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SHORT NOTE

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The modelled growth of mycorrhizal and non-mycorrhizal plants under constant versus variable soil nutrient concentration

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Abstract We studied the response of mycorrhizal and non-mycorrhizal plants to variation in soil nutrient concentration. A model for the relative growth rate (RGR) of plant biomass was constructed with soil nutrients as an explanatory variable. A literature survey was carried out to find the relative magnitudes of parameter values for mycorrhizal and non-mycorrhizal plants. Mycorrhizal plants had higher RGR at low nutrient concentrations and non-mycorrhizal plants at high nutrient concentrations. The RGR of mycorrhizal and non-mycorrhizal plants at constant versus log-normally distributed soil nutrient concentration were compared to see the effect of mycorrhizal status on responses to variation. Variation in nutrient concentration generally reduced RGR, especially in mycorrhizal plants. The RGR of a non-mycorrhizal plant may increase with variation where a growth function threshold exists, i.e. a soil nutrient concentration that must be exceeded to allow growth. Mycorrhizal plants appeared more sensitive to variation in nutrient concentration than non-mycorrhizal plants due to the higher affinity of mycorrhizal roots at low nutrient levels. However, this prediction may be reversed if mycorrhizal symbiosis considerably stabilises flow of nutrients to plant physiological processes, such that mycorrhizal plants experience less variation in soil nutrient concentration than non-mycorrhizal plants. Our results also attain broader significance by suggesting a general trade-off between competitive ability in a constant versus variable resource availability.

Keywords Jensen's inequality · Model · Relative growth rate · Trade-off

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Introduction

Soil nutrient concentration is spatially (e.g. Gupta and Rorison 1974; Jackson and Caldwell 1993; Marschner 1995; Fransen et al. 2001) and temporally (e.g., Davy and Taylor 1974; Gupta and Rorison 1974; Chapin et al. 1978; Ryel et al. 1996; Lodge et al. 1997; Ryel and Caldwell 1998) variable in all ecosystems. Plant species, and various life-history strategies within species, may differ with respect to response of the relative growth rate (RGR) of plant biomass to average soil nutrients (Tilman 1982; Marschner 1995). We expected, therefore, that plant species and life history strategies would also differ in their response to the variability of soil nutrients (Fransen et al. 2001).

Mycorrhiza, where carbon products of a host plant are traded off against soil nutrients provided by symbiotic fungi, widens the range of possible nutrient uptake strategies. Plants benefit from mycorrhiza mainly due to the increased absorption surface provided by fungal hyphae, but consequently lose a considerable proportion of their photosynthates to meet the carbon demand of the fungi (Smith and Read 1997). The growth of mycorrhizal and non-mycorrhizal plants, therefore, may respond differentially to soil nutrient concentration, as has been observed in several experiments (e.g. Pairunan et al. 1980; Thomson et al. 1986; Bougher et al. 1990; Titus and del Moral 1998). Tilman's (1982) theory of resource competition predicts that a plant able to maintain a positive net growth rate at the lowest concentration of the limiting resource will competitively replace others, and the ability to tolerate depleted resources is necessary for long-term success in competition. This suggests that mycorrhizal symbiosis should increase plant competitive success when the availability of nutrients rather than energy is limiting (Son and Smith 1988). However, if mycorrhizal and non-mycorrhizal plants respond to variation in a different way, the competitive outcome between mycorrhizal and non-mycorrhizal strategies may be altered (Fransen et al. 2001).

In this paper, we reanalyse published data on the growth of mycorrhizal and non-mycorrhizal plants under a range of soil nutrient concentrations to see how these two nutrient uptake strategies differ in terms of the response of RGR to nutrient concentration. We constructed a model of RGR and tested it for differences in mycorrhizal and non-mycorrhizal plants in their response to variable nutrient concentration. We further analysed the contribution of the model's parameters to the difference between RGR at constant versus variable nutrient concentration. Finally, we considered a trade-off between plant fitness in a constant and in a variable environment.

Model

We assume that the concentration of a limiting soil nutrient is a variable X and the values it takes are marked by x. The nutrient concentration is assumed to follow a log-normal distribution f_X, which fits well for soil nutrient availability's (Jackson and Caldwell 1993; Marschner 1995; Ryel et al. 1996) as nutrient level is low for most of the time or in the largest proportion of the habitat area and only rarely high (Hutchings and de Kroon 1994). The parameters μ and σ^2 define the expectation $E[f_X(x)] = \exp(\mu+\sigma^2/2)$ of the distribution (Lindgren 1976; Patel et al. 1976):

$$fX\,(x) = \frac{1}{\sigma x\sqrt{2\pi}} \cdot e^{\frac{(\ln x-\mu)^2}{2\sigma^2}} \tag{1}$$

The RGR (=$1/B\cdot \mathrm{d}B/\mathrm{d}t$) of the biomass of an individual plant, or a monoculture of plants, is a function of a random variable when it depends on the randomly varying nutrient concentration. We assume that the biomass loss rate is negligible and present the following variant of the Michaelis-Menten function for the RGR of plant biomass (DeAngelis 1992):

$$\frac{1}{B} \cdot \frac{\mathrm{d}B}{\mathrm{d}t} = \begin{cases} \frac{r(x-x_0)}{k+x-x_0}, & x > x_0 \\ 0, & x \le x_0 \end{cases} \tag{2}$$

Parameter r (in units time^{-1}) defines the maximum RGR at nutrient saturation, x_0 is the threshold nutrient concentration, which must be exceeded for a non-zero growth rate, and k is the half-saturation constant nutrient concentration. Parameters k and x_0 define the response of RGR to nutrient concentration and half the maximum rate is obtained in the resource concentration equal to the sum of half-saturation constant and the threshold, i.e., $x=k+x_0 \rightarrow 1/B\cdot \mathrm{d}B/\mathrm{d}t=r/2$. Parameters k and x_0 have the same unit as the nutrient concentration x. We used the RGR function (Eq. 2) as a non-linear transformation to the log-normal distribution (Eq. 1) to get a distribution of RGR values under variable nutrient availability. The derivation of the RGR distribution is presented in the Appendix. We were unable to find an analytical solution to the expectation of the RGR distribution and will, therefore, present numerical analysis for RGR expectation. We used the expected RGRs to compare how sensitive mycorrhizal and non-mycorrhizal plants are to variation in resource concentration.

We reanalysed published data on the growth of several plant species under different phosphorus availabilities to obtain RGR estimates for mycorrhizal and non-mycorrhizal treatments. We required that the experiments had at least four nutrient levels, but not at toxically high concentrations. The initial plant biomasses necessary for the calculation of RGR (Hunt 1990) were not reported in any of the studies we found. We used the lowest reported plant biomass of each study as an arbitrary initial biomass. This makes the numeric values of parameter estimates unreliable, but

Table 1 Parameter estimates for plant relative growth rate as a function of soil nutrient concentration. The table gives the species name, number and range nutrient treatments, duration of the experiment in days, the minimum plant biomass reported and the reference to literature. Treatments are: *AM* arbuscular mycorrhiza, *EM* ectomycorrhiza and *NM* non-mycorrhizal. The parameters of the growth model are: maximum relative growth rate r (day^{-1}), half-saturation constant k (units of nutrient concentration) and threshold nutrient concentration x_0 (unit of nutrient concentration). The lower and upper limit of the 95% confidence interval is given in parentheses for each parameter estimate. A threshold concentration could be determined only in two cases, others were not determined (*n.d.*) and assumed to be zero

Plant species	Experimental conditions	Treatment	r	k	x_0
Eucalyptus diversicolor	10 levels, 1 replicate 0–48 mg P/kg soil, 120 days, min. 0.09 g, Bougher et al. (1990)	EM	0.0397 (0.0346, 0.0447)	2.1071 (0.5369, 3.6773)	6.2890 (0.6146, 9.6332)
		NM	0.0447 (0.0391, 0.0562)	5.2194 (0.6217, 9.8170)	n.d.
Manihot esculenta	4 levels, 8 replicates 0.1–100 μM P, 42 days, min. 1.54 g, Howeler et al. (1982)	AM	0.0419 (0.0393, 0.0445)	0.3544 (0.2202, 0.4886)	n.d.
		NM	0.0444 (0.0411, 0.0476)	0.8944 (0.5493, 1.2395)	
Trifolium subterraneum	6 levels, 1 replicate 0–150 mg P/kg soil, 42 days, min. 0.79 g, Abbot et al. (1984)	AM	0.0854 (0.0384, 0.1325)	1.4083 (–17.801, 20.617)	n.d.
		NM	0.0954 (0.0420, 0.1489)	10.2652 (–10.890, 40.421)	
Trifolium subterraneum	7 levels, 1 replicate 0–2.4 g P/pot, 42 days, min. 2.72 g, Pairunan et al. (1980)	AM	0.0312 (0.292, 0.0331)	0.1518 (0.1064, 0.1972)	n.d.
		NM	0.0349 (0.0265, 0.0432)	0.3408 (0.0730, 0.6086)	
Trifolium subterraneum	7 levels, 1 replicate 0–280 mg P/kg soil, 42 days, min. 11.02 g, Thomson et al. (1986)	AM	0.0948 (0.0908, 0.0988)	6.4670 (4.1313, 8.8028)	n.d.
		NM	0.1073 (0.0938, 0.1208)	24.780 (11.488, 38.073)	
Trifolium subterraneum	4 levels, 1 replicate (0–0.67 mmol P/kg soil), 31–35 days, min. 0.075 g, Oliver et al. (1983); Oliver et al. unpublished data, cited in Smith and Read (1997)	AM	0.0320 (–0.0438, 0.1079)	0.1204 (–1.0360, 1.2769)	n.d.
		NM	0.0664 (0.0313, 0.1014)	0.6920 (0.0690, 1.3150)	

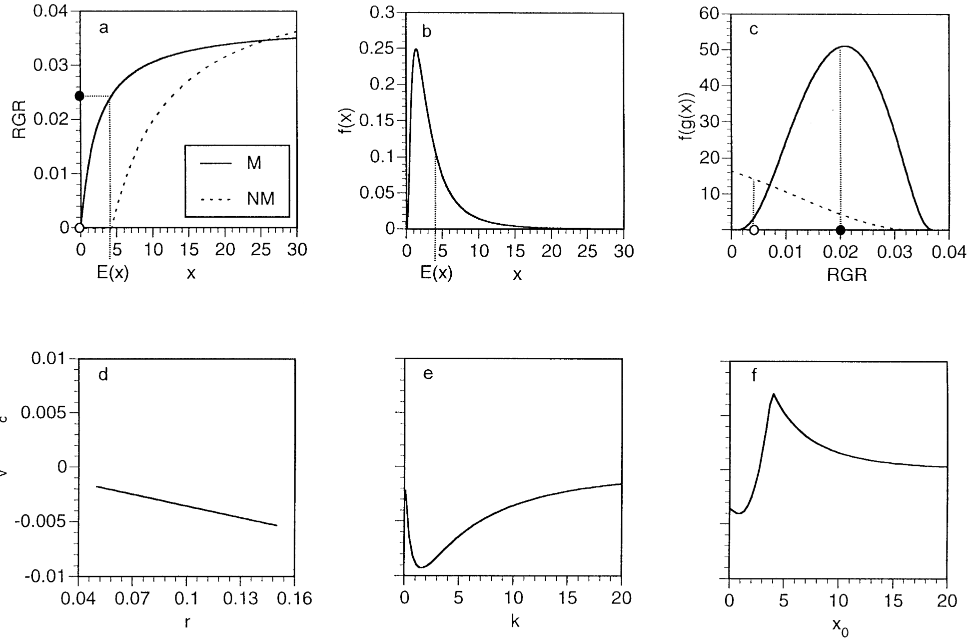

Fig. 1 **a** The relative growth rate (RGR) of mycorrhizal (*solid line*) and non-mycorrhizal plants (*dashed line*) at different availabilities of soil nutrient concentration *x*. The growth rate at a constant nutrient availability *E*(*x*) is denoted by *filled* and *open circles* for mycorrhizal and non-mycorrhizal plants, respectively. **b** The probability distribution *f*(*x*) of soil nutrient concentration is assumed to have a log-normal distribution with the expectation *E*(*x*) and coefficient of variation CV=1 (μ=1, $\sigma^2=\sqrt{\ln 2}\approx0.83$). **c** The probability distribution *f*(*g*(*x*)) of RGR for mycorrhizal (*solid line*) and non-mycorrhizal (*dashed line*) plants under variable nutrient concentration. The expected RGR of mycorrhizal and non-mycorrhizal plants are denoted with *filled* and *open circles*, respectively. Panels **d, e, f** present the difference between the RGR of plant biomass in variable (RGR$_V$) and constant (RGR$_C$) soil nutrient concentration with different parameter values. **d** Maximum growth rate *r*. Other parameter values: k=10, x_0=0. **e** Half-saturation constant *k*. Other parameter values: r=0.1, x_0=0. **f** Threshold nutrient concentration x_0. Other parameter values: r=0.1, k=10. The parameters of the log-normal distribution of nutrient concentrations are μ=1, $\sigma^2=\sqrt{\ln 2}$

does not affect the comparison of mycorrhizal and non-mycorrhizal treatments, as the difference of parameter value estimates does not change. The RGR function (Equation 2) was fitted to data and parameters estimated with 95% confidence intervals with a non-linear least squares method using Matlab's Optimisation toolbox (Coleman et al. 1999). A threshold concentration was determined only in the cases where the estimate had a positive value. Negative concentrations are not feasible and in those cases the threshold was given a fixed value of zero which does not have a confidence interval. The analysis is based on published treatment averages, not on the original data. This leads to large confidence intervals for parameter estimates, despite the good fit of the model.

We evaluated the contribution of the different parameters of the RGR model (Eq. 2) by studying how they affect the difference between expected RGR at constant versus variable nutrient concentration. This was done by plotting the difference between RGR at constant and RGR at variable nutrient concentration against a range of values for each of the parameters.

Results and discussion

The mycorrhizal plants in the reanalysed data set had a lower half-saturation constant (*k*) and lower or zero threshold concentration (x_0) than non-mycorrhizal plants (Table 1), suggesting that mycorrhizal plants are more responsive to soil nutrient concentration than non-mycorrhizal plants (Fig. 1a). Non-mycorrhizal plants, on the other hand, had a higher maximum growth rate than mycorrhizal plants (*r*) (Table 1).

Mycorrhizal plants would thus grow faster than non-mycorrhizal plants at low nutrient concentrations. Non-mycorrhizal plants, on the other hand, seem to respond slowly to increasing soil nutrient concentrations and growth may be retarded due to an uptake threshold for soil nutrients. Mycorrhizal fungi thus increase plant nutrient supply, but are also an additional carbon sink for the host plant (Jones et al. 1991; Eissenstat et al. 1993; Nielsen et al. 1998). At high nutrient levels, the relative benefits of mycorrhiza may decline, since the carbon allocation to fungi cannot yield additional nutritional advantages for the host-plant when it becomes saturated with nutrients (Son and Smith 1988; Peng et al. 1993; Tinker et al. 1994).

When nutrient availability is constant and below the threshold for growth of the non-mycorrhizal plant, the non-mycorrhizal plant has zero RGR while the mycorrhizal plant has a positive RGR (Fig. 1a). The situation changes when nutrient availability is variable (Fig. 1b), even if the mean availability remains the same. The mean RGR of the non-mycorrhizal plant becomes non-zero RGR (Fig. 1c) and that of the mycorrhizal plant decreases (Fig. 1c). This is due to a qualitative difference in the RGR functions. Mycorrhizal plant RGR *decelerates* for all nutrient availabilities, while the non-mycorrhizal plant RGR *accelerates* around the threshold for growth (Fig. 1a). This difference corresponds to different signs of the RGR function's second derivative, which Jensen's inequality (Ruel and Ayers 1999) predicts to determine the direction of the RGR difference in constant versus variable nutrient availability.

RGR is lower in variable than constant nutrient availability (Fig. 1d). The absolute difference increases linearly and the percentual difference in RGR values is independent of the maximum growth rate value. RGR is also higher in constant than in variable nutrient availability for all values of the half-saturation constant, but the response is non-linear, so that the difference between constant and variable availabilities is greatest at relatively low nutrient availability (Fig. 1e). The RGR difference between constant and variable nutrients is also non-linear in relation to the threshold concentration (Fig. 1f). Growth is faster in constant than variable nutrient availability when the threshold is low, but is faster at variable nutrient availability when the threshold is high (Fig. 1f). The half-saturation and threshold parameters determine a plant's responsiveness to soil nutrients. The difference between mycorrhizal versus non-mycorrhizal plant response to variation in soil nutrient concentration is, therefore, a consequence of a difference in responsiveness to nutrients, not of different maximum growth rates. High responsiveness increases RGR at low nutrient availability, but makes RGR decrease when nutrient availability is variable. In addition to the trade-off between growth in low and high nutrient levels (Table 1), our results suggest also a trade-off between the ability to grow in constant versus variable nutrient availability. The trade-off is especially notable under conditions where the nutrient variability increases the growth rate of non-mycorrhizal plants and decreases the growth rate of mycorrhizal plants. In nature, soil nutrient concentration is hardly ever stable, but the results of our theoretical analysis indicate possible differences on the optimal growth strategy in environments which differ in the variability of soil nutrient concentration.

In the present analysis, the variation in nutrient concentration was similar for mycorrhizal and non-mycorrhizal plants (i.e. nutrient flow to physiological processes was assumed to follow external availability). Although the variation in external nutrient concentration may be similar for all plants on a site, the extent it affects the plant growth may differ with mycorrhizal status. Mycorrhizal plants have been found to contain more nutrients per unit biomass than non-mycorrhizal ones (Stribley et al. 1980; Bolan 1991), which can be interpreted as luxury accumulation (Smith and Gianinazzi-Pearson 1988). The internal storage of nutrients is further increased by the volume of fungal hyphae (Bolan 1991). These mechanisms could buffer the flow of nutrients from fluctuations in external nutrient concentration, which could be expected to act for the benefit of mycorrhizal symbiosis under variable concentration of external nutrients (see Cui and Caldwell 1996a, b). Thus, it could be that mycorrhizal symbiosis still implies an increased physiological plasticity in a variable environment.

We argue that the results and insights of this analysis could also be extended to other mycorrhizal types and nutrients, as well as cross-species comparison of response to resource concentration. This is due to variability being a general property of all soil nutrients, and the uptake of all nutrients is likely to be non-linear with respect to nutrient concentration. This suggests that the influence of nutrient variation on average plant growth rate is a basic property of ecological systems.

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Appendix

For notational convenience, we first define $1/B \cdot \mathrm{d}B/\mathrm{d}t=g(x)=y$. The probability density function of RGRs $f_Y(y)$ was derived according to a general equation for the function of a continuous random variable (Lindgren 1976):

$$f_Y(y) = f_X\left[g^{-1}(y)\right] \cdot \left|\frac{\mathrm{d}g^{-1}(y)}{\mathrm{d}y}\right| \tag{3}$$

The probability density function of the dependent variable (nutrient availability in the present case) is f_X, while f_Y is the probability density function of RGR values. The inverse $g^{-1}(y)$ is derived from the RGR function $g(x)$ (Eq. 2) and is defined only for $x > x_0$. The RGR of plant biomass is zero when $x < x_0$ and the zero growth rate can, therefore, be accounted for in the resource availability distribution (Eq. 1) by multiplying it with a Heaviside step function $H(x-x_0)$:

$$H(x-x_0) = \begin{cases} 0, & x \leq x_0 \\ 1, & x > x_0 \end{cases} \tag{4}$$

This results in a new function $f_\mathrm{H}(x) = H(x-x_0)\, f(x)$, which will be used in the calculation of the RGR distribution. The inverse of $g(x)$ is for $x > x_0$:

$$g^{-1}(y) = \frac{rx_0 + yk - yx_0}{r-y}, x > x_0 \tag{5}$$

The derivative of the inverse is:

$$\frac{\mathrm{d}g^{-1}(y)}{\mathrm{d}y} = \frac{rk}{(y-r)^2} \tag{6}$$

The RGR distribution is obtained by substituting the right hand side of Eq. 5 for x in $f_\mathrm{H}(x)$ and multiplying it by the right-hand side of Eq. 6. This yields $f_\mathrm{Y}(y)$, where $H(y)$ is a Heaviside step function.

$$f_y(y) = \frac{H\left(\frac{ky}{r-y}\right)\sqrt{2rk}}{(r-y)(rx_0+ky-x_0y)\sigma\sqrt{\pi}} \cdot e^{-\frac{\left[\ln\left(\frac{rx_0+ky-x_0y}{r-y}\right)-\mu\right]^2}{2\sigma^2}} \tag{7}$$

The expected RGR was calculated numerically as:

$$E(Y) = \int_{-\infty}^{\infty} y \cdot f_Y(y)\mathrm{d}y \tag{8}$$

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