REPORT

The C : N : P stoichiometry of autotrophs – theory and observations

Göran I. Ågren
Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, PO Box 7072, SE-750 07 Uppsala, Sweden
E-mail: goran.agren@eom.slu.se

Abstract
Evolution has set biochemical constraints on the chemical composition of living organisms. These constraints seem to lead to increases in N : C and P : C ratios with increasing relative growth rate for all types of organisms. The N : P ratio also seems to decrease with relative growth rate for heterotrophs whereas autotrophs may show a more complex behaviour. Here I will show that, from biochemical considerations, N : C should increase linearly and P : C quadratically with relative growth rate in autotrophs with the consequence that N : P increases at low relative growth rates, passes a maximum and then decreases at high relative growth rates. These predictions are verified against observations for a freshwater alga (Selenastrum minutum) and a tree seedling (Betula pendula). Changes in temperature, light or other factors that affect the growth rate of autotrophs interact with nutrient supply in such a way that there are no simple rules for as to how N : P will change.

Keywords
Betula pendula, nitrogen, phosphorus, relative growth rate, RNA, Selenastrum minutum, specific growth rate, stoichiometry.


INTRODUCTION
Evolution has set biochemical constraints on the chemical composition of living organisms and these constraints become important when we want to understand the implications of human alterations to element cycles (Hessen et al. in press). Sterner & Elser (2002) have extensively explored causes and consequences of these constraints under the terminology of ecological stoichiometry. One of their conclusions is that organisms must change their C : N : P stoichiometry as a function of their growth rate. Higher growth rates are coupled not only to higher N : C and P : C but also to lower N : P in many heterotrophic organisms, including bacteria and arthropods (Elser et al. 2003; Makino et al. 2003). This is necessary because higher growth rates require more investment in rRNA to produce the proteins required for growth. As rRNA is one the major pools of P, the increasing content of rRNA will lead to a disproportionate increase in the concentration of P in the cells. This result is supported by both theoretical analysis and empirical data. But should we expect the same relationships for photautotrophs (‘autotrophs’ hereafter)? Terry (1980) showed that N : P increases for low growth rates and decreases for high growth rates of the alga Pavlova lutheri. Can these differences between animals and autotrophs be explained as a consequence of how they acquire different elements? Animals mainly get their food in packages where the element composition is determined by the food source. Autotrophs, on the contrary, acquire elements individually (e.g. CO₂, PO₄, NH₃, NO₃) and the acquisition of elements is linked in a chain; to get C the autotrophs require proteins and thus N, and to get proteins the autotrophs, like animals, require rRNA and thus P. It should not, however, be excluded that there are organisms other than autotrophs where the resource acquirement of elements can be linked in a chain in a similar way.

There is considerable empirical evidence for increasing N : C and P : C with increasing growth rate also in autotrophs. From a theoretical point of view, such a relationship follows as an immediate consequence of nutrient productivities (Ågren 1985a, 1988; Ågren & Bosatta 1998). However, both from theoretical and empirical data it is not clear how N : P should change with growth rate. A considerable difficulty in analysing N : P ratios in autotrophs stems from uptake above what is immediately required for growth (Ågren 1988). Autotrophs growing under N-limitation can take up considerable amounts of P for storage (and vice versa under N limitation) and
measured N : P ratios may therefore be quite misleading in terms of what the organism needs. Instead, the N : P ratio at the balance between N and P limitation, the critical N : P ratio, must be sought in experiments where both elements in turn are limiting under otherwise similar conditions. Unfortunately, such studies are rare. Previous analyses (Terry 1980; Terry et al. 1985) have shown for a marine alga that it is likely that the relationship between growth rate and the critical N : P is not monotonous but has a maximum. In the past, the theoretical foundation used to interpret these results has been the Droop equation (Caperon 1967; Droop 1974), which basically is a phenomenological formulation. I will here go further by using a theoretical analysis, which can be interpreted biophysically, and also apply the results to terrestrial autotrophs. The analysis will be restricted to C, N and P because these are much more strongly coupled than other elements (Knecht & Göransson in press).

Reflecting convention from terrestrial ecophysiology, all amounts are expressed in mass units (g or mg) and the term relative growth rate (rather than specific growth rate) for the growth rate per unit mass. For comparison, the Redfield ratios in mass units are N : C 176 mg g$^{-1}$, P : C 24 mg g$^{-1}$ and N : P 7.3 g g$^{-1}$.

**THEORY**

There is no unique way of decomposing an organism into its chemical constituents. It is, however, possible to distinguish certain major categories of functional groups that are directly linked to the growth of the organism. Photosynthesis requires large amounts of proteins (notably Rubisco) and proteins are synthesized by P-rich ribosomes. As these compounds can dominate the N and P stores in autotrophs, and proteins are synthesized by P-rich ribosomes. As these compounds but there is also structurally bound N. I will assume that these other N containing compounds are proportional to the amount of C with a factor $b_N$ such that the total amount of N in the organism ($N$) is

$$N = N_p + b_N C$$

(3)

Similarly, there is P in addition to that in ribosomes. It can be assumed that this additional P also is proportional to the amount of C (a factor $b_p$). Hence the total amount of phosphorus (P) in the organism is

$$P = P_a + b_p C$$

(4)

Note that the N and P included in the terms $\beta_N C$ and $\beta_P C$ are the minimum quantities required for proper functioning of the organism and do not include excess storage. For further considerations of which biochemical constituents correspond to the parameters $\beta_N$ and $\beta_P$ (see Geider & La Roche (2002) and Sterner & Elser (2002).

For organisms under stable and balanced growth [constant relative chemical composition and constant relative growth rate $\mu = 1/C(dC/dt) = 1/N(dN/dt) = 1/P(dP/dt)$], the element ratios N : C ($r_{NC}$) and P : C ($r_{PC}$) can be derived as functions of $\mu$ from eqns 1–4 (see Appendix).

$$r_{NC}(\mu) = \frac{\mu}{\phi_{CN}} + \beta_N$$

(5)

$$r_{PC}(\mu) = \frac{1}{\phi_{CN} \phi_{NP}} \mu^2 + \beta_P$$

(6)

As eqns 5 and 6 describe organisms growing at fixed relative growth rates, the organisms must also rely on external supplies of resources matching this relative growth rate; internal storages such as polyphosphates or nitrate would rapidly be exhausted and the relative growth rate cannot be maintained. This point is extensively developed by Ingestad (1982; see also Rhee 1980).

The N : P ratio ($r_{NP}$) formed from eqns 5 and 6 corresponds to the critical N : P ratio where N and P are simultaneously limiting growth

$$r_{NP}(\mu) = \frac{\mu \phi_{NP} + \beta_N \phi_{CN} \phi_{NP}}{\mu^2 + \beta_P \phi_{CN} \phi_{NP}}$$

(7)

Equations 5 and 6 show that N : C and P : C are increasing functions of the growth rate, as has been repeatedly observed. The N : P ratio will, on the contrary, increase linearly with $\mu$ for small values of $\mu$ and reach a maximum at $\mu_{max NP}$ and from then on decrease. For large values of $\mu$ the decrease is proportional to 1/$\mu$. The value of $\mu_{max NP}$, which is calculated from the condition $d\phi_{NP}/d\mu = 0$, is

$$\mu_{max NP} = \frac{\beta_P \phi_{NP}}{\beta_N \phi_{CN} - 1}$$

(8)
Depending on the value $\mu_{\text{max NP}}$ relative to the maximum relative growth rate, $\mu_{\text{max}}$, three possibilities exist:

1. $\mu_{\text{max NP}} > \mu_{\text{max}}$. In this case, increasing growth rates will always lead to increasing N : P. This is contrary to the observations for heterotrophs.

2. $\mu_{\text{max NP}} < \mu_{\text{max}}$. In this case, N : P will decrease with increasing $\mu$ for all $\mu$ of practical interest and the autotrophs behave as heterotrophs with respect to C : N : P stoichiometry.

3. $\mu_{\text{max NP}} < \mu_{\text{max}}$. In this case, N : P increases for small values of $\mu$, passes a maximum and then decreases as $\mu$ increases. Depending on the curvature of the $\lambda_{\text{NP}}(\mu)$-function, the N : P ratio can be more or less sensitive to changes in $\mu$.

**COMPARISON WITH OBSERVATIONS**

I will now compare the predictions from the theory section with observations. As will become clear below, such a comparison requires data from experiments where the organism has been subjected to N and P limitation under otherwise similar conditions. It is not difficult to find observations of either N or P limitation but studies where both elements have been made limiting are rare. I have used two such studies for a detailed analysis: one for a freshwater alga (*Selenastrum minutum* (Naeg.) Collins, Elrifi & Turpin 1985) and one for a tree seedling (*Betula pendula* Roth., Ericsson & Ingestad 1988; Ingestad et al. 1994). Multiple regressions of N and P concentrations against $\mu$ and $\mu^2$ were calculated ($c_n = a + b\mu + c\mu^2$). For both species, the quadratic term was not significant ($P > 0.79$) in the regression with N concentration whereas the linear term was not significant ($P > 0.37$) for P concentration. All other terms (except the constant term in the regression for N concentration for *B. pendula*) were highly significant ($P < 0.001$) and $r^2$ values exceed 0.88.

The regressions and the observed data are shown in Fig. 1 and the resulting parameter estimates are given in Table 1. The observations conform well to the theoretically predicted linear relationship between N concentration and relative growth rate and the quadratic relationship (without linear term) between P concentration and relative growth rate, respectively. The observed N : C and P : C ratios for the non-limiting elements are also included in Fig. 1. It is clear that there exists a considerable capacity for excess uptake of the non-limiting element, a capacity that is much larger for *S. minutum* than *B. pendula*. Another way of looking at the excess uptake is by comparing the critical N : P ratio with those observed. As can be seen in Fig. 1, observed N : P ratios all fall well above the critical line under P limitation.

**Figure 1** N : C, P : C, and N : P ratios as functions of relative growth rate for *S. minutum* and *B. pendula* under N- and P-limited growth. Regressions between N : C and P : C vs. relative growth rate are shown as solid lines. The solid lines in the N : P vs. $\mu$ graphs are the critical N : P ratios. The Redfield ratio is shown as a broken line in the graphs for *S. minutum*. ©2004 Blackwell Publishing Ltd/CNRS
limitation and well below under N-limitation, with the exception of some P-limited points for B. pendula, but the classification of these points as N-limited is questionable. The excess uptake decreases with increasing relative growth rate, which is most clearly seen in the decreased deviation between actual N : P and the critical N : P at high values of μ.

In addition to the two studies discussed above, I have tested regressions of the form \( c_2 = a + b_1 \mu \) and \( c_2 = a + b_2 \mu^2 \) (n = N or P) on five other experiments (Table 2). In all cases, both the linear and the quadratic regression fit the data well but a linear regression model fits the data best in five of the seven cases under N limitation and the quadratic regression model fits the data best in five of the seven cases under P limitation. The five additional experiments are only represented by a few data points and whether the linear or the quadratic models will give the best fit can in several cases depend on a single data point.

**DISCUSSION**

The first implication of these analyses is that the relationship between organism N and relative growth rate are different than those between organism P concentration and relative growth rate. The relation for N is linear whereas the relation for P is quadratic. This agrees with the theoretical predictions based on the assumption that autotroph growth requires protein (N based) and proteins presuppose rRNA (P based). Both of these growth-related processes are linear but they combine multiplicatively leading to the quadratic relation between P and relative growth rate. The observed linear relationship between N concentration and relative growth is the N productivity (Ågren 1985a) but its extension to other elements is, on the basis of this analysis, less obvious. I have previously suggested that a linear relationship between autotroph nutrient concentration and relative growth rate also should apply to elements other than N (Ågren 1988). This might still be a relevant approximation because the curvature in the P concentration–relative growth rate curve is small and it will require higher quality data to observe it than is available in many cases. Although the experiments included in Table 2 indicate a quadratic rather than a linear relationship for P, the linear regression is a good description. Other experiments (eucalyptus, Kirschbaum et al. 1992; three grass species, Ryser et al. 1997) reveal no curvature or have a clear curvature (Pavlova lutheri, Terry 1980) in the relationship between relative growth rate and P concentration (data not shown).

However, the choice between functions to describe data should not be made only on the basis of goodness-of-fit to data but also with regard to underlying principles and explanatory power. In that respect, because the parameters in eqns 1–4 can be related to underlying biological properties, the equations suggested in this paper offer more prospects than a phenomenological function like the Droop equation. Moreover, it is possible to extend the present analysis in logical ways. It is, for example, possible to

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>( \Phi_{CN} ) (g mg(^{-1}) day(^{-1}))</th>
<th>( \Phi_{CP} ) (g mg(^{-1}) day(^{-1}))</th>
<th>( \beta_N ) (mg g(^{-1}))</th>
<th>( \beta_P ) (mg g(^{-1}))</th>
<th>( \mu_{max NP} ) (day(^{-1}))</th>
<th>( r_{NP} (\mu_{max NP}) ) (mg mg(^{-1}))</th>
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<tbody>
<tr>
<td><em>S. minutum</em></td>
<td>0.0101</td>
<td>8.55</td>
<td>48.4</td>
<td>3.69</td>
<td>0.258</td>
<td>16.6</td>
</tr>
<tr>
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<td>0.00318</td>
<td>2.25</td>
<td>8.441</td>
<td>1.84</td>
<td>0.091</td>
<td>12.4</td>
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<tr>
<td><em>C. acutus</em></td>
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</tr>
<tr>
<td><em>E. globulus</em></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. minutum</em></td>
<td>0.931/18</td>
<td>0.897/18</td>
<td>0.826/21</td>
<td>0.898/21</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. pendula</em></td>
<td>0.931/10</td>
<td>0.896/10</td>
<td>0.831/16</td>
<td>0.881/16</td>
<td></td>
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<tr>
<td><em>E. globulus</em></td>
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<td>0.958/9</td>
<td>0.830/8</td>
<td>0.890/8</td>
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<td><em>S. minutum</em></td>
<td>0.955/6</td>
<td>0.888/6</td>
<td>0.831/6</td>
<td>0.704/6</td>
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<td>0.943/4</td>
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<td>0.983/5</td>
<td>0.957/4</td>
<td>0.990/4</td>
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</table>

*The values from the three lowest relative growth rates with P limitation were excluded from the analysis because of decreasing P : C with increasing relative growth rate.*

### Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>N limited</th>
<th>P limited</th>
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<tbody>
<tr>
<td></td>
<td>Linear</td>
<td>Quadratic</td>
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<tr>
<td><em>S. minutum</em></td>
<td>0.939/18</td>
<td>0.982/21</td>
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<td>0.831/16</td>
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<tr>
<td><em>E. globulus</em></td>
<td>0.981/9</td>
<td>0.830/8</td>
</tr>
<tr>
<td><em>S. minutum</em></td>
<td>0.955/6</td>
<td>0.831/6</td>
</tr>
<tr>
<td><em>E. globulus</em></td>
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<td>0.826/6</td>
</tr>
<tr>
<td><em>C. meneghiana</em></td>
<td>0.853/6</td>
<td>0.897/4</td>
</tr>
<tr>
<td><em>A. lagunensis</em></td>
<td>0.902/5</td>
<td>0.957/4</td>
</tr>
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</table>

<table>
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<tr>
<th>Source</th>
<th>Linear</th>
<th>Quadratic</th>
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<tbody>
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<td></td>
</tr>
<tr>
<td>Ericsson &amp; Ingestad 1988; Ingestad 1994</td>
<td></td>
<td></td>
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<tr>
<td>Ericsson 1994</td>
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<td>Shaﬁk et al. 1997</td>
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<td>Liu et al. 2001</td>
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</table>
explore the consequences of partitioning the N and P pools in another way. As ribosomes are also rich in N (N : P = 3 on a mass basis, Sterner & Elser 2002) increasing allocation to ribosomes in the organism results also in increasing allocations of protein N. Let N : P in ribosomes be \( \beta_{\text{NP}} \). Equation 3 is then replaced by

\[
N = N_p + \beta_{\text{NP}} P_a + \beta_N C
\]  

and a derivation along the lines in the Appendix shows that eqn 5 should be replaced by

\[
\eta_{\text{NC}}(\mu) = \frac{\beta_{\text{NP}}}{\Phi_{\text{CN}} \Phi_{\text{NP}}} \mu^2 + \frac{1}{\Phi_{\text{CN}}} \mu + \beta_N
\]  

The equation for \( \eta_{\text{PC}} \) remains unchanged. The consequences of introducing this additional N pool is thus to also make the \( \eta_{\text{NC}} \) function quadratic in \( \mu \). However, the term \( \beta_{\text{NP}} \mu/\Phi_{\text{NP}} \) is at most \( \mu \approx 0.2 \) and the quadratic term will probably not be distinguishable from the linear term with current quality of data.

The numerical values for the parameters found with data analysed in this paper all point to case 3, i.e. there should be a clear maximum in the relationship between N : P and relative growth rate. This is in contrast to what seems to be the case for heterotrophs, where N : P decreases monotonically with relative growth rate. The parameters describing the interactions between the elements (\( \Phi_{\text{CN}} \) and \( \Phi_{\text{NP}} \)) can also be compared with what can be predicted from biochemical properties. Ågren (1985b) estimated from observed rates of the catalysing capacity of Rubisco that \( \Phi_{\text{CN}} \) should have a value of 0.02 gC (mgN\(^{-1}\)) day\(^{-1}\), which is just a factor of 2 higher than observed for \( S. \) minutum. Sterner & Elser (2002) give values for the rate of protein synthesis by ribosomes. From their values we get \( \Phi_{\text{NP}} \) of 1.1 mgN (mgP\(^{-1}\)) day\(^{-1}\). This is a factor of two lower than the value given in Table 1 for \( B. \) pendula and a factor of seven lower for \( S. \) minutum. Given the crude approximations used to arrive at these values, the agreement between the values obtained from biochemical considerations and whole organism observations is not unreasonable, although this point deserves further evaluation.

A second observation relates to the problems of identifying the requirements of different elements for growth. As can be seen from the sometimes large distances between the critical N : P ratio and the observed values for the non-limiting element in Fig. 1, autotrophs have large capacities for excess uptake, a capacity that varies both between species and between elements. Element ratios obtained under the limitation of one of the elements are therefore likely to lead to exaggerated expected requirements of the other element. It is only when using results from conditions where both elements in the ratio are from limiting conditions that proper limiting ratios can be obtained. In the case of N and P, the N : P ratios derived from P-limited conditions with an excess of N are closer to the critical N : P ratio than N : P ratios obtained under N limitation. This makes sense because the excess N that \( S. \) minutum takes up under P limitation and low growth rates corresponds to an uptake of \( \sim 50 \) mg g\(^{-1}\) of N and this approximately doubles the N : P ratio relative to what is required at the critical level. On the contrary, the decrease in N : P by more than an order of magnitude under N limitation corresponds to an excess uptake of \( \sim 100 \) mg g\(^{-1}\) of P. Expressed on a molar basis, the excess uptakes are approximately the same, which indicates that the limitation on excess uptake might be a question of handling ion balances.

A further complication in understanding the critical N : P in autotrophs is variability between tissues. For example, a more detailed analysis of the data for \( B. \) pendula shows that the critical N : P is considerably higher in leaves than in stems and roots (data not shown). The relative contribution of different tissues will change with the size of the plant and the whole-plant critical N : P will then be changing not only with growth rate but also with plant size. The possibility of truly identifying the critical N : P in any given situation may therefore be limited and a single critical N : P might therefore serve as an approximate substitute.

The variations in stoichiometry shown in Fig. 1 are all accomplished by manipulating the rate of nutrient supply and thereby the relative growth rate at otherwise constant environmental conditions. If the other environmental

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**Figure 2** Critical N : P ratios calculated for \( S. \) minutum and \( B. \) pendula for conditions corresponding to estimated parameter values (solid lines), when \( \Phi_{\text{CN}} \) has been halved (broken lines), and when both \( \Phi_{\text{CN}} \) and \( \Phi_{\text{NP}} \) have been halved (dotted lines).
conditions change, so will all the stoichiometric relations. Factors, other than supply rates of nutrients, that decrease growth rates tend to increase N : C and P : C (Sterner & Elser 2002), but effects on N : P are not well studied. Figure 2 shows variations in N : P when environmental factors change. If light intensity changes, this should only affect the rate of carbon fixation per N, i.e. \( \phi_{CN} \). However, if temperature changes, all rate processes should change, i.e. \( \phi_{CN} \) and \( \phi_{NP} \). To illustrate this, I have halved \( \phi_{CN} \) alone as well as \( \phi_{CN} \) and \( \phi_{NP} \) together. Both changes result in increased critical N : P at low relative growth rates and decreased critical N : P at high relative growth rates with the effects of \( \phi_{CN} \) most pronounced at low relative growth rates and those of \( \phi_{NP} \) at high relative growth rates. What is less trivial is that changing only the interaction between C and N (\( \phi_{CN} \)) affects N : P at low relative growth rates, whereas changing equally the interaction between C and N and N and P has an effect on N : P over the entire span of relative growth rates. There are, therefore, no simple relationships between N : P and growth rates when nutrient supply rates change. If temperature changes, all rate processes should change, i.e. \( \phi_{CN} \) and \( \phi_{NP} \). To illustrate this, I have halved \( \phi_{CN} \) alone as well as \( \phi_{CN} \) and \( \phi_{NP} \) together. Both changes result in increased critical N : P at low relative growth rates and decreased critical N : P at high relative growth rates with the effects of \( \phi_{CN} \) most pronounced at low relative growth rates and those of \( \phi_{NP} \) at high relative growth rates. What is less trivial is that changing only the interaction between C and N (\( \phi_{CN} \)) affects N : P at low relative growth rates, whereas changing equally the interaction between C and N and N and P has an effect on N : P over the entire span of relative growth rates. There are, therefore, no simple relationships between N : P and growth rates when nutrient supply rates interact with other rate determining factors. The changes in \( \phi_{CN} \) and \( \phi_{NP} \) used here are fairly large in order to clearly illustrate qualitative effects. What is further required is an incorporation of different feedback mechanisms that might offset changes in one single process.

The results in Fig. 2 also emphasize the conclusion from Elser et al. (2000) that autotrophs from terrestrial and aquatic environments differ with respect to nutrient : C ratios but not with respect to N : P ratios. Eliminating the variability resulting from excess uptake shows that the fundamental biochemistry of the two types of autotrophs should be quite similar. If the two taxa used for Fig. 2 are representative for aquatic and terrestrial environments, and this seems reasonable, the growth environment has at least two major effects that need to be explained: the higher maximum relative growth rate and the larger excess uptake in aquatic taxa than in terrestrial taxa. A deeper understanding of these facts will probably require a detailed biochemical analysis along the lines of, for example, Sterner & Elser (2002) and Geider & La Roche (2002).

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REFERENCES


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APPENDIX. DERIVATION OF EQNS 5 AND 6

Substitute \( N_p \) from eqn 3 into eqn 1 and divide through with \( C \):

\[
\frac{1}{C} \frac{dC}{dt} = \mu = \phi_{CN} \frac{N}{C} - \phi_{CN} \beta_N = r_{NC} \phi_{CP} - \phi_{CN} \beta_N
\]

(A1)

and solve for \( r_{NC} \) to obtain eqn (5).

Differentiate eqn 3 with respect to time and use eqn 2 to eliminate \( dN_p/dt \) and eqn 4 to eliminate \( P_a \):

\[
\frac{dN}{dt} = \frac{dN_p}{dt} + \beta_N \frac{dC}{dt} = \phi_{NP} P_a + \beta_N \frac{dC}{dt}
\]

\[
= \phi_{NP} (P - \beta_P C) + \beta_N \frac{dC}{dt}
\]

(A2)

Divide through with \( C \) and use the \( \mu = 1/C(dC/dt) = 1/N(dN/dt) \):

\[
\frac{1}{C} \frac{dN}{dt} = \frac{N}{C} \frac{dN}{dt} = r_{NC} \mu = \phi_{NP} (\eta_C - \beta_P) + \beta_N \mu
\]

(A3)

Solving eqn A3 for \( r_{NC} \) and using eqn 5 to eliminate \( r_{NC} \) gives eqn 6.