Short Communication
Plant stoichiometry in relation to relative growth rate

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Abstract

Plants need certain proportions between elements for proper growth and functioning. These proportions vary with growth conditions and it has generally been found that with increasing relative growth rates P:N should increase (the growth rate hypothesis). However, the proportions between N and other elements change with growth rates, and how this determines which element is limiting growth is not well studied, but it is possible that limitations of other elements could restrain plant growth more than N. Using results from nine studies with birch plants (*Betula pendula*) with different limiting elements (N, P, K, S, Mg, Zn, Mn, Fe and Cu) under steady-state growth, I have investigated how the switch, defined as the ideal proportion, between which element is limiting growth varies with relative growth rate. The ideal proportion of element:N increases with increasing relative growth rate for K, P, Zn and Mn but a slight decline for Mg and S. The changes in element:N ratios are strongest at low relative growth rates. The consequences of these results for plant properties under global change are discussed.

Keywords: ecological stoichiometry, relative growth rate, *Betula pendula*, nitrogen, ideal nutrient proportions, stoichiometric plasticity

植物化学计量与相对生长速率的关系

摘要：植物的正常生长和功能需要特定比例的元素，这些元素比例会随着生长条件的变化而变化。生长速率假说认为，随着相对生长速率的增加，磷氮比(P:N)也随之增加。然而，氮(N)与其他元素之间的比例如何随生长速率的变化而变化，以及这些变化如何决定生长受限的元素，目前尚未得到充分研究。事实上，其他元素的缺乏可能比N更显著地限制植物的生长。基于9项关于白桦(*Betula pendula*)的研究结果，本研究探讨了在不同限制元素(N、P、K、S、Mg、Zn、Mn、Fe和Cu)的条件下，植物在稳定生长状态下的反应机制；探究了元素限制生长的"转换点"，即不同元素与N的理想比例如何随相对生长速率的变化而变化。研究结果发现，随着相对生长速率的增加，K、P、Zn和Mn与N的理想比例增加，而Mg和S与N的理想比例则略有下降。这些元素与N比例的变化在相对生长速率较低时最为显著。本文还讨论了在全球变化背景下这些结果对植物特性可能产生的影响。

关键词：生态化学计量学，相对生长速率，白桦(*Betula pendula*)，氮，理想元素比例，化学计量可塑性

INTRODUCTION

Plants require many elements in fairly restricted proportions for proper growth. It is well established that as a plant relative growth rate increases, the plant phosphorus concentration increases relative to plant nitrogen concentration; P:N increases (e.g. Niklas 2006; Niklas *et al.* 2005). This is called the growth rate hypothesis (Sterner and Elser 2002), and can be understood from how phosphorus and nitrogen interact during vegetative growth (Ågren 2004). With increasing atmospheric carbon dioxide concentration, concentrations of other elements than carbon will decrease through dilution. Meta-analyses of experiments with elevated CO_2 (e.g. Deng *et al.* 2015; Yue *et al.* 2017) show that plant N concentration decreases more than P concentrations. Studies on the effects on other elements are scarce and have mainly focused on the decreasing nutritional value of food crops (e.g. Loladzle 2002, 2014). Ågren and Weih (2020) showed that the relation between N combined with P and other elements could have scaling exponents that were both smaller and larger than one, indicating that other elements could be increasing both slower and faster than N and P in plants. Here, I will use a series of laboratory experiments with varying relative growth rates under the limitation of one of nine important elements, n (N, P, K, S, Mg, Zn, Mn, Fe and Cu) to investigate potential consequences of shifts in the relations between elements on plant growth. The main question is to see how much stoichiometric plasticity (e.g. Sistla and Schimel 2012) will be required, here expressed as changes in n:N ratios as growth conditions change. The effects of changing growth conditions will be expressed as changes in the relative growth rate of the plant.

MATERIALS AND METHODS

Theory

The basis for this analysis is the concept of nutrient productivities (Ågren 1985, 1988). Here, the relative plant growth rate, $r = (1/W)(dW/dt)$, as a function of the limiting plant nutrient concentration $c_m = m/W$ is described by the following relations, where W is the plant biomass and m is the whole-plant nutrient content:

$$r = \begin{cases} r = 0 & c_m < c_{m,\min} \\ r = P_m(c_m - c_{m,\min}) & c_{m,\min} < c_m < c_{m,\mathrm{opt}} \\ r = r_{\max} & c_m \geq c_{m,\mathrm{opt}} \end{cases}$$

(1)

where $c_{m,\min}$ is the minimum plant nutrient concentration required for growth, P_m is the nutrient productivity (the rate of plant production per unit nutrient m, $(dW/d)/m$) and $c_{m,\mathrm{opt}}$ is the plant nutrient concentration beyond which plant relative growth rate no longer increases beyond $r_{\max} = P_m(c_{m,\mathrm{opt}} - c_{m,\min})$. The parameters will depend on external factors such as light intensity, CO_2 and temperature. I will only investigate the middle relation, the response region, because it is only in this region that meaningful changes in nutrient proportions will occur. Equation (1) can be inverted to give the plant nutrient concentration required to achieve a given relative growth rate

$$c_m(r) = \frac{r}{P_m} + c_{m,\min}$$

(2)

From Equation (2), I calculate the ratio, $I_{m\mathrm{N}}(r)$, between the plant nutrient concentrations of m and N, where the two elements simultaneously are limiting according to Equation (2), the ideal nutrient proportions (Ågren 1988)

$$I_{m\mathrm{N}}(r) = \frac{c_m(r)}{c_{\mathrm{N}}(r)} = \frac{r/P_m + c_{m,\min}}{r/P_{\mathrm{N}} + c_{\mathrm{N,min}}}$$

(3)

This ratio shows at which proportion between element m and N the growth limitation will change from one element to the other. As the ratio depends on the relative growth rate, the switch in limitation can change with environmental conditions and the rate of supply of the growth-limiting elements.

Differentiating Equation (3) with respect to r will show how the ideal proportion of m:N will change as the relative growth rate changes

$$\frac{dI_{m\mathrm{N}}(r)}{dr} = \frac{1}{P_m P_{\mathrm{N}}} \frac{P_{\mathrm{N}} c_{\mathrm{N\,min}} - P_m c_{m,\min}}{(r + P_{\mathrm{N}} c_{\mathrm{N,min}})^2}$$

(4)

which shows that the ideal proportions are always monotonically increasing or decreasing depending on whether $P_{\mathrm{N}} c_{\mathrm{N,min}} - P_m c_{m,\min} > 0$ or <0. Positive values mean that c_m needs to increase faster than $c_{\mathrm{N:}}$ when the relative growth rate increases. Note, in the limit $r \to 0$, $I_{m\mathrm{N}} \to c_{m,\min}/c_{\mathrm{N,min}}$.

Data

To test Equation (3), I have used data from a series of steady-state experiments with silver birch seedlings (*Betula pendula* L.). In these experiments, one of the
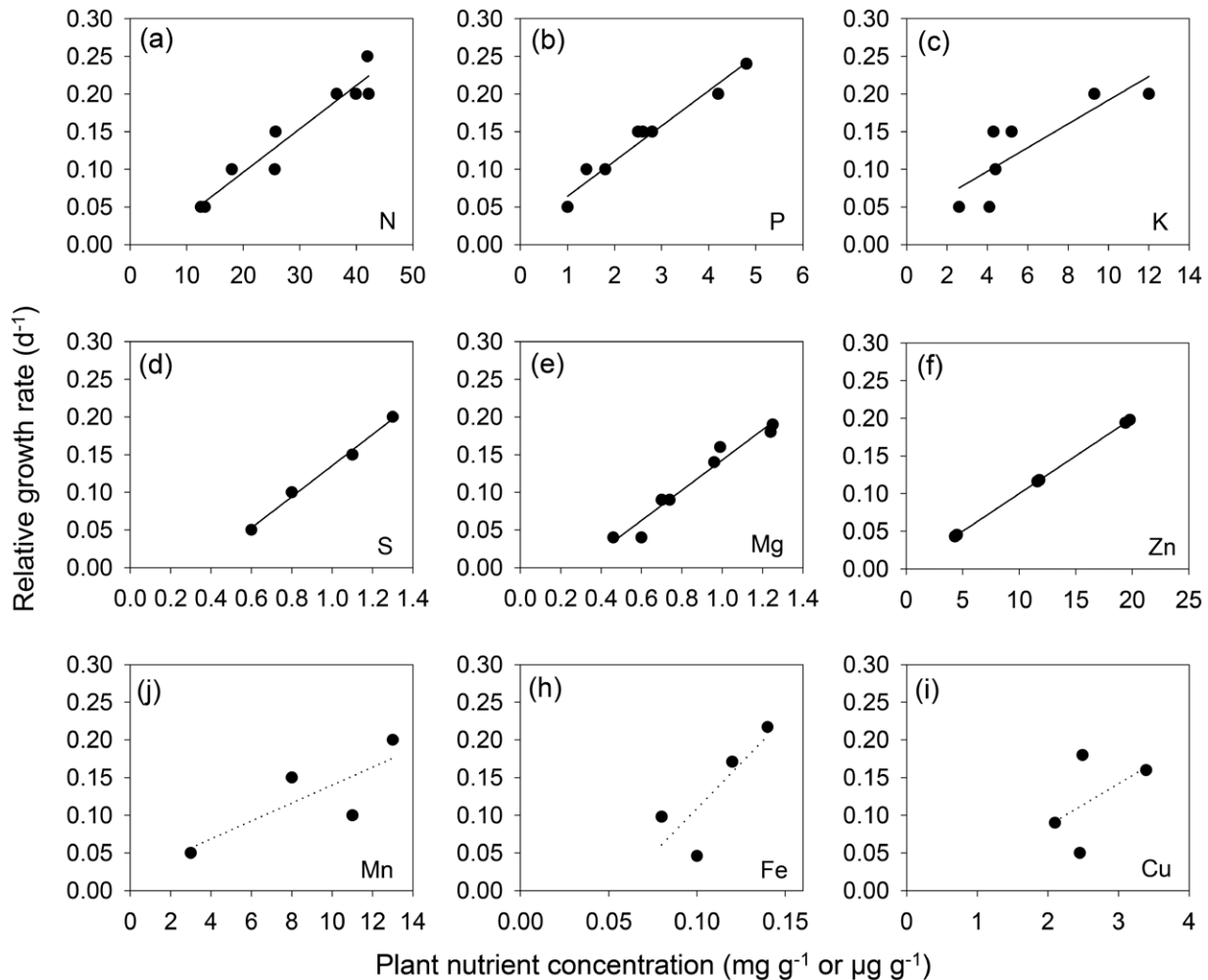
Figure 1: Observed relations between whole-plant nutrient concentrations and relative growth rates when grown under the limitation of one element at a time. Data sources are given in Table 1. The line is the regression line and estimated parameters (P_n and $c_{n,\min}$) and r^2 values are given in Table 1. Units for plant nutrient concentrations are mg g^{-1} (N, P, K, S and Mg) and µg g^{-1} (Zn, Mn, Fe and Cu). Regressions that are not significant at $P = 0.05$ are dotted.

elements N, P, K, S, Mg, Zn, Mn, Fe or Cu has been limiting growth and supplied at an exponentially increasing rate, r, and all other elements supplied in excess; with this technique the relative growth rate becomes equal to the exponential supply rate of the limiting element, r. All the experiments have been performed under otherwise similar conditions (Ingestad and Lund 1979), where the experimental technique also is explained in detail.

RESULTS

Graphs with the observed relations between relative growth rate and the limiting whole-plant nutrient concentration are given in Fig. 1 and the corresponding parameters (P_m and $c_{m,\min}$) are given in Table 1. Parameters have been estimated with Sigmaplot 14.03. P_m's are the slopes of the linear regression lines and c_m

is calculated as $-$intercept/P_m. $c_{m,\text{opt}}$ has been estimated as the c_m value at which the regressions extrapolate to $r_{\max} = 0.26$ day^{-1}, the value observed in the N experiments (Ingestad *et al.* 1994a). The linear relation between r and c_m fits very well with r^2 ranging from 0.51 (Cu) to 1.00 (Zn) and is significant ($P < 0.05$) for all elements except Mn, Fe and Cu.

Some elements (P, K, Zn, Mn) show an increase in m:N with increasing relative growth rate, while the other investigated elements (S, Mg, Fe, Cu) show a decline. In all cases, the changes are not drastic and are strongest at the lowest growth rates (Fig. 2).

DISCUSSION

There are changes in the ideal element:N ratios, both increasing and decreasing, with relative

Table 1: Estimated parameters P_n, $c_{n,min}$, $c_{n,opt}$ and P_n, $c_{n,min} - P_N c_{n,min}$ for nine elements

Element n	Pn	$c_{n,\mathbf{min}}$	$c_{n,\mathbf{opt}}$	r^2	$P_n, c_{n,min} - P_N c_{n,min}$	Data source
N, mg	0.0058 $P < 0.05$	3.29	48.12	0.93	—	Ingestad *et al.* (1994a)
P, mg	0.18 $P < 0.001$	0.42	3.48	0.96	0	Ericsson and Ingestad (1988)
K, mg	0.034 $P < 0.01$	1.09	8.67	0.70	>0	Ericsson and Kähr (1993)
S, mg	0.21 $P < 0.01$	0.35	1.60	0.99	>0	Ericsson T and Kähr M (Personal communication, 8 December 2008)
Mg, mg	0.20 $P < 0.001$	0.29	1.58	0.95	>0	Ericsson and Kähr (1995)
Zn, µg	0.010 $P < 0.001$	2.83	28.83	1.00	>0	Göransson (1999)
Mn, µg	0.012 $P < 0.1$	1.25	23.10	0.64	<0	Göransson (1994)
Fe, µg	2.41 $P < 0.1$	0.055	0.16	0.67	>0	Göransson (1993)
Cu, µg	0.056 n.s.	1.02	5.70	0.26	>0	Göransson (1998)

Units are for P_n g mg^{-1}day^{-1} or g µg^{-1}day^{-1} and for $c_{n,min}$ and $c_{n,opt}$ mg g^{-1} or µg g^{-1} depending on element. The data for N are from the experiments with daily quantum flux of 22 mol m^{-2}. r^2 refers to the fit of the linear regressions to the data in Fig. 1 Abbreviation: n.s. = not significant. $P > 0.05$ but $P < 0.1$.
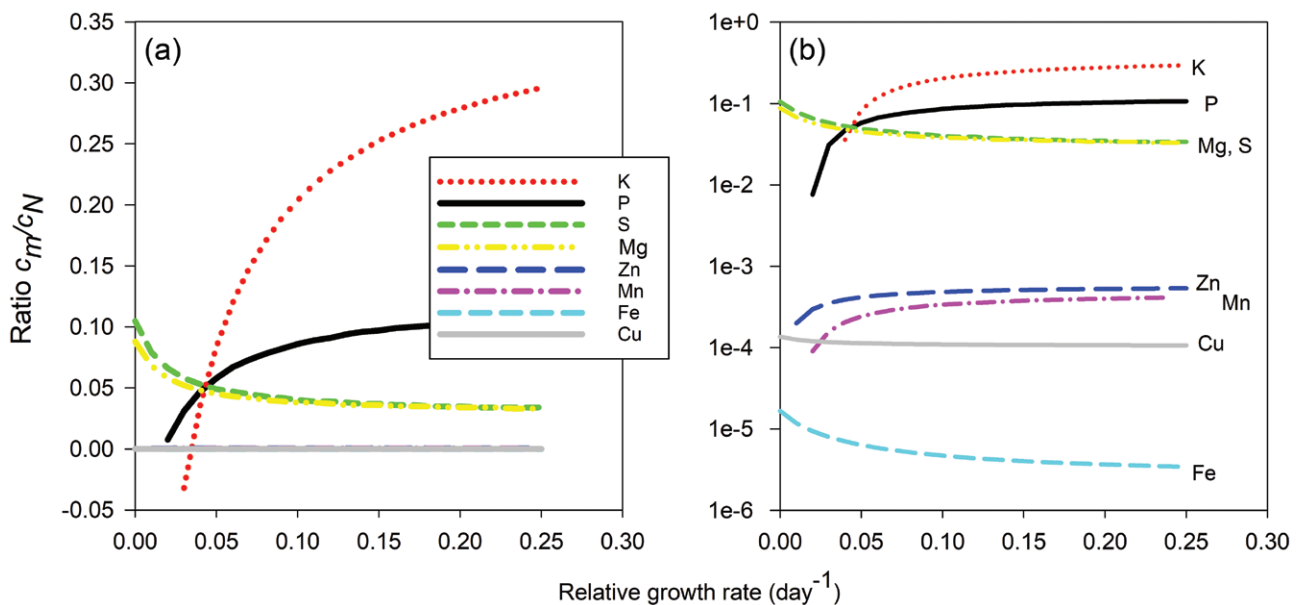

Figure 2: The ideal proportions of different elements relative to N calculated from Equation (3). K, P, Mg, Fe and S give almost identical curves (a). Using a log scale (b) separates the curves for K and P and Zn and Mn.

growth rates for all elements, in particular at low relative growth rates. However, with the exception of K, changes in the ideal *n:N* are small over the entire range of relative growth rates, suggesting that changing growth conditions might not be a challenge to the stoichiometric plasticity of plants.

Only plants growing in marginal habitats (low values of r) may be sensitive to shifts in limiting elements. The precise magnitude of the changes is uncertain because of difficulties in the parameter estimations. In particular, estimates of $c_{m,\min}$ are uncertain and should be based on more observations at very low growth rates. The result that some $c_{n,\min}$ are negative further stresses the importance of additional studies of slow-growing plants. Additional studies on other organisms and other elements than N as limiting may help in understanding the mechanisms. Other relations between plant relative growth rate and nutrient concentrations (e.g. Moriconi and Santa-Maria 2013) could also be substituted for Equation (1). It should be emphasized that the analysis has been on vegetatively growing plants, and other stoichiometric rules and relations may apply under reproductive growth. Changes in growth conditions, for example, light and temperature, will change the parameters used in this analysis but the method should be applicable for understanding the effects of growth conditions. With increasing light intensity, P_N increases (Ingestad et al. 1994a, 1994b) but no information is available for $c_{m,\min}$ and other elements.

In this study, the ideal N:P changes between 9 and 32 by mass over the range of relative growth rates. This is similar to the observations by Güsewell et al. (2003) in a study of plant populations in wetlands where the shift between N and P limitation is at N:P ratios of around 20. In another study with wetland graminoids, Güsewell (2005) found that the shift between P and N limitation for growth occurred in the N:P range of 15–45. The observations for N:P, N:K and N:Mg (means 9, 2 and 8, respectively) found by Knecht and Göransson (2004) are comparable to the ratios found here but indicating N limitation in their investigated plants.

I have expressed the stoichiometric relations with N as the basis. It is straightforward to replace N with any other elements should that be of interest.

The relative growth rate has been used as a basis for the analysis because it has been the driving variable in all the experiments. Because N is a strong driver of plant growth, the results should also be applicable to situations where N availability is changing, resulting in changes in growth rates. This result is important as we live in a world with increasing N deposition (Galloway et al. 2004). However, Mason et al. (2002) suggest that in spite of increasing N deposition, the N availability may actually be declining in many ecosystems. A global meta-analysis by Mao et al. (2020) indicates that N additions can lead to decreases

in P, K, Ca and Mg:N. A further complication is that stoichiometric couplings are important not only for plant growth rates but also for responses to temperature and water availability as discussed by Tian et al. (2019).

The increasing nitrogen deposition in combination with an increasing atmospheric CO_2 concentration can cause changes in both plant production and plant quality with potentially negative consequences also for human health because of decreasing content of important micronutrients (e.g. Fe, Se) (Ebi and Loladze 2019).

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