# A Model for Optimal Mycorrhizal Colonization along Altitudinal Gradients

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Mycorrhizal associations are generally favourable for vascular plants in nutrient-poor conditions. Still, non-mycorrhizal plants are common in high arctic and alpine areas, which are often poor in nitrogen and phosphorus. The relative proportion of mycorrhizal plants has been found to decrease along with increasing altitude, suggesting that the advantage of the mycorrhizal symbiosis may change along an altitudinal gradient. This may be related to the environmental factors that possibly constrain the amount of photosynthesized carbon to be shared with mycorrhizal fungi. We propose a simple optimization model for root colonization by fungal symbionts and analyze the advantages of mycorrhizas in relation to the nutrient use efficiency of photosynthesis (PNUE), the kinetics of nutrient uptake and the soil nutrient levels. Our model suggests that mycorrhizas are not usually favoured at low PNUE values. At low nutrient levels, mycorrhizas may be advantageous if they have a lower threshold concentration of nutrient uptake ($x_{min}$) compared to non-mycorrhizal roots. If mycorrhizal roots have a higher maximum capacity of nutrient uptake ($V_{max}$), mycorrhizas can be favourable for the host plant even at relatively low nutrient concentrations and at relatively low PNUE. Consequently, the possible patterns along altitudinal gradients essentially depend on PNUE. If the soil nutrient concentration is constant and PNUE decreases, the advantage of mycorrhizal symbiosis declines independently of the nutrient uptake kinetics. If PNUE remains constant and the soil nutrient concentration decreases along with increasing altitude, the emerging colonization pattern (either increasing, decreasing or intermediate) depends on the nutrient uptake kinetics. Additionally, if both PNUE and the soil nutrient concentration decrease, several patterns may emerge, depending on the nutrient uptake kinetics.

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## List of symbols

$R$ = total number of roots

$p$ = proportion of roots colonized by mycorrhizal fungi

$N_{nm}$ = nutrient uptake rate by non-mycorrhizal roots

$N_m$ = nutrient uptake rate by mycorrhizal roots

$C_{nm}$ = carbon cost of non-mycorrhizal roots

$C_m$ = carbon cost of mycorrhizal roots

$\alpha$ = nutrient use efficiency of photosynthesis (PNUE)

$N_i$ = nutrient uptake rate of non-mycorrhizal (i = nm) or mycorrhizal (i = m) roots

$x$ = external mineral nutrient concentration

$x_{min}$ = minimum value of $x$ leading to zero net uptake

$V_{max}$ = maximum nutrient uptake capacity of a root

$K_m$ = half-saturation constant

# 1 Introduction

Mycorrhizas benefit vascular plants because symbiotic fungi increase the absorption surface of roots and offer to their host plants better access to soil mineral nutrients (Koide 1991). Some mycorrhizal fungi are also able to utilize the soil organic nitrogen and phosphorus pools (Mitchell and Read 1981, Northup et al. 1995, Näsholm et al. 1998, Joner and Johansen 2000, Koide and Kabir 2000), even though there may be differences between mycorrhizal types. However, mycorrhizas also imply a considerable cost to the host plant, as mycorrhizal roots may consume a 2.5-fold amount of host carbon compared to non-mycorrhizal roots (Jones et al. 1991). The dependency on symbiosis varies between the taxonomic groups of both plants and fungi. Of the main mycorrhizal types, plants that form ecto- or ericoid mycorrhizas are more or less dependent on symbiosis and, hence, heavily mycorrhizal in natural conditions (Newman and Reddell 1987). Plants that form arbuscular mycorrhiza (AM) are often less dependent on their fungal symbionts and may perform well even without symbiotic fungi (Trappe 1987).

Because of their high nutrient uptake capacity due to the increased absorption surface and possible enzyme activity (Smith and Read 1997), mycorrhizas should be especially advantageous for vascular plants in nutrient-poor conditions.

However, certain relatively infertile habitats are distinctly colonized by non-mycorrhizal plants, including saline soils (Allen et al. 1989), ruderal landscapes (Allen 1989) and arcto-alpine areas (Gardes and Dahlberg 1996, Smith and Read 1997). There are observations to suggest that genera normally associated with AM are often non-mycorrhizal in high arctic (Bledsoe et al. 1990, Kohn and Stasovski 1990, Väre et al. 1992), antarctic (Christie and Nicolson 1983) and high alpine areas (Haselwandter and Read 1980, Read and Haselwandter 1981). The relative coverage of mycorrhizal plant species decreases (Väre et al. 1997) and the levels of mycorrhizal infection possibly also decrease with increasing altitude (Haselwandter 1979, Haselwandter and Read 1980, Väre et al. 1997). Haselwandter (1979) and Väre at al. (1997) both discussed the possibility that this might be due to the reduced photosynthetic production and decreased supply of carbon to the fungal symbiont. Along altitudinal and latitudinal gradients, the dominant mycorrhizal types also change with the vegetation types, which are both apparently determined by climatic conditions and soil composition, e.g. organic matter accumulation (Read 1984), but in the high alpine zone, mycorrhizal infections are rare and slight (Read and Haselwandter 1981, Smith and Read 1997). Additionally, herbaceous plants native to high altitudes have higher root/ shoot ratios compared to low-altitude plants,

which has been proposed to indicate a functional replacement of mycorrhizas (Körner and Renhardt 1987). These observations suggest that 1) the advantage of mycorrhizal symbiosis changes along an altitudinal gradient, and 2) this pattern may be related to environmental constraints, e.g. mean temperature and soil nutrient levels, which change along the gradient.

Consequently, a possible approach for studying the advantages or, alternatively, disadvantages of mycorrhizal associations is to analyze how the mineral nutrient use efficiency of photosynthesis, the varying soil nutrient concentration and the nutrient uptake kinetics of the roots may influence the benefits of mycorrhizal symbiosis for the host plant. For this purpose, we will present a simple model where the benefit of mycorrhizas is proportional to the net carbon gain of the host plant. From the model, we will deduce how optimal colonization of roots by mycorrhizal fungi may change along environmental gradients and, finally, discuss the predicted patterns specifically in relation to altitudinal gradients.

## 2 Benefits and Costs of Mycorrhizas for the Host Plant

We assume a root system with $R$ roots, of which fraction $p$ are mycorrhizal and $1-p$ non-mycorrhizal. 'Root' is here defined as a nutrient-absorbing root unit, and the word could be replaced by such terms as short root, fine root or rootlet. The average nutrient gain per unit time by a non-mycorrhizal root is $N_{nm}$ and by a mycorrhizal one $N_m$, where $N_m > N_{nm}$, and $C_m$ is the average carbon demand of a mycorrhizal root per unit time and $C_{nm}$ that of a non-mycorrhizal root ($C_m > C_{nm}$). Thus, the mycorrhizal root is assumed to have a higher nutrient gain, mainly due to the increased absorption surface, and for the same reason, it is assumed to consume more carbon. The net carbon gain of a plant with a fraction of $p$ mycorrhizal roots is defined as

$$C(p) = \alpha R(p\, N_m + (1-p)\, N_{nm}) \\ - R\,(p\, C_m + (1-p)\, C_{nm}) \qquad (1)$$

where $\alpha$ is the nutrient use efficiency of photosynthesis (PNUE) (Kanazawa 1985, Larcher 1995), $N(p) = R(p\, N_m + (1-p)\, N_{nm})$ is the total nutrient gain of the whole plant, and the last term $R\,(p\, C_m + (1-p)\, C_{nm})$ represents the carbon loss to the root system (Tuomi et al. 2001).

The two main terms on the right-hand side of Eq. 1, i.e. gross carbon gain and carbon cost of the root system, are linear functions of $p$. If mycorrhizal roots are more effective in nutrient absorption, i.e. $N_m > N_{nm}$, but have a greater carbon demand, i.e. $C_m > C_{nm}$, the net carbon gain, $C$, will increase with $p$ for

$$\alpha > (C_m - C_{nm})/(N_m - N_{nm}) \qquad (2)$$

If $\alpha$ assumes smaller values, $C$ will decrease as a function of p. In other words, in terms of the net carbon gain, the nutrient use efficiency of photosynthesis determines whether a mycorrhizal condition ($p=1$) or a completely non-mycorrhizal condition ($p=0$) would be most economical for the carbon balance of the plant (see also Fitter 1991, Tuomi et al. 2001).

We used the kinetics of nutrient uptake at different soil nutrient concentrations to determine the nutritional benefits, i.e. $N_m > N_{nm}$, that the plant obtains from mycorrhizal associations. Nutrient uptake as a function of the external concentrations of mineral nutrients is often presented in terms of the Michaelis-Menten kinetics:

$$N_i = \frac{V_{max}\,(x - x_{min})}{K_m + (x - x_{min})} \qquad (3)$$

where $N_i$ = uptake rate of non-mycorrhizal (i = nm) or mycorrhizal (i = m) roots, $V_{max}$ = maximum uptake capacity of a root, $x$ = external mineral nutrient concentration, $x_{min}$ = minimum value of $x$ leading to zero net uptake, and $K_m$ = half-saturation constant (e.g. Marschner 1995). There are several ways in which this function may explain our assumption of the higher nutrient uptake of mycorrhizal compared to non-mycorrhizal roots, i.e. that $N_m > N_{nm}$: i) mycorrhizal roots may have a lower threshold value ($x_{min}$) below which uptake ceases (Mosse et al. 1973, Bougher et al. 1990), ii) they may have a higher maximum absorbing capacity, $V_{max}$ (Cress et al. 1979, Plassard et al.

1994, Eltorp and Marschner 1996), or iii) they may have a higher affinity of uptake (lower $K_m$), leading to more effective absorption from the low concentrations in the soil solution (Cress et al. 1979, Thomson et al. 1986). When these possibilities are studied in the present model by replacing the $N_m$ and $N_{nm}$ obtained from Eq. 3 in the condition 2, we get three cases indicating how the advantage of mycorrhizal symbiosis may change along a gradient of the external availability ($x$) of mineral nutrients in the soil (Fig. 1A–C).

Fig. 1. indicates the parameter areas of $\alpha$ and $x$ where selection is expected to favour mycorrhizal plants ($p=1$) or, alternatively, non-mycorrhizal plants ($p=0$). These theoretical results can be used to deduce how the mycorrhizal status of plants may change along environmental gradients when the nutrient use efficiency and the soil nutrient concentration change along the gradient (Table 1). To deduce this, we assumed that mycorrhizal roots consume 20% more carbon than non-mycorrhizal roots (Smith and Read 1997), defined as root respiration/time ($C_{nm}=2.5$ and $C_m=3$ mmol $CO_2$ g root dwt$^{-1}$ d$^{-1}$; Nielsen et al. 1998). For non-mycorrhizal plants, we used the following kinetic parameters in the Michaelis-Menten equation: $x_{min}=1.5$ µmol, $V_{max}=32$ µmol P g root dwt$^{-1}$ d$^{-1}$, and $K_m=2.5$ µmol. For mycorrhizal plants, the following values were used: $x_{min}=0.5$ µmol (Fig. 1A), $V_{max}=97$ µmol P g root dwt$^{-1}$ d$^{-1}$(Fig. 1B), and $K_m=1.6$ µmol (Fig. 1C). The soil phosphate concentration axis reaches up to 10 µmol (Larcher 1995, Marschner 1995, Nielsen et al. 1998), and $\alpha$ was defined as the carbon fixed/phosphorus absorbed (mmol $CO_2$ g shoot dwt$^{-1}$/µmol P g root dwt$^{-1}$). All these parameter values were calculated on the basis of Nielsen et al. (1998) by using the average parameter values of *Phaseolus vulgaris* at the 28th growth date. The results are presented for a nutrient use efficiency ($\alpha$) gradient and a soil phosphate concentration gradient, where the minimum of the phosphate ($x$) axis is set to 1.5 µmol, and we hence compare mycorrhizal and non-mycorrhizal plants only for positive nutrient uptake rates (Fig. 1). Note further that in Eq. (3) $K_m$ is defined in relation to $x_{min}$, and hence the plant with lower $x_{min}$ actually achieves 1/2 $V_{max}$ at lower $x$-value.

These parameter values are used for scaling
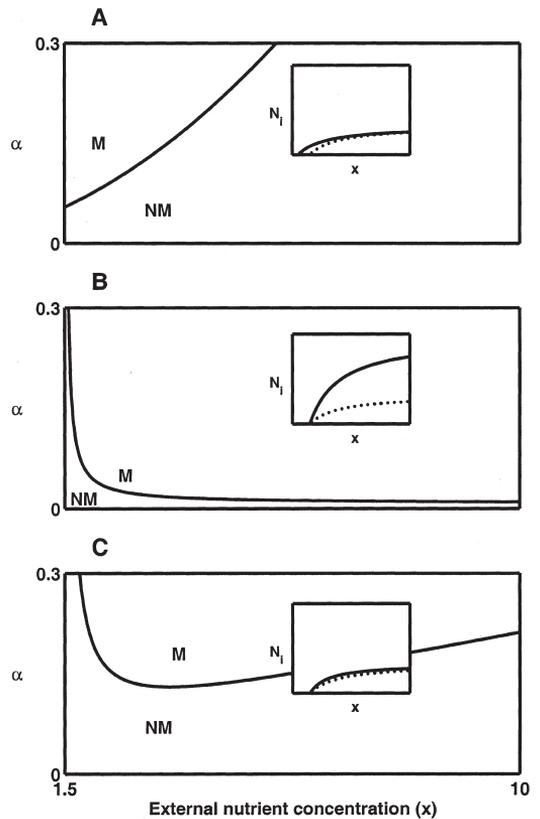


**Fig. 1.** Parameter areas where plants are predicted to be mycorrhizal (M) or non-mycorrhizal (NM). A. Mycorrhizal roots have a lower threshold of external nutrient concentrations for nutrient uptake (lower $x_{min}$), B. mycorrhizal roots have a higher maximum capacity of nutrient uptake at high external nutrient concentrations (higher $V_{max}$), and C. mycorrhizal roots are better absorbers at low external nutrient concentrations (i.e. have lower half-saturation constants of nutrient uptake, $K_m$). $\alpha$=mineral nutrient use efficiency of photosynthesis (mmol $CO_2$ g shoot dwt$^{-1}$/µmol P g root dwt$^{-1}$), $x$=external nutrient concentration (µmol). The small figures in the boxes show the differences in the Michaelis-Menten nutrient uptake curves in each case ($N_i$=nutrient uptake rate) as a function of the external nutrient concentration ($x$). Solid line=mycorrhizal plants, dotted line=non-mycorrhizal plants.

purposes, but they do not affect the major qualitative patterns concerning the relative advantages or, alternatively, disadvantages of mycorrhizal plants as compared to non-mycorrhizal plants. Note further that we have scaled the key parameters on the basis of a laboratory study of an AM plant species (Nielsen et al. 1998), which is why the relevant range of the $\alpha$ axis, for example, might be different in natural conditions and in the presence of different soil nutrients (however, see further discussion). Though the findings of Nielsen et al. (1998) constitute a limited basis for parameterization, the advantage of using only them was that they provided us sufficiently detailed data for calculations. Most papers dealing with the carbon economy of mycorrhizal plants do not present adequate information for this purpose, and parameterization on the basis of several data sets was thus found unsatisfactory. Additionally, the advantage of parameterization on the basis of AM is that it probably does not overestimate the carbon cost because ectomycorrhizal plants, for example, may be many times more costly than AM plants (e.g. Jones et al. 1991, Smith and Read 1997). Moreover, phosphate was chosen as the study nutrient because its transfer is especially important in AM symbiosis (Smith and Read 1997) and because most papers on nutrient uptake kinetics also deal with phosphate uptake (Mosse et al. 1973, Cress et al. 1979, Thomson et al. 1986, Bougher et al. 1990). However, the main patterns and conclusions drawn from the present theoretical analysis should hold for any mineral nutrient that limits the carbon economy of mycorrhizal and non-mycorrhizal plants along environmental gradients.

# 3 Optimal Root Colonization along Environmental Gradients

## 3.1 Effects of Uptake Kinetics

If the nutrient uptakes of mycorrhizal and non-mycorrhizal roots differ in one of the Michaelis-Menten parameters ($x_{min}$, $K_m$ or $V_{max}$), the nutrient uptake of mycorrhizal roots will be more efficient for the studied range of soil nutrient concentrations (see nutrient uptake curves in Figs. 1A–C). However, because the relative benefit in terms of acquired nutrients varies along the soil nutrient levels, differences in the parameters of nutrient uptake kinetics yield several patterns in relation to $\alpha$ values and soil nutrient concentrations which favour mycorrhizal or, alternatively, non-mycorrhizal plants (Figs. 1A–C).

If mycorrhizal roots have a lower minimum threshold value ($x_{min}$), the difference in nutrient uptake between mycorrhizal and non-mycorrhizal roots is most conspicuous under conditions of low nutrient availability (Fig. 1A). Hence, mycorrhizal symbiosis is favoured at low soil nutrient concentrations, provided that $\alpha$ is high enough, while at higher nutrient concentrations only the non-mycorrhizal strategy prevails. If mycorrhizal roots have a higher maximum absorbing capacity ($V_{max}$) than non-mycorrhizal roots at high soil nutrient concentrations, the difference in nutrient uptake capacity between mycorrhizal and non-mycorrhizal roots increases as soil fertility increases (Fig. 1B). Consequently, a very high $\alpha$ is required for mycorrhizal symbiosis to take place in poor soils, but as the nutrient concentration increases, the advantage of mycorrhizas increases quite steeply. At sufficiently low $\alpha$ values, only the non-mycorrhizal strategy is favoured. If mycorrhizal roots have a higher affinity of uptake, leading to a lower half-saturation constant ($K_m$), the difference in nutrient uptake between mycorrhizal and non-mycorrhizal plants is largest at intermediate availability of mineral nutrients and the difference decreases towards both poor and rich soils (Fig. 1C). Thus, mycorrhizal symbiosis is favoured at intermediate nutrient concentrations and at relatively high values of $\alpha$.

## 3.2 Predicted Patterns along Environmental Gradients

In Table 1, we present possible deduced patterns of mycorrhizal colonization along an environmental gradient 1) when the nutrient use efficiency of photosynthesis ($\alpha$) decreases but the external nutrient concentrations remain constant, and 2) when $\alpha$ changes and the soil nutrient con-

**Table 1.** Different patterns of mycorrhizal symbiosis in relation to the kinetics of nutrient uptake and mineral nutrient use efficiency of photosynthesis ($\alpha$). The patterns of mycorrhizal colonization along the environmental gradient refer to the patterns depicted in Fig. 2: A. M → NM, B. NM → M, and C. NM → M → NM. These patterns have been deduced from Fig. 1A–C depicting situations where $\alpha$ and/or soil nutrient availability change along the gradient and mycorrhizal plants (M) differ in the kinetics of nutrient uptake from non-mycorrhizal plants (NM): $x_{min}$ = minimum soil nutrient-level for zero net nutrient uptake, $V_{max}$ = maximum nutrient uptake capacity, and $K_m$ = half-saturation constant.

|  | Change in $\alpha$ along the gradient | Pattern of mycorrhizal colonization along the gradient |
|---|---|---|
| 1. Soil nutrient-level constant along the gradient | - | A |
| 2. Soil nutrient-level decreases along the gradient | | |
| i) $x_{min}$ lower among mycorrhizal plants | - | A, B |
| | 0 | B |
| | + | B |
| ii) $V_{max}$ higher among mycorrhizal plants | - | A |
| | 0 | A |
| | + | B, C |
| iii) $K_m$ lower among mycorrhizal plants | - | A, C |
| | 0 | A, B, C |
| | + | B, C |

centration decreases along the gradient. The patterns have been deduced from Fig. 1 for different cases of nutrient uptake kinetics.

If the external nutrient levels remain constant (1), the kinetics does not affect colonization patterns because the advantage of mycorrhizas consistently decreases with decreasing $\alpha$ (Fig. 1A–C). As a consequence, mycorrhizal plants should prevail in the lower parts of the environmental gradient and non-mycorrhizal plants in the upper parts (Fig. 2A) when $\alpha$ decreases along the gradient but the nutrient levels remain constant. In the latter case with decreasing soil nutrient levels (2), however, kinetics is relevant, and a number of patterns of mycorrhizal colonization are possible (Table 1, Fig. 2A–C). Below these, three possibilities are treated separately:

i) Mycorrhizal roots have lower minimum threshold values of nutrient uptake (i.e. lower $x_{min}$). If mycorrhizal roots can absorb nutrients from lower concentrations than non-mycorrhizal roots, mycorrhizas may be favoured in poor soils, but only in the presence of sufficiently high $\alpha$ (Fig. 1A). If the soil nutrient concentration decreases along the environmental gradient, the pattern can be from a non-mycorrhizal to a mycorrhizal state (Table 1, Fig. 2B) or from a mycorrhizal to a non-mycorrhizal state if the soil nutrient concentration is also relatively low at high $\alpha$ values and if $\alpha$ decreases steeply with slightly decreasing nutrients (Table 1, Fig. 2A). If $\alpha$ remains constant or increases with decreasing nutrients, the patterns along such gradients change from non-mycorrhizal to mycorrhizal states (Table 1, Fig. 2B).

ii) Mycorrhizal roots have a higher maximum capacity of nutrient uptake (i.e. higher $V_{max}$). If mycorrhizal roots have a higher maximum capacity of nutrient uptake, very high $\alpha$ is required to favour mycorrhizas in extremely nutrient-poor conditions, but as the soil nutrient levels increase, mycorrhizal symbiosis is favoured even at relatively low values of $\alpha$ (Fig. 1B). If $\alpha$ decreases or remains constant at a declining soil nutrient concentration along the gradient, mycorrhizas are favoured in

A

B

C

Environmental gradient
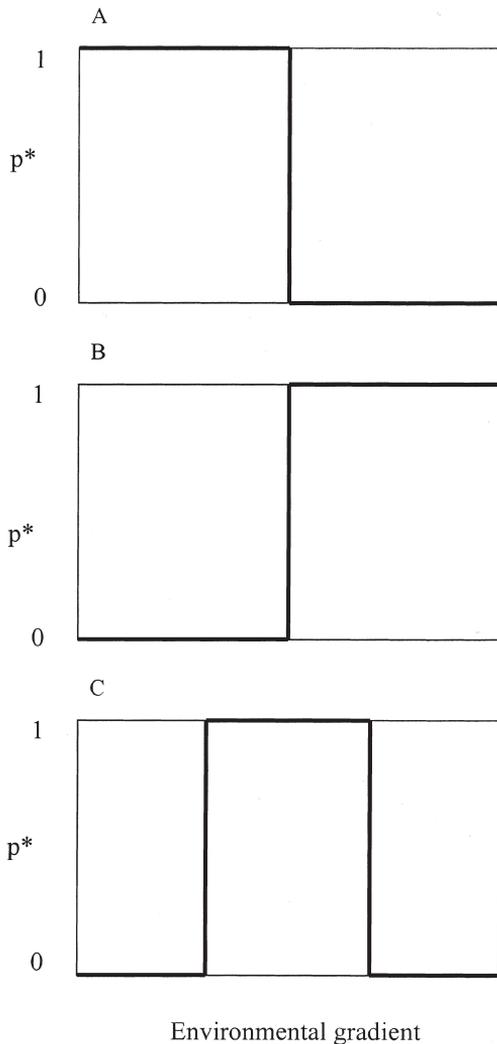
**Fig. 2.** Three patterns of optimal mycorrhizal colonization ($p^*$) along an environmental gradient. Mycorrhizas ($p = 1$) are favoured in the lower (A), higher (B) and middle (C) parts of the gradient. In Table 1, these patterns are related to possible changes in the mineral nutrient use efficiency of photosynthesis and in external nutrient concentrations along the gradient.

the lower parts of the gradient but not in the upper parts (Table 1, Fig. 2A). In contrast, if $\alpha$ increases with decreasing external nutrient concentrations, a reverse pattern (Table 1, Fig. 2B) is obtained or, alternatively, an intermediate pattern is possible

(Table 1, Fig. 2C).

iii) Mycorrhizal roots have a lower half-saturation constant (i.e. lower $K_m$). When mycorrhizal roots have a lower half-saturation constant, mycorrhizas are favoured at intermediate soil nutrient concentrations, but only at relatively high $\alpha$ values (Fig. 1C). With decreasing soil nutrients along an environmental gradient, several patterns may emerge. Constant or decreasing $\alpha$ either leads to a change from a mycorrhizal to non-mycorrhizal condition (Table 1, Fig. 2A) or results in an intermediate pattern (Table 1, Fig. 2C). Increasing $\alpha$ along declining soil nutrient levels leads to a change from a non-mycorrhizal to a mycorrhizal condition along the gradient (Table 1, Fig. 2B) or possibly results in an intermediate pattern (Table 1, Fig. 2C).

Consequently, the advantage of mycorrhizal symbiosis for the host plant may vary considerably along gradients of decreasing soil nutrient levels, depending on the kinetics of nutrient uptake and the covariation between photosynthetic nutrient use efficiency and soil nutrient concentrations along the gradient.

# 4  Discussion

## 4.1  Kinetics of Nutrient Uptake

Nutrient uptake is a similar process in mycorrhizal and non-mycorrhizal roots in the sense that both absorb nutrients from soil solution, and uptake is a selective, energy-demanding process through cell membranes (Smith and Read 1997). Mycorrhizal symbiosis increases the absorption surface of the root, which allows mycorrhizal plants better access to soil nutrients (Koide 1991). In the case of relatively immobile nutrients, e.g. phosphate, the main limitation of nutrient acquisition is the diffusion of nutrient molecules from soil (Bolan 1991), and the increased absorption surface provided by fungal hyphae can thus be especially important.

However, nutrient uptake kinetics may still influence the relative benefit of mycorrhizas along nutrient availability gradients. As nutrient uptake occurs through the binding sites of the root or fungal membranes, the nutrient uptake rate may

be affected by 1) the affinity of the binding sites to nutrients and 2) the number of binding sites. At low nutrient concentrations, affinity is crucial, and high affinity may lead to a lower half-saturation constant ($K_m$) or a lower threshold concentration of nutrient uptake ($x_{min}$). At high nutrient concentrations, the number of binding sites becomes important and determines the maximum nutrient uptake capacity ($V_{max}$) (Marschner 1995). Additionally, mycorrhizal roots may be more efficient in exploring the soil because a mycorrhizal root with a large hyphal network is more likely to capture nutrient ions in nutrient-poor soil than a non-mycorrhizal root. This may, consequently, yield lower $x_{min}$ or $K_m$ for mycorrhizal roots.

We analyzed three theoretical possibilities of how nutrient uptake kinetics might differ between mycorrhizal and non-mycorrhizal plants. Both a lower half-saturation constant ($K_m$) (Cress et al. 1979, Plassard et al. 1994, see also Thomson et al. 1986, Bougher et al. 1990) and a higher maximum absorption capacity ($V_{max}$) (Cress et al. 1979, Plassard et al. 1994, Eltorp and Marschner 1996) of mycorrhizal plants have been reported. Among arbuscular mycorrhizal plants, there is not much evidence of lower $x_{min}$ (Bolan 1991), but Mosse et al. (1973) demonstrated that some study plants were able to absorb labelled phosphate from soils where non-mycorrhizal plants did not absorb any, which suggests that a lower $x_{min}$ can be possible among AM plants. It is more probable that a lower $x_{min}$ of mycorrhizal roots could result in a situation where the roots are able, through, for example, enzyme activity, to access or more efficiently utilize other nutrient sources compared to non-mycorrhizal roots, regardless of whether these nutrients are inorganic (Bolan 1991, Smith and Read 1997) or organic (Mitchell and Read 1981, Northup et al. 1995, Näsholm et al. 1998, Koide and Kabir 2000). If $x$ or the external mineral nutrient concentration includes these different nutrient sources, this would imply a lower threshold concentration of nutrient uptake for mycorrhizal roots.

Consequently, mycorrhizal roots may have a higher nutrient uptake than non-mycorrhizal roots due to differences in either $x_{min}$, $V_{max}$, or $K_m$. Despite this, the benefit derived by the host plant from mycorrhizas is ultimately determined by the value of the acquired nutrients for the carbon gain of the host and by the additional carbon cost caused by fungal hyphae, which together define the optimal strategy to maximize the net carbon gain at different nutrient concentrations (Fig. 1A–C). The mineral nutrient use efficiency of photosynthesis ($\alpha$) is the key parameter in our model. This parameter defines how valuable the acquired mineral nutrients are for carbon assimilation (Kanazawa 1985, Larcher 1995) and, hence, how much plants benefit from their better access to soil nutrients due to mycorrhizal associations. Along altitudinal gradients, the average nutrient concentrations of plants increase (for a review, see Körner 1989), which is probably related to the slow growth rates of alpine plants (Fitter 1997, Körner 1999). This may be a result from decreasing PNUE along increasing altitude because photosynthesis and growth processes are limited by declining temperatures, and nutrients are not diluted into new biomass. In the following discussion, we will assume that an increasing altitude implies either constant or decreasing nutrient use efficiency of photosynthesis combined with either 1) constant or 2) decreasing soil nutrient levels (Table 1).

A remark of caution is that we have derived the expected patterns of mycorrhizal colonization exclusively from the potential advantage of mycorrhizal symbiosis for the host plant. Consequently, plants are predicted to be mycorrhizal only if the net carbon gain of mycorrhizal plants is expected to be higher than that of non-mycorrhizal plants. This is a plausible assumption in conditions where mycorrhizas represent mutualistic symbiosis and mycorrhizal fungi hence do not function as parasitic symbionts (for a discussion, see Johnson et al. 1997, Tuomi et al. 2001). However, this may be a simplified assumption because mycorrhizal plants have not always been found to derive any benefit from mycorrhizal associations (e.g. Fitter 1991).

## 4.2 Mycorrhizal Colonization along Altitudinal Gradients

On the basis of the relatively scarce literature, mycorrhizal colonization of plants is generally poor in high alpine conditions (Haselwandter and Read 1980, Read and Haselwandter 1981,

Smith and Read 1997). Additionally, observations of high arctic and antarctic areas show the same trend (Christie and Nicolson 1983, Bledsoe et al. 1990, Kohn and Stasovski 1990, Väre et al. 1992). Dalpé and Aiken (1998) found AM spores and mycorrhizal associations in the Canadian High Arctic, but only 28% of the root samples were infected, the infection levels of the roots were relatively low (2–15%) and arbuscules were detected only occasionally. Väre et al. (1997) calculated, based on the data reported by Oksanen and Virtanen (1995), that the relative coverage of non-mycorrhizal plant species increases along with altitude in the northern Fennoscandian mountains. In addition, plant genera which form AM at lower altitudes may be non-mycorrhizal at higher altitudes (Read and Haselwandter 1981, Smith and Read 1997). These observations tend to suggest that, at the level of plant communities, the main pattern would be from mycorrhizal to non-mycorrhizal communities along increasing altitude.

At lower elevations, changes in mycorrhizal associations also take place. Mycorrhizal colonizations of *Vaccinium myrtillus* and *V. vitis-idaea* have been found to decrease along increasing altitude (Haselwandter 1979, Haselwandter and Read 1980). In contrast, Väre et al. (1997) found constant and even increasing colonizations among a few ericoid and AM species in Finnish Lapland, but their gradient length was remarkably shorter compared to the previous studies. At the plant growth form level (Table 2), mainly decreasing colonization patterns have been detected (Haselwandter 1979, Haselwandter and Read 1980, Väre et al. 1997), but there are also reports of increasing (Väre et al. 1997) and intermediate (Read and Haselwandter 1981) patterns (Table 2). These data on colonization patterns along increasing altitude are few in number and do not suggest any general invariable direction of change. It should, however, be noted that when only long gradients (1245–1300 m) are included, the trend of mycorrhizal colonization is always decreasing (Haselwandter 1979, Haselwandter and Read 1980) or intermediate (Read and Haselwandter 1981). Additionally, dominant mycorrhizal types may change along increasing altitude. For example, AM is a dominant type at the lowest altitudes and in mineral soils, whereas the ericoid type dominates at higher altitudes in organic soils, where

nutrients are mainly bound in an organic form (Read 1984). This emphasizes the importance of climate for the formation of vegetation zones and their specific mycorrhizal types along increasing altitude and latitude.

Along altitudinal gradients, air temperature decreases due to decreasing air pressure (Körner 1999). This implies a lower effective temperature sum during the growing season at high altitudes compared to low altitudes and thus, possibly, less photosynthates to be shared with the symbiotic fungi at high altitudes as Haselwandter (1979) and Väre et al. (1997) have proposed. The low mean temperature also slows down the mineralization rate (Rehder and Schäfer 1978) and soil concentrations of available phosphate (and nitrogen) decrease along increasing altitude (Widden 1987, Kyllönen 1988, Körner 1999), and the proportion of nutrients bound in organic matter increases. Consequently, the ability to utilize organic phosphate forms may become increasingly important towards higher altitudes. This utilization is known to be relatively efficient among ericoid and ectomycorrhizal fungi (Mitchell and Read 1981, Smith and Read 1997), but less efficient among AM fungi (Joner and Johansen 2000, but see Koide and Kabir 2000). Certain non-mycorrhizal arctic plants have also been shown to be able to exploit organic P forms (Kroehler and Linkins 1991).

Our model predicts that if the nutrient use efficiency of photosynthesis ($\alpha$) decreases and the soil nutrient levels remain constant, the emerging pattern is from a mycorrhizal to a non-mycorrhizal state along the environmental gradient (Fig. 1. A–C) independently of the nutrient uptake kinetics. However, these figures differ qualitatively. If mycorrhizal roots have lower $x_{min}$ or $K_m$, mycorrhizal symbiosis is optimal only if $\alpha$ is high enough. However, in the case of lower $x_{min}$, mycorrhizas are favoured at low nutrient concentrations, but in the case of lower $K_m$, symbiosis is favoured at intermediate nutrient levels (Fig. 1A, C) and the non-mycorrhizal strategy is optimal for a relatively wide range of $\alpha$ values. Contrary to this, if mycorrhizal roots have higher $V_{max}$, mycorrhizal symbiosis is favoured for most $\alpha$ values (Fig. 1B). Different mycorrhizal types might have different kinetics, at least when a lower $x_{min}$ can be reached by using organic nutrient sources, as

**Table 2.** List of published papers about mycorrhizal colonization patterns along an altitudinal gradient. Plant species: *C. hypnoides* = *Cassiope hypnoides*, *S. herbacea* = *Salix herbacea*, *S. proc.* = *Sibbaldia procumbens*, *V. alpina* = *Veronica alpina*, *V. myrtillus* = *Vaccinium myrtillus*, *V. vitis-idaea* = *Vaccinium vitis-idaea*. Ericaceous plants form ericoid mycorrhizas and forbs and grasses are either AM- or non-mycorrhizal. The letters in parentheses in the column 'Colonization pattern' refer to Fig. 2. ¥ = values deduced from the figure. * = statistically significant. NS = non-significant. µg mg dwt$^{-1}$ = root glucosamine concentration as µg/mg of root dry weight. Note: these patterns are not from a completely mycorrhizal to a totally non-mycorrhizal state and that statistical significances were not given in papers of Haselwandter (1979), Haselwandter and Read (1980) and Read and Haselwandter (1981).

### A. Pattern at species level

| Study area | Gradient length | Species | Mycorrhizal type | Colonization pattern and range along the alpine gradient | |
|---|---|---|---|---|---|
| Finnish Lapland[a] | 400 m | *C. hypnoides* | Ericoid | Increasing (B) | 33% → 71% * |
| | | *V. vitis-idaea* | Ericoid | Increasing (B) | 25% → 66% * |
| | | *S. proc.* | Arbuscular mycorrhiza | Constant | 67% → 77% NS |
| | | *V. alpina* | Arbuscular mycorrhiza | Constant | 36% → 25% NS |
| | | *S. herbacea* | Ectomycorrhiza | Constant | 100% → 100% NS |
| Austrian Alps[b] | 1245 m | *V. myrtillus* | Ericoid | Decreasing (A) | 3.38 → 0.83 µg mg dwt$^{-1}$ |
| | | *V. vitis-idaea* | Ericoid | Decreasing (A) | 3.11 → 0.85 µg mg dwt$^{-1}$ |
| Austrian Alps[c] | 1300 m | *V. myrtillus* | Ericoid | Decreasing (A) | 3.4 → 0.8 µg mg dwt$^{-1}$ ¥ |

### B. Pattern at plant growth form level

| Study area | Gradient length | Growth form | Colonization pattern and range along the alpine gradient | |
|---|---|---|---|---|
| Finnish Lapland[a] | 400 m | Ericaceous shrubs | Increasing (B) | 34% → 51% * |
| | 300–400 m | Forbs and grasses | Decreasing (A) | 38% → 19% NS |
| Austrian Alps[d] | 1300 m | Forbs and grasses | Intermediate (C) | 20% → 42% → 13% |
| Austrian Alps[b] | 1245 m | Ericaceous shrubs | Decreasing (A) | 3.25 → 0.77 µg mg dwt$^{-1}$ |
| Austrian Alps[c] | 1300 m | Forbs and grasses | Decreasing (A) | 78% → 33% of studied plant species AM |

[a] Väre et al. 1997, [b] Haselwandter 1979, [c] Haselwandter and Read 1980, [d] Read and Haselwandter 1981

especially ericoid and ectomycorrhizal plants are able to do (Mitchell and Read 1981, Smith and Read 1997). This might be compatible with the observations that ericaceous heaths prevail below the high alpine zone (Read 1984, Oksanen and Virtanen 1995, Smith and Read 1997) and that the optimum of ericoid mycorrhizal plants might hence occur at low nutrient concentrations, but slightly higher $\alpha$ values. As both higher $V_{max}$ and $K_m$ have been detected in mycorrhizal roots (Cress et al. 1979, Thomson et al. 1986, Bougher et al. 1990, Plassard et al. 1994, Eltorp and Marschner 1996), they are also possible explanations. The abundance of mycorrhizal symbiosis in all but the highest alpine conditions (lowest $\alpha$) in the case of higher $V_{max}$ seems reasonable on the basis of the present model (Fig. 1B).

If both $\alpha$ and the soil nutrient concentration decrease with altitude, or if $\alpha$ remains constant and the soil nutrient concentration decreases, then different patterns along gradients emerge, depending on the kinetics of nutrient uptake (Fig. 1A–C). Combinations of low $\alpha$ values and low nutrient concentrations, as in the Figs. 1A–C, still favour non-mycorrhizal plants in all cases. It appears that a decreasing pattern (Fig. 2A) might result from all the kinetics studied, with certain qualitative differences. However, in the cases of lower $x_{min}$ and $K_m$, increasing patterns along an altitudinal gradient (Fig. 1A) are also possible, and with lower $K_m$, an intermediate colonization pattern may also emerge (Fig. 1C). An intermediate pattern would require $\alpha$ either to be constant or to decrease only slightly along the nutrient gradient (Fig. 2C). A colonization pattern of this kind was found in one altitudinal study, where the lowest site was a fertilized hay meadow (Read and Haselwandter 1981, Table 2) with especially high nutrient concentrations. In laboratory studies, mycorrhizal associations are known to suffer from high nutrient levels, and mycorrhizal colonizations may similarly also decline at very low nutrient levels (Amijee et al. 1989, Koide and Li 1990, Koide 1991). Thus, this pattern can hardly exist without an especially nutrient-rich lower part of the gradient. Additionally, if $\alpha$ is constant or decreases only slightly along the nutrient gradient, lower $x_{min}$ in mycorrhizal plants will yield an increasing mycorrhizal pattern along increasing altitude

(Fig. 1A, Table 1). The same pattern is possible in a case of lower $K_m$ if the nutrient concentration decreases only slightly (Fig. 1C, Table 1). Even though Väre at al. (1997) reported a phenomenon of this kind from ericaceous shrubs (Table 2), the results may not be extensively generalized because the studied gradient was relatively short (400 m), and no increasing colonization patterns have been reported at the plant community level (Smith and Read 1997).

Finally, note that other factors may also contribute to the success of non-mycorrhizal plants in arctic and alpine conditions. For instance, non-mycorrhizal arctic sedges are known to be able to utilize organic nitrogen and phosphorus (Kroehler and Linkins 1991, Chapin et al. 1993, Kielland 1994). In high-altitude conditions, a non-mycorrhizal strategy might also have a nutritional advantage of this kind. Additionally, at high altitudes, physical disturbance of soil by frosts and winds might play some role, because mycorrhizal colonizations may be reduced in disturbed soils, possibly due to breakage of the hyphal network (Jasper et al. 1989, McLellan et al. 1995).

## 4.3 Conclusions

Our model predicts that the advantage of mycorrhizas for the host plant is essentially dependent on the nutrient use efficiency of photosynthesis (PNUE). Decreasing PNUE with a constant soil nutrient concentration yields the pattern from a mycorrhizal to a non-mycorrhizal condition independent on the nutrient uptake kinetics. In relation to the decreasing soil nutrient concentration, different patterns may arise, depending on the nutrient uptake kinetics and PNUE. Provided that PNUE and the soil nutrient concentration either remain constant or decline with increasing altitude, several patterns of mycorrhizal symbiosis would be possible. Thus, our model emphasizes the potential importance of PNUE over the nutrient uptake kinetics for the advantage of mycorrhizal symbiosis. The existing data from plant communities along altitudinal gradients support the decreasing pattern of mycorrhizal colonization. At the plant species level, the existing data of mycorrhizal colonizations along the altitudinal gradient are sparse and inconclusive (Table 2),

even though the longest gradients measured have yielded decreasing colonization patterns among mycorrhizal plants.

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