extra fungal growth. This loss of inorganic N uptake by the plant corresponds to lost growth of,:

$$\Delta C_{Pi} = r_m \Delta C_m \frac{\Delta N_i}{\Delta N_i + \Delta N_o} \frac{P_N}{\mu_P} \quad (13)$$

The decrease in plant growth calculated in Eq. (13) must be subtracted from the plant growth calculated in Eq. (1) to assess the full effect of mycorrhizae on plant growth.

The parameters in the model (see Table 1) are difficult to estimate with any accuracy, but we have chosen values that are approximately representative for a boreal spruce (*Picea abies*) coniferous forest (Skogaby) in southern Sweden (Ågren and Andersson 2012). Parameter values for turnover of fungal biomass and exoenzymes were taken from Schimel and Weintraub (2003). The construction costs ($\gamma_m = 1$ and $\gamma_m = 0.8$) for fungal biomass and enzymes were taken as in-between cost for fast-growing and slow-growing roots, respectively for nitrogenous compounds (Ågren and Andersson 2012, p. 107). $\gamma_m = 1$ implies that the allocation to fungal biomass cannot exceed $e_m = 0.5$. The N:C ratio in enzymes is taken as that of an average protein (Sterner and Elser 2002) and for fungal biomass from Cleveland and Liptzin (2007). We estimate the parameter K_o from the priming experiment by Fontaine and others (2004, Table 1). Of 495 units of C added, 365 is lost in respiration, corresponding to $e_m = 0.222$. The priming has released an extra 140 units of C, corresponding to an extra degradation of 140/0.222 = 630 units of C. Thus, 630 = ΔC_f units of SOC is degraded from an addition of 495 = ΔC_a units of C. Inserted in Eq. (4) this gives K_o. We estimate K_i to give equal uptakes of organic and inorganic N when $e_m = e_e$ and middle inorganic soil N, see below. (Because of the uncertainty in parameters, the results should been seen as qualitative rather than quantitative). We focused on the effects of changing the availability of soil inorganic

Table 1. List of Parameters Used in the Model and Default Values Applied

Symbol	Meaning	Default value
BUE	Biomass use efficiency (nitrogen uptake per unit increase in fungal biomass)	0.084 y^{-1}
C_s	Amount of soil organic matter carbon	99 Mg C ha^{-1}
EUE	Enzyme use efficiency (nitrogen uptake per unit enzyme produced)	1.047×10^{-4} y^{-1}
e_e	Mycorrhizal allocation to enzyme production	Variable
e_m	Mycorrhizal allocation to biomass production	Variable
e_r	Mycorrhizal allocation to respiration	Variable
γ_e	Construction cost of enzymes	0.8 g C g^{-1} C
γ_m	Construction cost of fungal biomass	1.0 g C g^{-1} C
K_i	Mycorrhizal rate of inorganic nitrogen uptake	1.18 m^2 g^{-1} C y^{-1}
K_o	Enzymatic rate of degradation of soil organic matter	1.885×10^{-3} m^2 g^{-1} C y^{-1}
μ_e	Turnover rate of enzymes	18 y^{-1}
μ_m	Turnover rate of mycorrhizal biomass	14 y^{-1}
μ_p	Turnover rate of plant biomass	0.2 y^{-1}
N_i	Soil inorganic nitrogen	0.1,1,10 g N m^{-2}
N_s	Amount of soil organic matter nitrogen	584 kg N ha^{-1}
NUE	Nitrogen use efficiency Amount of plant carbon fixed per unit nitrogen uptake	800 g C g^{-1} N
P_N	Plant nitrogen productivity	80 g C g^{-1}N y^{-1}
r_e	Nitrogen/carbon ratio of enzymes	0.435 g N g^{-1} C
r_m	Mycorrhizal nitrogen/carbon ratio	0.106 g N g^{-1} C
r_s	Soil organic matter nitrogen/carbon ratio	0.059 g N g^{-1} C
s	Degree of saprotrophy	0–1

N by using three levels of N_i (0.1, 1, 10 g m^{-2}). Other parameters are such that, at the middle N level and without augmentation, the fungal supply of N to the plant (ΔN_p) comes in equal amounts from inorganic and organic sources. The low (0.1 g m^{-2}) and high (10 g m^{-2}) inorganic N values chosen are admittedly unrealistic for spruce forests, but we wanted to explore a wide range of conditions. All changes in biomass were expressed per unit C transferred from the plant to the fungus. It should be noted that with the default parameters used (Table 1), a strong augmentation factor was obtained whereby, for each unit of C obtained from the plant, the fungus obtained an extra 0.376 units of C from SOM. The augmentation is a form of priming (Kuzyakov and others 2000).

All calculations were performed with Mathcad 15.0 (Parametric Technology Corporation, Needham, MA, USA), except the values in Table 2 that were calculated in Excel.

Results

According to the model, the extra transfer of N to the plant from the mycorrhizal fungus (ΔN_p) depends on how much of the C delivered by the plant (ΔC_a) to the fungus is allocated to biomass growth (e_m) and on the soil N_i level (Figure 2). The most striking feature is that it is only for N_i = 10 that we find any positive effect for the plant. In effect, $N_i \geq 2.6$ is required for any fungal allocation to be beneficial for the plant, with or without augmentation. Above this limit, when e_m is small, there is no positive N delivery to the plant because the enzyme production consumes more N than is gained from the increased N uptake. Under high-enough soil inorganic N and large enough e_m, the plant gains N from the association with the fungus. The effect of the augmentation factor (that is, letting the fungus also take up and use SOM C) is marginal, because it means both larger fungal biomass and increased enzyme production, and hence increased inorganic N uptake and also increased organic N uptake but also further N costs. With our parameter choices the fungus is a liability to the plant at all allocations (the red and black lines fall below the green line in Figure 2) except a high inorganic N levels; the negative values for $\Delta N_p/\Delta C_a$ even suggest that the plant should be feeding the fungus with N.

The parameter K_o plays a crucial role in determining the N delivery to the plant; see Figure 3. When there is no access to SOM, K_o = 0, the fungus immobilizes N than to such an extent that the plant is not compensated for its C delivery to the

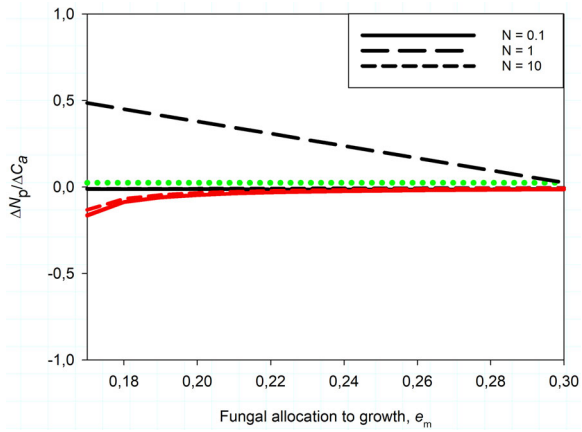

Figure 2. Amount of nitrogen (N) transferred to the plant per unit carbon (C) supplied by the plant to the mycorrhizal fungus as a function of fungal allocation to biomass growth (e_m) for three levels of inorganic N (N_i; 0.1, 1, 10 g m^{-2}). Red lines = with augmentation. Black lines = no augmentation. Green dotted line shows the breakpoint where enough N is supplied to the plant to compensate for the C exported to the fungus (Color figure online).

fungus. When SOM degradation is switched on, $K_o > 0$, enzyme production is also switched on with its associated N cost such that that the net delivery of N from the fungus to the plant decreases further, except at high inorganic N. This occurs more strongly under augmentation; having $s = 0$ has the same effect as having $K_o = 0$, Eq. (6). As K_o increases, with augmentation the organic N uptake increases providing the plant more N. Similarly, higher inorganic N increases the delivery of N to the plant.

The transfer efficiency, Figure 4, reflects the net N uptake in Figure 2 and is only positive for high soil inorganic N and high allocation to fungal biomass, when C is only allocated to fungal biomass the transfer efficiency can approach 1.

The model also shows the simultaneous changes in plant and fungal biomass resulting from an allocation ΔC_a (Figure 5). As a consequence of the results shown in Figure 2, increasing e_m leads to an increasing plant biomass increase with a simultaneous increasing fungal biomass as soon as e_m and soil inorganic N are large enough to allow a net transfer of N to the plant. With augmentation, a larger e_m is required to result in a positive plant biomass increase.

The mycorrhizal fungus causes a drain of C from the plant. One part of this is a direct drain, ΔC_a, and the other is an indirect drain caused by fungal immobilization of soil inorganic N, which the plant could otherwise have taken up and used for growth

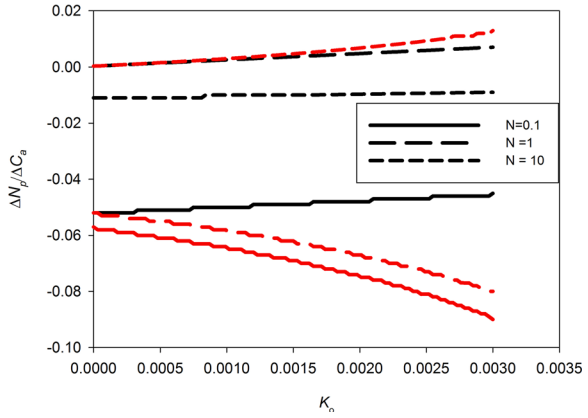

Figure 3. Amount of N transferred to the plant per unit of C supplied from the plant to the mycorrhizal fungus as a function of fungal capacity to degrade SOM (K_o) for three levels of inorganic N and with or without augmentation. Red lines = with augmentation. Black lines = no augmentation (Color figure online).

[Eq. (13)] (Figure 6). The importance of lost growth because of fungal immobilization of N_i seems to be considerably larger than the direct cost of C allocated from the plant (1 unit) to the fungus (Figure 6). This cost is also larger at high N availability and augmentation has a strong effect. However, the growth gained from the mycorrhizal association can still be much larger than this lost growth, cf. Figure 5 (note differences in scales). This cost is greater at high inorganic N, as the absolute uptake of N_i by the fungus is larger.

We investigated the sensitivity to parameter choices by running a Monte Carlo simulation.

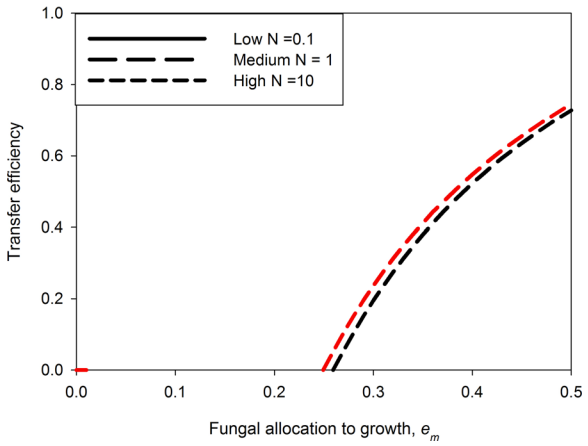

Figure 4. Transfer efficiency, fraction of N taken up by the mycorrhizal fungus that is transferred to the plant, as a function of fungal allocation to growth (e_m) for three levels of inorganic N (0.1, 1, and 10). The results are almost identical whether augmentation is considered or not.

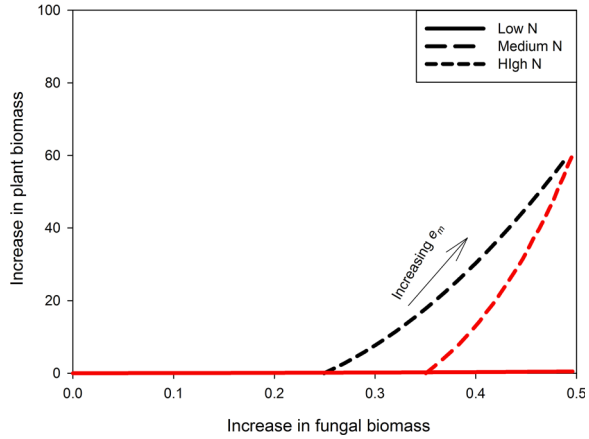

Figure 5. Relationship between plant and fungal biomass as a result of a carbon allocation ΔC = 1 from the plant to the fungus, as a function of fungal allocation to biomass growth (e_m) for three different levels of inorganic nitrogen (N_i; 0.1, 1, 10 g m^{-2}). For e_m = 0, the increase in fungal biomass is 0. Black lines: Without augmentation (the increases in plant biomass are very small). Red lines: With augmentation (Color figure online).

Starting from the default parameter values in Table 1, we drew 1000 parameter values from uniform distributions ranging from 0.5 × default value to 1.5 × default value (with P_N/μ_p combined to NUE, K_o/μ_e into EUE and K_i/μ_m into BUE). Depending on N_i, but with no effects of s, 131–652 parameter combinations resulted in positive ΔC_p, which were used for the sensitivity calculations. The sensitivity to a parameter was defined as the slope of the regression between $\ln(\Delta C_p)$ and

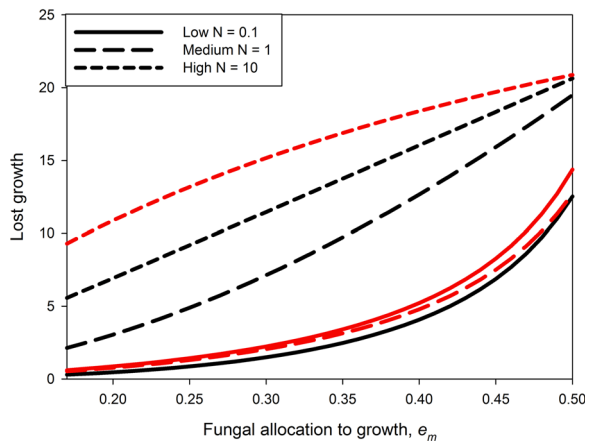

Figure 6. Lost plant growth as a result of fungal consumption of inorganic nitrogen (N_i) as a function of fungal allocation to biomass growth (e_m) at three different levels of N_i (0.1, 1, 10 g m^{-2}). Black lines = no augmentation. Red lines = with augmentation (Color figure online).

ln(parameter) (Table 2 and Figure 7). Three parameters (NUE, EUE and e_m) emerged as being more sensitive than the others. Interestingly, two of the more sensitive parameters were associated with different efficiencies: the efficiency of the plant to use N (NUE) and the efficiency of the fungus to use plant C to produce exoenzymes (EUE). The high sensitivity to e_m is a result of e_m controlling the partitioning between fungal biomass and enzyme production.

Discussion

Plant allocation of C to mycorrhizal fungi can pay off with increased plant N (the right-hand side of Eq. (10) is positive), with an extra uptake of 0.025 units of N sufficing to compensate for 1 unit of carbon. The fungal allocation to biomass or exoenzymes of the plant-derived C has a large effect on the N return to the plant; see Figure 2. The parameter space where the fungus is a drain on the plant appears large, mainly because of the stoichiometric mismatch between the low-N SOM source for the fungus and the high-N requirement of building fungal biomass and, in particular, exoenzymes.

Neither models nor experiments can cover all aspects of a real system. We made the simplification that the plant in a mycorrhizal symbiosis had no alternative, more advantageous uses of the C allocated to the fungus. However, growing more plant roots could have been an alternative to increase the uptake of N_i and possibly also of organic N. The fungus competes with the plant for N_i uptake. We overestimated this effect because part of the uptake by the fungus would probably have been lost by leaching or taken up by plants other than the symbiotic partner plant. We also took a plant perspective by assuming that the symbiosis is driven by the plant's need to obtain more N. An alternative, but interesting, starting point, could have been to assume that the fungus delivers nutrients to the plant in exchange for C, but this would require quite a different model. Starting from a fungal perspective might also require a long-term perspective, where a fungal N delivery to a plant could increase plant growth, with subsequent larger capacity to provide the fungus with C.

Parameters for the model were difficult to estimate with any accuracy, but literature values approximately representative of a boreal coniferous forest were chosen. However, the results must be viewed with caution as they depend on our parameter choices and there is considerable uncertainty in many; for example, it is likely that we used too large a value for K_o. Nitrogen use efficiency of the plant is also a critical factor, Table 2, and our value of 400 g C g^{-1} N is considerably higher than the values of around 100 g C g^{-1} N in the literature (Vitousek 1982), although its absolute value is not likely to be important for the qualitative results. On the other hand, the critical stoichiometric relations of SOM and fungal biochemistry should be fairly accurate.

The immobilization of soil inorganic N by the fungus could be the major C cost for the plant because of lost growth. Because of the rapid turnover of fungal mycelium, most of this immobilized N_i will be returned to SOM and thus unavailable to the plant only in the short term. In the longer term, this N can be taken up as organic N by other colonizing mycorrhizal mycelium or mineralized by saprotrophs but, because of rapid turnover of fungal biomass, it should not show up as a large increase in fungal N biomass. This lock-in of N in forms not available to non-mycorrhizal plants could confer a competitive advantage to mycorrhizal plants (Blagodatskaya and others 2011). The exact magnitude of this lock-in depends strongly on the extra uptake of C from SOM generated by the production of enzymes.

With our parameters, for each unit of C delivered from the plant, the fungus can, depending on allocation, obtain up to 0.4 units extra of C from SOM (note that this mechanism is a positive feedback, where the more C the fungus allocates to enzymes, the more C it gains and the more C can be allocated to enzymes). This return on investment in enzymes is in the range of observations of

Table 2. Results of the Sensitivity Test

Parameter	Sensitivity		
N_i	0.1	1	10
C_s	0.2299	− 0.2325	− 0.0334
BUE	0.0605	− 0.2541	1.2067
EUE	1.7237	1.9521	1.9175
e_m	− 3.1671	− 3.9635	− 0.1152
r_m	− 0.1029	0.0597	0.0452
r_s	− 0.4812	− 0.2698	− 0.1497
r_e	− 0.1672	0.5313	− 0.2000
γ_m	− 0.0427	− 0.3167	− 0.0009
γ_e	− 0.7311	− 0.2421	− 0.2793
NUE	0.5652	0.8478	0.7826
n	130	146	651

The sensitivity was calculated as the slope of the relationship between ln(ΔC_p) and ln(parameter). n = number of simulations out of 1000 that give positive ΔC_p. For symbols and abbreviations, see Table 1.

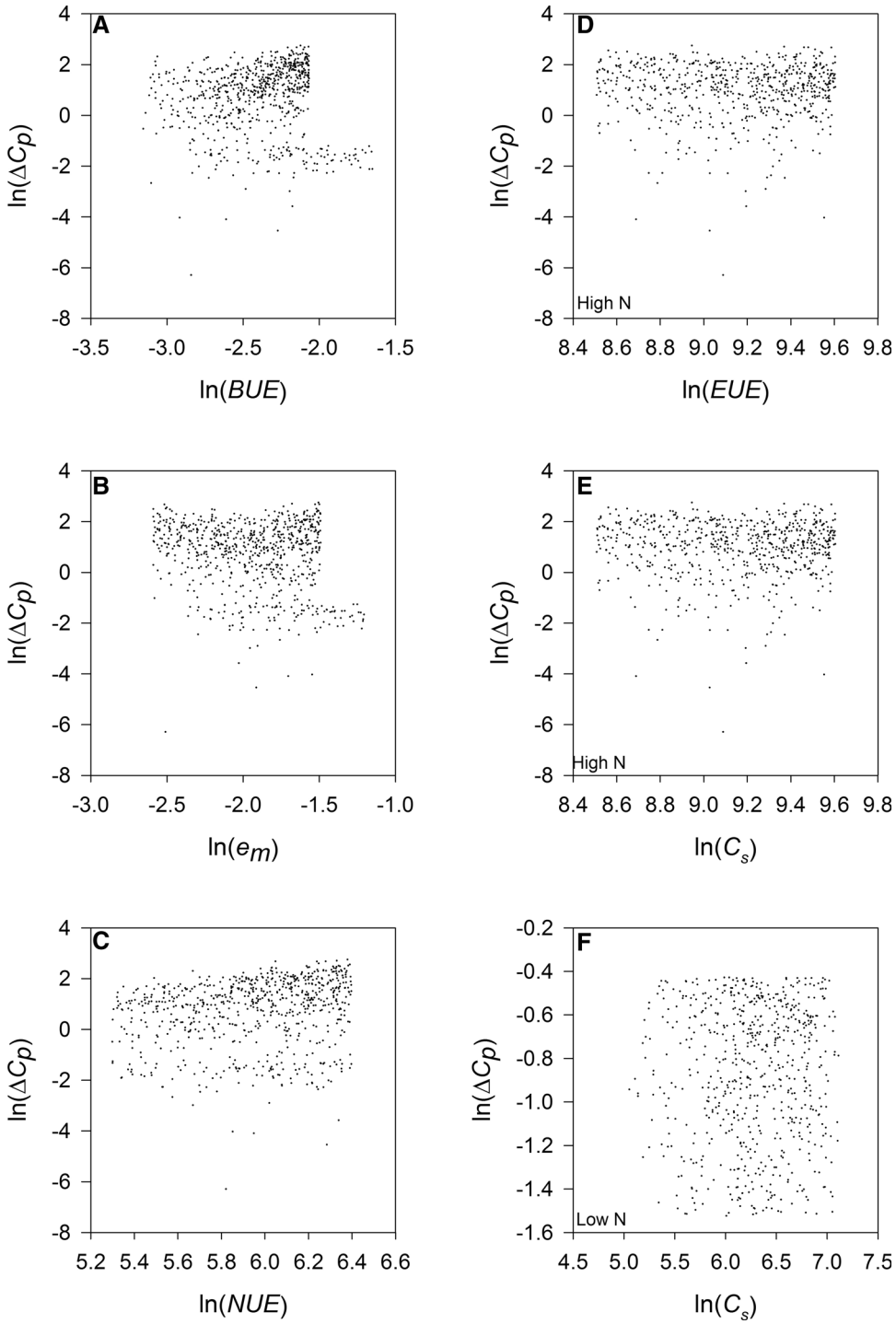

Figure 7. Relationship between $\ln(\Delta C_p)$ and ln(parameter) for high soil inorganic nitrogen (N_i) value of 100 g C g^{-1} N, (**A–E)** and low N (**F**). The slopes of the relationships (see Table 2) are a measure of the sensitivity to the parameter. Each point represents a random selection of parameters (in all, 1000 values). NUE = P_N/μ_p and EUE = K_o/μ_e.

priming. In an experiment (Blagodatskaya and others 2011), addition of glucose to soil caused an extra release of C that was 2- to 200-fold the amount of C added (see also Näsholm and others 2013 and Boberg and others 2010). In contrast, the fungal uptake of organic N is not in competition with the plant, because this N is inaccessible to the plant except when mediated by the fungus. A crucial aspect that needs further investigation is therefore how much SOM C the mycorrhiza gains

by obtaining plant C (the parameters K_o and s). Increasing the parameter K_o (that is, increasing enzyme efficiency) is beneficial to both the plant and the fungus; the curves in Figure 5 will be displaced to the right and upwards. The question is whether the mycorrhizal fungus simply takes up C and N in the proportions available in SOM, or whether it can shift its enzyme production to specifically target the release of C or N from SOM. More research needs to be devoted to the stoichiometric requirements of mycorrhizal fungi and their enzymes. Less N sequestration in fungal mycelium and larger N supply to the plant or less N sequestration in mycelium may result if the fungi can reduce its uptake of SOM C and more specifically target SOM N.

One surprising result is that the mycorrhizal fungus seems to be most beneficial to the plant at high inorganic N levels (Figure 2); the N return for an investment in C is always highest at high inorganic N), which contradicts conventional wisdom (Orwin and others 2011; Wyatt and others 2014). This result seems also to contradict the common observation that N (or P) fertilization decreases mycorrhizal abundance (Treseder 2004). This contradiction might be resolved by reducing the focus on the quantitative effects; in low-N conditions the extra N obtained by the plant through the mycorrhizal association could be what allows the plant to survive, that is, the association with the fungus increases the fundamental niche of the plant (Peay 2017). Our model also shows that at low soil inorganic N content, the plant benefits most if the fungus can increase its allocation to uptake of inorganic N (Figure 2). A critical aspect is therefore whether the plant can control fungal use of the allocated C. Another aspect is the extent to which the plant can control the degree of mycorrhizal infection in response to environmental condition (for example, soil N and P and atmospheric CO_2, Treseder 2004), which could modify the rate of C transfer from the plant. Bever (1999) and Bever and others (2009) analyzed from an evolutionary perspective how and why plants may preferentially select for the most beneficial symbiont. Bever (2015) showed that plants, indeed, allocate preferentially to the symbiont giving the highest return. With low inorganic N, it is best for the plant if less C goes to the N-costly enzyme production. Studies on arbuscular mycorrhiza show that plants at least can prefer an association with the fungal species that delivers most nutrients (Kiers and others 2010). The competition for nutrients between plant individuals is also a factor that could result in individuals benefiting from mycorrhizae.

Our results show a more plant-favorable association with mycorrhizal fungi than Näsholm and others (2013) found in their model analysis. This discrepancy is mainly due to the large increase in N uptake caused by depolymerization of SOM, an aspect not included in the Näsholm model where soil N availability is a fixed parameter. We must also emphasize that our model suggests that the major benefit to the plant from its mycorrhizal symbiosis is not that it gets access to the otherwise inaccessible soil organic pool, but that the fungus enhances uptake of inorganic N.

One observation is that plants with higher NUE should benefit more from mycorrhizal associations. In a meta-analysis Hoeksema and others (2010) found that C4 grasses respond more strongly to associations with mycorrhiza than C3 grasses and Saxena and Ramakrishna (1984)showed that C4 grasses indeed have higher NUE than C3 grasses.

The augmentation factor seems to be of less importance in determining the benefit to the plant of engaging in mycorrhizal associations, although this depends on the efficiency of the enzymes (Figure 3). However, it is not clear whether mycorrhizal fungi even use SOM as a source of C. Hobbie and others (2013) suggest that mycorrhiza acquires SOM C only as a result of uptake of amino acids, whereas the remaining mycorrhizal C comes from the host plant. Our modeling results suggest that for the mycorrhizal fungus to be most useful to its plant host it should not have saprotrophic capabilities as the use of SOM C by the fungal partner in the association increases N immobilization. Fungal use of soil C may also change the stability of soil C if the fungi feed on labile soil C, but return recalcitrant C as dead fungal biomass (Clemmensen and others 2013). This provides an additional, potentially important process, in the plant–soil system (Wurzburger and others 2017).

Our model is not intended for quantitative comparisons with field data, but rather to explore qualitatively the implications of the mycorrhizal interaction between plant and fungus. Three major considerations emerge. First, optimal use by the fungus of C supplied by the plant does not coincide with optimal conditions for the plant. This could be a problem for the development of the symbiosis. Second, it is important to determine whether C obtained by the fungus directly from the plant is used in the same way as C taken up from SOM and to what extent the fungus can use soil organic C in its metabolism. Third, it is not known whether the plant uses the fungus mainly to obtain more inorganic soil N or organic soil N. In summary, our

analysis indicates several gaps in the current understanding of plant–mycorrhizal symbiosis.

ACKNOWLEDGEMENTS

This work was partly funded by a ''Strong research environment grant'' from FORMAS (2011-1747) to PB and RH. We thank Björn Lindahl, the editor and anonymous reviewers for valuable comments on a previous version of the manuscript.

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