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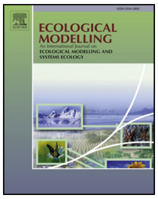

Why do forests respond differently to nitrogen deposition? A modelling approach

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ABSTRACT

Elevated reactive nitrogen deposition can result in declines in belowground C allocation to mycorrhiza, potentially threatening the sustainability of forest ecosystems, especially with regard to ongoing global environmental changes. Previous studies showed that the vulnerability of mycorrhiza differs in different forests. In this paper, we introduce a model that explains such differences as resulting from the optimization of belowground tree C investment in forests with inorganic or organic N economy. According to the model, the optimization of belowground tree C investment in forests with organic N economy is governed by indirect competition between trees for available forms of N. We predict decreasing C investment in mycorrhiza with N deposition in systems dominated by an organic N economy. In contrast, in forests with inorganic N economy the optimization of belowground tree C investment is governed by direct competition between trees for available forms of N. We show that C investment in mycorrhiza does not depend on N deposition in the case of inorganic N economy. Parameterizing the model with data from spruce and beech temperate forests, we show that spruce forests are more sensitive to N deposition with a decrease of tree investment in mycorrhiza, which seems to be consistent with empirical findings. As mycorrhizae are essential for nutrients and water acquisition in trees, we suggest our approach could contribute to predicting the responses of forests to global environmental changes.

1. Introduction

Nitrogen (N) is one of the key elements for plant growth and metabolism. Primary production used to be generally limited by N in most northern temperate and boreal forests (Tamm, 1991; Vitousek and Howarth, 1991), so nitrogen was historically the most common limiting nutrient for these forests. However, anthropogenic activities have led to a tenfold rise in nitrogen production compared with the late 19th century (Galloway et al., 2003). Transportation and intensive agriculture produce the majority of anthropogenic nitrogen leaking to the environment, mostly in simple inorganic forms (NO_x, NH_y), hereafter referred to as reactive N. Most forest ecosystems in the northern hemisphere are strongly affected by reactive nitrogen deposition (Bobbink and Hettelingh, 2010; de Vries et al., 2009; Galloway et al., 2003) with negative impacts on biodiversity (Riofrío-Dillon et al., 2017; Vitousek et al., 1997) and deep changes in forest soils due to the decline of fine root biomass, and changes in foliar chemistry and mycorrhiza (Bobbink and Hettelingh, 2010; Lupi et al., 2013; Novotný et al., 2016). Growth of both arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) has been shown to be suppressed by N fertilization in experiments and observational studies (Bahr et al., 2013; Högberg, 2006; van Diepen et al., 2010). However, the vulnerability of trees or forests to the deteriorative effects of reactive nitrogen deposition is variable (Boot et al., 2016; Carter et al., 2017; Rotter et al., 2017; Talbot et al., 2008) and is supposed to increase with N limitation (Bobbink and Hettelingh, 2010; Meunier et al., 2016). Despite significant progress in recent years, the mechanisms which cause different forest responses to deposition are still not fully described and understood. Following the plant economy theory (Bloom et al., 1985), plants should preferentially invest assimilated carbon to the structures that acquire the most limiting resources. This explains the reduction of the biomass of fine roots and mycorrhizae when some previously limited nutrient becomes easy available (Bloom et al., 1985; Johnson, 2010). Biological market theory predicts that the increased availability of limiting nutrient affects exchanges between mycorrhizal fungi and plants so that symbiosis turns into commensalism or parasitism (Konvalinková et al., 2017; Wyatt et al., 2014). However, recent studies emphasized the possible key role of the type of mycorrhizae

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(ectomycorrhiza — EM or arbuscular mycorrhiza - AM) and plant–-microbe interactions in ecosystem response to deposition (Carter et al., 2017; Dean et al., 2014). The vulnerability of mycorrhiza through excess reactive N input threatens forest resistance and functioning because the acquisition of important nutrients, such as N and P, as well as water uptake are mostly achieved through fine roots and their symbiotic interaction with mycorrhizae (Lindahl et al., 2007; Read and Perez-Moreno, 2003; Talbot et al., 2008). To the best of our knowledge, at the moment no theory relates C allocation from plants to mycorrhizal partners with plant N acquisition strategy and N mobility in soil. Here we develop such theory.

1.1. *Initial question and conceptual model*

We expect an increase in the impacts of reactive nitrogen deposition on temperate forests, as reactive nitrogen inputs are expected to remain high in the western hemisphere in the near future (Posch et al., 2015) and interactions with others stressors, such as drought and tropospheric ozone are likely (Carter et al., 2017). Despite the awareness of the importance of deposition on forest biodiversity and functioning, there are still many open questions about the mechanisms that underlie the effects of reactive nitrogen in various forests. The main question we ask in this paper is which processes cause various reactions of tree bellowground C investment to myccorhiza under reactive nitrogen deposition. We first construct a conceptual model to link the type of N economy in forests and competition among trees. Efforts to reach maximum competitive fitness in the given circumstances then determine the optimization of plant belowground investment. We show that optimal belowground investment predicts how forests react to reactive nitrogen deposition. To represent the difference between competition for mobile and immobile forms of soil nitrogen, we use the concepts of within- and between-cycle competition (Loreau, 1998) (Fig. 1). To translate our conceptual model (Fig. 1) in mathematical form, we first extend the classical Droop model (Droop, 1975, 1974) to include plants investment in mycorrhizae under different levels of reactive nitrogen deposition. We then parameterize our model for temperate spruce and beech forests. Finally, we discuss the results of our model in the context of empirical findings from the literature, type of mycorrhiza, biological market theory and plant C allocation strategies.

1.2. *Competition for N in forests with inorganic or organic nutrient economy*

The classification of forests on the basis of dominant mycorrhizal type into arbuscular mycorrhiza (AM) forests (with *Acer sp., Fraxinus sp. and Prunus sp.*) and ectomycorrhizal (EM) forests (with *Picea sp., Pinus sp.*) is of key importance with regard to N nutrient economy (Phillips et al., 2013; Lin et al., 2016). Higher concentrations of mineral forms of N (NH_4^+, NO_3^-) occur in AM forests. In addition, more freely living saprotrophic organims can be found in AM forests than in EM forests, and the net N mineralization and nitrification rates are higher (Phillips et al., 2013; Lin et al., 2016). It seems that for N uptake through mycorrhiza, inorganic forms of N are more important in AM forests and organic forms of N in EM forests.

The higher concentration of inorganic forms of N, characteristic for AM forests, is connected to the activity of freely living saprotrophic microorganisms (Lin et al., 2016). Because AM fungi have limited hydrolytic activity, they seek out primarily nitrogen released by freely living saprotrophic organims (Lindahl and Tunlid, 2015). At the same time, the absolute and relative uptake rates of inorganic N by AM trees was higher than by EM trees (Liese et al., 2017). Moreover, inorganic forms of N in AM soils are relatively mobile (Phillips et al., 2013). It is therefore usually thought that AM forests specialize in the uptake of inorganic forms, and in this context one can talk about an inorganic N economy (Phillips et al., 2013; Lin et al., 2016). In contrast, EM mobilize N straight from soil organic matter (SOM) through the production of extracellular enzymes, which makes EM trees less dependent on freely living saprotrophic organisms (Brzosek et al., 2015; Lindahl and Tunlid, 2015). EM fungi can take up such released organic forms of N, including those that do not dissolve well (Chen et al., 2016; Hobbie at al., 2012; Lin et al., 2016; Phillips et al., 2013). It is usually thought that the uptake of organic forms of N dominates in EM forests, therefore one can talk about an organic N economy (Phillips et al., 2013; Lin et al., 2016; Liese et al., 2017).

We think that the differences between inorganic and organic N economy, in the way mycorrhizal fungi are engaged in N uptake, are of key importance for understanding the sensitivity of decrease of

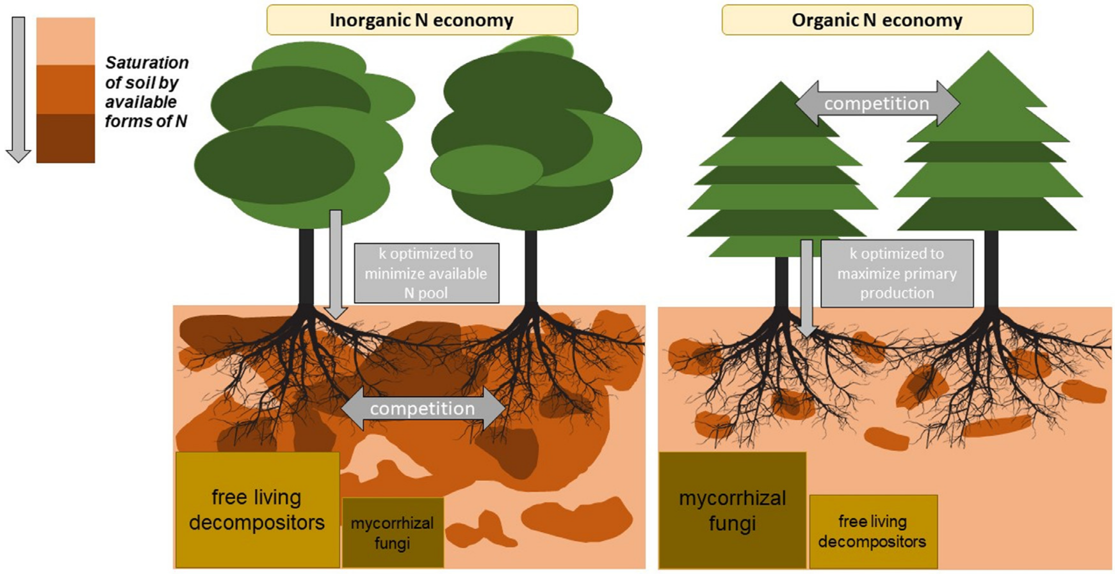

Fig. 1. The relationships between natural nitrogen mobility, tree investment to mycorrhizae and competition in Inorganic or Organic N economy. Left: inorganic and mobile forms of nitrogen prevail in the case of inorganic N economy, resulting in a relatively global pool of available nitrogen. Arbuscular mycorrhizal fungi support the uptake of inorganic forms of nitrogen. Right: in the case of organic N economy, nitrogen is mostly locked in less mobile organic matter, resulting in local available nitrogen pools. Trees acquire mainly dissolved organic forms of nitrogen released from organic matter by ectomycorrhizal fungi. Figure based on Loreau (1998), Phillips et al. (2013) and Soudzilovskaia et al. (2015).

bellowground C investment to mycorrhiza under reactive nitrogen deposition in various forests.

In AM forests, we assume that AM trees take up more mobile forms of inorganic N (Phillips et al., 2013). We suppose that in the soils of AM forests there exist relatively large numbers of areas where AM trees are in direct competition with other AM trees or microorganisims for mobile inorganic N. AM fungi function here as scavengers who seek out places with higher concentrations of inorganic N (Lin et al., 2016) (Fig. 1). In contrast, for EM species such patches are small and mainly connected to places of enzyme exudation by EM, where available forms of N are released. Such released organic forms of N are then absorbed by EM trees near the place of release. In other words, direct competition for released organic N between EM trees or EM trees and microorganisms is less likely. In view of the preferred forms of absorbed N, AM soils appear to be more homogeneous with larger areas of available inorganic forms, whereas EM environments are more heterogenous with smaller active areas of enzyme release and the subsequent absorption of organic forms of N.

For the analysis of plant strategies for belowground C investment during N uptake as a limiting factor, we used the model of within- and between-cycle competition introduced by Loreau (1998) (Fig. 1). Hereafter we will talk about available N, by which we mean all forms of nitrogen in the soil that plants can absorb even though mycorrhizal fungi act as mediators during this process.

The concepts of within- and between-cycle competition were introduced to predict the consequences of selection for different functional and demographic traits of organisms for the evolution of ecosystem properties (Loreau, 1998). Within-cycle competition describes competition between plants when the soil limiting nutrient is relatively mobile and hence the soil nutrient pool is more homogeneous. Under these conditions, trees compete for the limiting nutrient directly. The organism with the lowest steady-state nutrient level in soil (Na* in our model) eventually outcompetes all the others (R* rule, Tilman, 1982). Up to 80% of plant N and P is provided by mycorrhizal fungi (Van Der Heijden et al., 2015), and nutrition by these elements depends on plant belowground C investment. We therefore expect some level of belowground C investment to result in the lowest steady-state nutrient level, i.e. plant optimal strategy. We assume that this example describes competition between trees for inorganic forms of N in AM forests, and therefore that it corresponds to inorganic N economy (Fig. 2). In contrast, between-cycle competition occurs in spatially-structured environments, leading to a local pool of available form of limiting nutrient in the vicinity of plant roots (Fig. 1). In such a setting, trees do not compete for nutrient directly, and their competitive success is related to their ability to compete for space (Loreau, 1998). We assume that competition for space is realized within the life of each plant and also between generations. The colonization success of each plant strategy depends on its relative contribution to the plant population's seed pool. Seed production can depend on either plant biomass or plant net primary production (de Mazancourt et al., 2001). A positive correlation between primary production and seed production is likely in perennial plants (Mole, 1994). Therefore, under between-cycle competition, the tree species with the maximal steady-state primary production (*NPP** in our model) should eventually outcompete all others. The optimal level of belowground C investment from the perspective of plant strategy, is the one which maximizes primary productionin this example. We assume that this case describes EM forests with organic N economy (Fig. 2).

1.3. Hypotheses and objectives

Based on the literature, forests that are traditionally considered as strongly N limited should be more sensitive to reactive nitrogen deposition, including a decline in mycorrhizae (Bobbink and Hettelingh 2010; Meunier et al., 2016) probably due to restricted plant belowground investment (Bahr et al., 2013; Högberg et al., 2010). These forests belong to the organic N economy in connection with the dominance of EM fungi. In the conceptual model, belowground C investment in these forests is driven by between cycle competitions, i.e. indirect competition between trees for available forms of N. Therefore we hypothesize *that reactive nitrogen deposition influences belowground plant investment (C allocation) in mycorrhizae more strongly if the competition between trees for available forms of N is indirect (organic nutrient economy) rather than direct (inorganic nutrient economy).*

2. Model describtion

The Droop model was originally derived as a tool for describing the growth of a unicellular phytoplankton species with different internal concentrations of limiting nutrients (Droop, 1975, 1974). However, because of its simplicity, it has been widely used for a variety of other living systems, including terrestrial plants (Cherif and Loreau, 2010). We modified the Droop model to include the feedback between plant investments to mycorrhizae (term *k.C* in Eq. 1) in acquiring available nitrogen (limiting nutrient) and the internal concentration of nitrogen in living biomass:

$$\frac{dC}{dt} = \bar{\mu}_N \cdot \left(1 - \frac{q_{Nm}}{q_N}\right).\ C - m.\ C - k.\ C \tag{1}$$

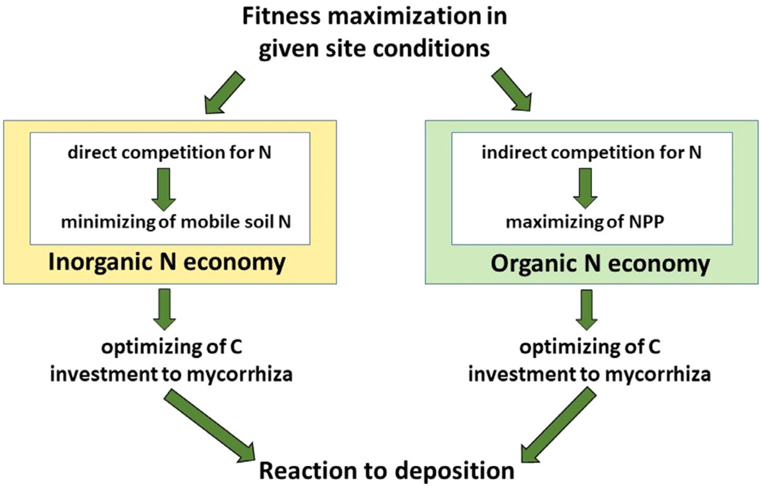

Fig. 2. Fitness maximization in a set of given environmental conditions and its relationship to the reaction of trees to reactive nitrogen deposition.

$$\boldsymbol{\frac{dq_N}{dt} = e_1.\, k.\, N_a \;-\; \bar{\mu}_N.\left(1 - \frac{q_{Nm}}{q_N}\right).\, q_N} \tag{2}$$

$$\boldsymbol{\frac{dN_a}{dt} = D_N + e_2.\, k.\, L_N + m_o.\, L_N - e_1.\, k.\, N_a\ .\ C} \tag{3}$$

The production of plant green biomass *C* increases with the quota of N (assumed to be the limiting nutrient) in green biomass q_N in relation to a minimal quota q_{Nm} (Eq.1). Green biomass is lost at a constant rate *m*, and plants invest part of their assimilated carbon at a constant rate *k* into N acquisition (Eq.1). For the purpose of our paper, we assume that plant investment is mainly received by mycorrhizal fungi, which improve N supply to plants through two mechanisms:

(1) an increase in the rate of N uptake by extending the active surface area of the root system due to its interconnection with the mycelium of mycorrhizal fungi, this mechanism corresponds with "scavenging" of nutrients by mycorrhizal fungi as described by Lambers et al. (2008);
(2) an increase in the available forms of N in the soil solution due to the enzymes released to the soil by mycorrhizal fungi, this mechanism corresponds with "mining" of nutrients by mycorrhizal fungi as described by Lambers et al. (2008) and others (e.g. Zak et al., 2019).

The efficiency of the first mechanism with regard to carbon investment is measured by the dimensionless coefficient e_1, and the efficiency of the second mechanism, by the dimensionless coefficient e_2. The change in the internal N quota q_N depends on the rate of N uptake by plants (through myccorhizae) and the consumption of N by growing biomass. The rate of N uptake is co-determined by the available N pool in the soil (N_a, Eq. 2). The change in the available N pool in soil (N_a) is determined by the rate of nitrogen deposition (D_N), the rate of available N release from the biodegradable pool of N in the soil (L_N) and the rate of N uptake. The rate of decay of the L_N is governed by two processes: the contribution of mycorrhizal fungi directly supported by plants (second term in Eq. 3) and the contribution of microorganisms living in the soil (third term in Eq. 3). Eqs. 1–3 thus link primary production, investment of primary producers in mycorrhizae and nitrogen deposition. All dynamical variables and parameters of the model are listed in Table 1.

3. General model analysis

3.1. Impact of nitrogen deposition on primary production

The equilibrium solutions of Eq 1–3 are shown in the Supporting Information (AE1–AE3). At equilibrium, net primary production can be expressed as:

$$\boldsymbol{NPP^* = \frac{(\bar{\mu}_N - m - k).\,(k.\ \ e_{N2}.\, L_N + m_0.\, L_N + D_N)}{\bar{\mu}_N.\, q_{Nm}}} \tag{4}$$

Eq. 4 shows that if other parameters are constant, then *NPP** increases linearly with the enhancement of decay efficiency e_2 or reactive nitrogen deposition D_N. In contrast, *NPP* first increases and then decreases with plant investment in mycorrhizal fungi *k* (further discussed in section 4.2).

3.2. Deposition decreases plant investment in mycorrhizae in forests with organic N economy

We assume (Section 2.2 and Fig. 1), that the competition between trees in forests with organic N economy should select for carbon allocation to mycorrhizae, k_{max}, that maximizes primary production. We find k_{max} by taking the derivative of Eq. 4 with respect to *k*, setting the derivative to zero and solving for k. We find:

$$k_{max} = \frac{((\bar{\mu}_N - m).\, e_2 - m_o).\, L_N - D_N}{2.\, e_2.\, L_N} \tag{5}$$

Eq. 5 shows that k_{max} is positive when the rate of nitrogen mineralisation m_o is very small. It declines as D_N increases, which means that higher deposition should lead to selection for lower values of plant investment in mycorrhizae. The value of *k* that maximizes *NPP* increases with the efficiency of N release from soil by myccorhizae e_2, especially when e_2 is small (Fig. 2, Supporting Information, AE 4).

The derivative of k_{max} with respect to D_N in Eq. 5 gives:

$$\frac{dk_{max}}{dD_N} = -\frac{1}{2.\, e_2.\, L_N} \tag{6}$$

Thus, k_{max} declines more steeply with reactive nitrogen deposition when the efficiency of releasing N from soil by myccorhizae e_2 is smaller. Thus mycorrhizae less effective in mining of N from forest soil should be more sensitive to the impact of reactive nitrogen deposition. In other words, if the system remains in a steady state, plants first reduce their investment in less effective mycorrhizal fungi in response to reactive nitrogen deposition. Eq. 6 also shows that reactive nitrogen deposition could cause the decline of mycorrhizal fungi especially if the biodegradable pool of N in soil is small.

3.3. Deposition does not affect investment in mycorrhizae in forests with inorganic N economy

We suppose that the competition between tress in inorganic N economy (Section 2 and Fig. 1) selects for carbon allocation to

Table 1
Dynamical variables and parameters of the model.

Dynamical variable	Description	Units
$\boldsymbol{C}$	green biomass (needles or leaves)	kg C ha^{-1}
$\boldsymbol{q_N}$	quota of N related to carbon in green biomass	kg of N per kg of carbon
$\boldsymbol{N_a}$	pool of available N in soil solution	kg of N ha^{-1}

Parameters	**Description**	**Units**
$\mathbf{q_{Nm}}$	minimal quota of N	kg of N per kg of carbon
$\boldsymbol{D_N}$	atmospheric deposition of N	kg of N ha^{-1} yr^{-1}
$\mathbf{L_N}$	biodegradable pool of N in soil (mostly in organic forms)	kg of N ha^{-1}
$\bar{\mu}_N$	maximal theoretical growth rate of green biomass	yr^{-1}
m	green biomass loss rate due to litterfall	yr^{-1}
k	carbon investment in belowground (roots and mycorrhiza), related to green biomass	yr^{-1}
$\mathbf{e_1}$	efficiency of plant investment to mycorrhizae for N uptake from soil solution	dimensionless
$\mathbf{e_2}$	efficiency of plant investment to mycorrhizae for releasing N from organic matter or mineral matter to soil solution	dimensionless
$\mathbf{m_o}$	rate of N release in available forms (related to L_N)	yr^{-1}

mycorrhizae k_{min}, which minimizes soil available N. To derive k_{min} we differentiate $N_a{}^*$ along k in AE 2 (Supporting Information) and find the minimum:

$$k_{min} = \sqrt{\bar{\mu}_N . m} - m \tag{7}$$

A positive value of k_{min} requires that the maximal growth rate is larger than the green biomass loss rate . Eq. 7 shows that reactive nitrogen deposition D_N would not influence optimal carbon allocation to mycorrhizae in a pure within cycle.

4. Impacts of reactive nitrogen in spruce and beech forests

4.1. Model parameterization

We argue that organic N economy is a good approximation for spruce forests. However, inorganic N economy is a less sufficient approximation for beech forests because of the connections between such forests and EM fungi (Phillips et al., 2013), even though other tree species — for example maples, with which AM fungi are connected, can also occur (Phillips et al., 2013). Nonetheless, in many important aspects beech forests are closer to forests with inorganic N economy than spruce forests with regard to N and C supply (Vesterdal et al., 2009; 2013), the concentration of inorganic forms of N and the speed of nitrification (Trum et al., 2011). We chose beech forests because we did not find appropriate data for parameterization from forests with dominant maple, linden or ash, which are closest to organic N economy in the temperate region. We estimated most parameters with data from long-term monitored spruce and beech forests in Europe (see Table S1 for spruce forests and Table S2 for beech forests in Appendix section).

The values of parameters k and e_2, which are included in Eq. 4–5 and 7, were not available from existing data. Carbon allocation to mycorrhizal fungi k is positively and linearly related to average annual belowground NPP (Hobbie, 2006). Therefore, we derived the value of k as the theoretical upper limit of plant carbon investment in mycorrhizae, which is equal to the overall plant investment in the belowground system for temperate spruce (0.36; fraction related to green biomass) and beech forests (0.2; fraction related to green biomass) according to Ågren and Andersson (2012). Although this theoretical upper limit is likely to overestimate real investment, Meyer et al. (2010) found that fungi can receive up to 25% of plant assimilates. Richardson et al. (2010) presented a wide range of 0.01–0.5 (fraction related to NPP) as tree C-allocation to fine roots.

The efficiency of N release to soil solution by myccorhizae e_2 was estimated from Eq. 4, using estimates of the other parameters and values of NPP from the literature (Ågren and Andersson, 2012). The resulting values of coefficient e_2 are probably underestimated because overestimated values of k (the upper limits of tree investment in mycorrhizae) were used to determine them. This could affect simulations in section 4.2, where we deal with the impact of nitrogen deposition on the optimal plant investment in mycorrhizae. However, a sensitivity analysis of k_{max} (k_{min} does not depend on e_2) with regards to e_2 (Fig. 3) shows that: i) an increase in e_2 ($e_2 = 0.25$ for spruce and 0.21 for beech) leads to only small changes in k_{max}, and ii) larger nitrogen deposition steepens the slope of k_{max} with e_2 as shown by Eq. 6. The sensitivity analysis revealed that the value of k_{max} determined using underestimated e_2 will be only slightly different from the estimate of k_{max} based on real (and to us unknown) e_2.

4.2. Simulations

We find that the relationship between NPP* and carbon allocation to mycorrhizae k differs in shape between spruce and beech forests (Fig. 4). Our model predicts a unimodal relationship in spruce forests, but a near-linear relationship in beech forests (Fig. 4). Both cases were simulated for ecologically relevant values of k according to Richardson et al. (2010). The derivative of NPP with respect to k (Supporting Information, AE 5) reveals that the shape of curves is determined by the value of the growth rate μ_N relative to the biomass loss rate (m), the rate of N mineralization (m_0) and k, such that larger values of μ_N lead to more linear shapes.

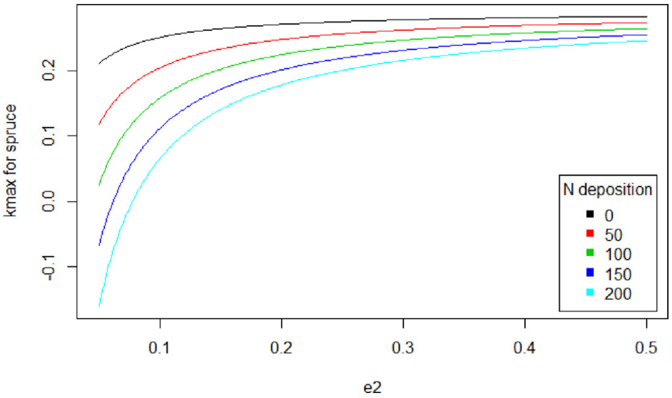

Fig. 3. Changes in relative optimal tree investment in mycorrhiza (related to NPP) as a function of the efficiency of releasing of N from soil by myccorhizae (e_2) in the case of between-cycle competition (spruce forests).

From Eq. 5 it follows that forests with organic N economy should be sensitive to reactive nitrogen deposition if k is optimized to maximize NPP*. In this case, plant investment in mycorrhizae declines with increasing D_N. In contrast, the k in forests under inorganic N economy is unaffected by D_N.

The relationship between k and reactive nitrogen deposition is presented in Fig. 4 for both forests (beech and spruce) and both competition types (between and within). If we take the values reported in the literature for belowground NPP (Ågren and Andersson, 2012) as the upper limits of plant investment in mycorrhizal fungi and express them as a fraction of NPP, we obtain 0.43 for coniferous forests and 0.06 for deciduous forests. Comparing these estimates with the lines for k_{max} or k_{min} obtained from simulations (Fig. 4), we conclude that our results are consistent with the assumption that spruce forests experience between-cycle competition and beech forests experience within-cycle competition.

5. Discussion

Net primary production increases with nitrogen deposition and mycorrhizal efficiency of releasing nitrogen to available form (e_2). In general, the relationship between net primary production and plant investment to mycorrhiza has a unimodal shape where net primary production achieves maximum values under intermediate values of plant investment. Model parameterization with long-term forest data shows such a unimodal curve for spruce forests, whereas NPP increases with plant investment in beech forests for the whole range of realistic values. The more linear shape of the curve is due to a higher difference between growth rate and green biomass loss.

In the following, we work with the two hypothesized scenarios for N economy (Fig. 1). The organic N economy occurs when nitrogen is prevalently locked in soil organic matter. We assume that in this case mycorrhizae are the key to locked N by releasing a variety of SOM-decaying enzymes and that most of the released available N is immediately captured by mycorrhiza and transported further to the roots. Direct competition for released nitrogen in soil solution is then marginal, and above ground competition for space plays a crucial role. Trees that maximize net primary production are expected to produce more seeds and be better competitors for space; investment to mycorrhiza should thus maximize net primary production. In this case, our model predicted that nitrogen deposition causes a decline in plant investment to mycorrhiza. This decline was steeper with low values of

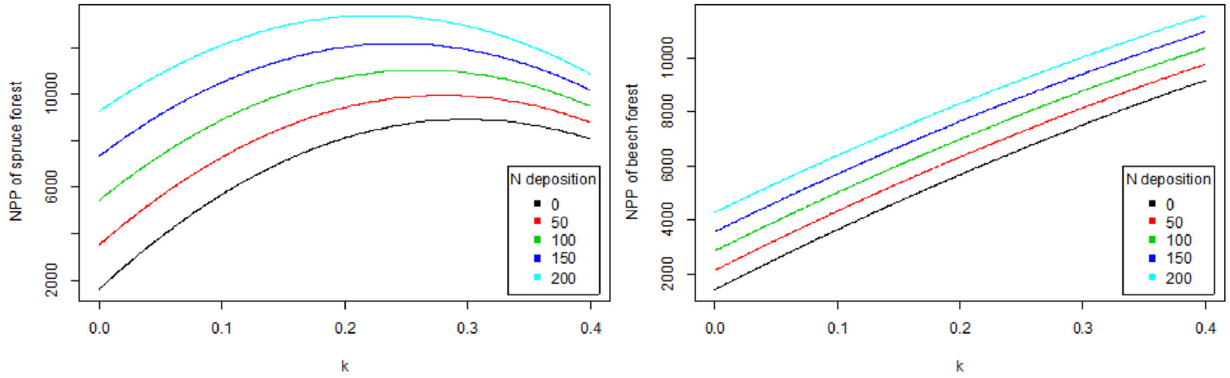

Fig. 4. Changes in NPP as a function of tree investment in mycorrhiza (k) in spruce and beech forests for different nitrogen deposition rates (D_n).

efficiency of N release to available form by mycorrhiza (e_2).

On the other hand, inorganic N economy corresponds to forests with significant concentrations of mobile forms of N. Free (non-symbiotic or non-directly symbiotic) living soil microorganisms contribute significantly to releasing N to available forms and mycorhizzae are crucial to support root uptake of these N forms by plants. Trees that minimize available pool of N in the soil should win competition in such environments, so that their investment to mycorrhiza should minimize the available pool of N in the soil, following the R*-rule (Tilman, 1982). Our model predicted that this optimal investment does not depend on nitrogen deposition.

5.1. Comparison of model results with empirical data in literature

We predict that reactive nitrogen deposition should cause a decline in plant investment to mycorrhiza in forests with organic N economy and the dominance of EM fungi, which is consistent with our hypothesis. EM tree species are able to take up organic as well as inorganic forms of N (Hawkins et al., 2015), but in colder temperate and boreal forests organic forms make up more than 50% of available N (Jones and Kielland 2002). This means that the uptake of organic forms of N dominates in forests with organic N economy. Forests with organic N economy usually react to an increase in inorganic forms with a decline in mycorrhiza. Inputs of inorganic forms of N at typical EM trees, such as spruce of pine, led to a decrease in the diversity and growth of mycelia EM fungi (Cox et al., 2010; Wallander et al., 2010). For Norway spruce *Picea abies* (L. H.Karst.), decreases in EM root tips abundance, mycelial growth, EM extramatrical mycelium and species richness were observed in connection with increased input of inorganic forms of nitrogen (Bahr et al., 2013; Kjøller et al. 2012; Nilsson and Wallander, 2003; Peter et al., 2001). This impairment can be explained as the result of the decrease in plant belowground C allocation. A drop of tree investment to soil biota was observed also in a fertilization experiment in a pine forest (Högberg et al., 2010). Recently, it has been emphasized that ectomycorrhiza of the conifers is more negatively affected by increasing N than ectomycorrhiza of broadleaf trees (Lilleskov et al., 2019; van der Linde et al., 2018). This is in line with our analysis, where coniferous forests are more close to organic N economy. Increasing carbon investment from trees into mycorrhiza would, even in the case of high N availability (when the increase in production along with a further rise in N in assimilation organs is minimal or zero), lead to a decrease in plant productivity in the case of organic N economy (Fig. 4). In view of competition settings (maximizing production with organic N economy), this would create a competitive disadvantage. An open issue is the possibility of increasing EM root tip abundance at certain EM tree species after adding organic forms of N (Avolio et al. 2009). This may be explained by the fact that organic forms of N contain C as well, which can be the source for the observed growth in EM tip abundance, i.e. this growth may not have to be supported by the plant. However, studies dealing with the reactions of mycorrhiza to increased input of organic forms of N in EM tree species, that is, for organic N economy, are still rare. A recent study by Clin et al. (2018) confirmed the decrease in species richness and changes in species composition of EM fungi after adding organic forms of N, which is consistent with the effects of adding inorganic forms of N.

Our model predicts that net primary production increases with nitrogen deposition (Eq. 4) in spite of reduced investment to mycorrhizae in case of organic N economy. However, mycorrhizae are indeed essential for the acquisition of other important nutrients, such as phosphorus, and for water uptake as well as for the immobilization of some risk elements (Brunner, 2001; Lindahl et al., 2007; Read and Perez-Moreno, 2003). We therefore expect further negative impacts of reduced belowground investment on net primary production in EM forests, which we did not directly consider in our approach. Some studies indeed demonstrated that AM trees react to higher availability of inorganic forms of N by increased growth. In contrast, in the case of EM trees higher availability of inorganic N led to various reactions including higher mortality. Recent studies demonstrated the switch from fertilization to damage effect of nitrogen deposition if a threshold was exceeded in both spruce forests and temperate beech forests (Braun et al., 2017). The deposition of more than 26 kg N ha^{-1} y^{-1} (beech) or 20–22 kg N ha^{-1} y^{-1} (spruce) was negatively correlated with tree basal area increment. Maximum growth was recorded in 1994 for beech and in 1985 for spruce in Baden-Württemberg (Meining et al., 2008). Higher drought sensitivity caused by nitrogen deposition was also proven, however, all these effects were co-determined by other factors connected with tree nutrition, such as foliar P and *K* content (Braun et al., 2017). Results suggest that the negative effects of nitrogen deposition stem from the decline of nutrients and water uptake, which could result from a decline in belowground investment.

Meining et al. (2008) showed that beech forests are also vulnerable to nitrogen deposition although to a lesser degree than spruce forests. As mentioned previously, we expect beech forests to be closer to inorganic N economy than spruce forests, but not perfect representatives, especially considering the dominance of EM fungi in most beech forests (depending on the other trees present).

Previous research confirmed that EM plants allocate more C than AM to their fungal partners (Soudzilovskaia et al., 2015), which is consistent with our results under the assumption that spruce forests are closer to organic N economy and beech forests are closer to inorganic N economy (Fig. 5). EM forests generally store more C in soil, with global consequences for carbon storage. The accumulation of C in forest soils seems to be significantly governed by EM with a clear correlation between EM and the amount of C stored in soil (Averill et al., 2014). This implies that the reduction of C investment to EM as described for organic N economy could negatively influence global soil carbon storage.

5.2. Comparison of our results with the biological market theory approach

Plant growth and resource use has been traditionally analysed by

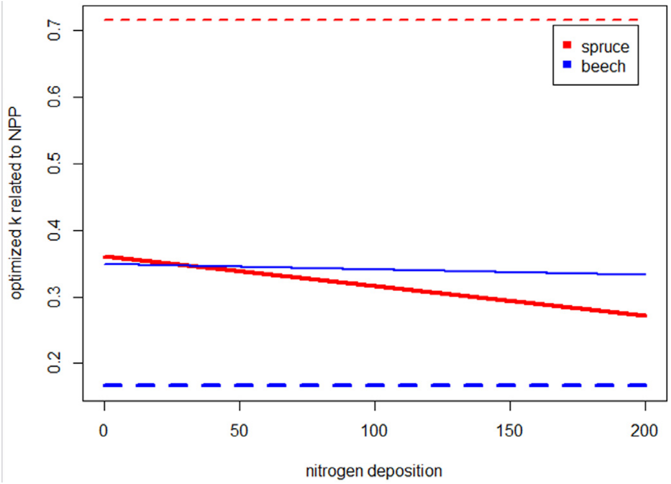

Fig. 5. Changes in optimal tree investment in mycorrhizae with increasing reactive nitrogen deposition. Dashed lines correspond to optimization of k under within-cycle competition (k_{min}); solid lines correspond to optimization of k under between-cycles competition (k_{max}). Blue colour stands for beech forests, red colour for spruce forests. The values of k_{min} are not affected by D_N. The most likely scenarios are highlighted by thicker lines.

economic theory, which assumes that plants should preferentially allocate C to such structures that acquire the resource which limits plant growth the most (Bloom et al., 1985; Johnson, 2010). The efforts of plants to eliminate limits to growth are equivalent with the idea of the maximization of growth. We showed that maximization of growth could be a favourable competition strategy only in forests with organic N economy and that a more homogenous distribution and higher mobility of the limiting nutrient in soil could lead to direct competition for the limiting nutrient in soil (Tilman, 1982), as described in inorganic N economy. The other approach which uses the economical analogy for the explanation of the principles of C allocation to MF and partner discrimination is biological market theory (Wyatt et al., 2014). This theory shows that under high availability of the limiting nutrient, the trade between the plant and its symbiotic partner may cease. Plants aim to maintain the best price for the limiting nutrient, which means lowest acquiring/C invested ratio, and thus select for the most efficient fungal partner (Werner and Kiers, 2015; Wyatt et al., 2014). In the terms of our model, the trees allocate C preferentially to partners with the highest e_2 (Fig. 2). Our model was not designed to compare investment in partners differing in efficiency. Eq. 5 of our model predicts a drop in plant C allocation to MF with a decrease in e_2 under between-cycle competition. Moreover, this drop is more pronounced under increasing nitrogen deposition (Fig. 2). This seems be consistent with the findings of biological market theory that higher availability of the limiting nutrient may destroy the biological market. In fact, it was demonstrated that trees and fungi usually have more partners in mycorrhizal cooperation (Kennedy, 2010; Bücking et al., 2016). Franklin et al. (2014) work with this multiple-partner structure of EM symbiosis. In their model each fungus and plant is allowed to individually adjust its strategy in terms of internal C-N allocation in trading with its multiple symbiotic partners. This model system was subsequently analysed along a gradient of increasing available soil N focusing on EM forests, which corresponds to deposition by reactive nitrogen in forests with organic N economy (indirect competition for available N). To compare the results based on the analysis of our model with the multiple symbiotic partners' model, we assume that EM production is an increasing function of k. The multiple symbiotic partners model, like our model, predicts a decrease in EM production with increasing available reactive N. However, this only happens once a certain concentration of reactive N is reached. Until that point EM production shows a growing tendency (Franklin et al., 2014). However, the multiple symbiotic model uses absolute values of EM production, while in our model plant investment into mycorrhizal fungi is expressed as a fraction of NPP. The multiple symbiotic partners model is more complex because it includes more partners into establishing the flow of C from plant to fungus. It uses maximization of production as the criterion of plants for maximizing their own fitness. Our model describes the overall plant investment of C into mycorrhizal fungi. On the other hand, the advantage of our model is that in spite of its simplicity it includes feedback between the amount of invested C and received N, which is furthermore influenced by the current availability of N. Our model also makes a difference between two strategies trees use to maximize their own fitness in connection with the characteristics of the pedoenvironment (organic or inorganic N economy).

6. Conclusions

Although simple, our model explains different responses of forests to reactive nitrogen deposition in belowground investment of trees to mycorrhizal fungi, crucial for forest sustainability. Our input assumption was that some differences in natural soil N cycle (relative importance of inorganic or organic forms of N for plant N uptake), as previously described in forests with organic or inorganic soil economy, are closely associated with the way trees compete. This competition is decisive for the optimization of plant belowground investment into mycorhizal fungi and thus also for the reaction of ecosystems to N deposition. Consistently with empirical findings, we find that forests with organic N economy (e.g. spruce forests) are more sensitive in that N deposition should reduce tree investment in mycorrhizal fungi. Our approach offers a simple framework to link the type of N economy in soils, competition among trees and optimal investment to mycorrhizal fungi. Further research is necessary to extend our knowledge about the role of phosphorus, mycorrhizal networks transporting nutrients between trees or functional shifts in mycorrhizal community in response of forests to reactive nitrogen deposition.

Data Accessibility

All used data (for estimates the values of model parametrs in simulations) are available in published articles and books stated in References and Supporting Information. No other data were used for this article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109034.

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