



On relating physical limits to the carbon: nitrogen ratio of unicellular algae and benthic plants

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Abstract

Unicellular algae such as phytoplankton and benthic microalgae have an elemental ratio of carbon to nitrogen to phosphorus (C/N/P) of approximately 106:16:1, known as the Redfield ratio. Benthic plants, including benthic macroalgae and seagrass, have a significantly different and more variable C/N/P ratio, with a median of 550:30:1, herein called the Atkinson ratio. In this paper, the implications of physically limited light absorption and nutrient uptake, combined with the biological constraint of a relatively fixed elemental stoichiometry, are investigated. Calculations reveal that: (1) for randomly oriented convex-shaped unicellular algae, if nutrient uptake is a linear function of surface area and light absorption is a linear function of projected area, then the ratio of light absorption to nutrient uptake is constant; (2) for benthic plants, the ratio of the rates of light absorption to nutrient uptake varies depending on plant morphology and hydrodynamic conditions; and (3) underlying other environmental influences, there is a constant factor of four difference in the ratio of the rates of light absorption to nutrient uptake of benthic plants, relative to unicellular algae, that can be attributed to the two- and three-dimensional environments they respectively experience. The contrasting geometric properties of unicellular algae and benthic plants, combined with the biological constraint of a relatively fixed stoichiometry, appear to exert a significant evolutionary pressure on the magnitude and variability of their C/N ratios.

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1. Introduction

A large number of studies have been conducted on the influence of the size and shape of unicellular algae on nutrient uptake (Munk and Riley, 1952; Pasciak and Gavis, 1975; Karp-Boss et al., 1996) and light absorption (Kirk, 1976). Other studies have investigated the effect of shape and roughness on nutrient

uptake (Hurd, 2000) and light absorption (Enriquez et al., 1994) by photosynthetic benthic communities.

Unicellular algae and benthic plants use light energy to fix carbon (C) and combine the carbon with elements such as nitrogen (N) and phosphorus (P) at relatively constant stoichiometric ratios (Kirk, 1994). C/N/P ratios of unicellular algae are typically around 106:16:1, a ratio called the Redfield ratio (Redfield et al., 1963). The C/N/P ratios of benthic plants are larger and more variable, with a median C/N/P ratio of 550:30:1 (Fig. 1), called the Atkinson ratio (Atkinson and Smith, 1983).

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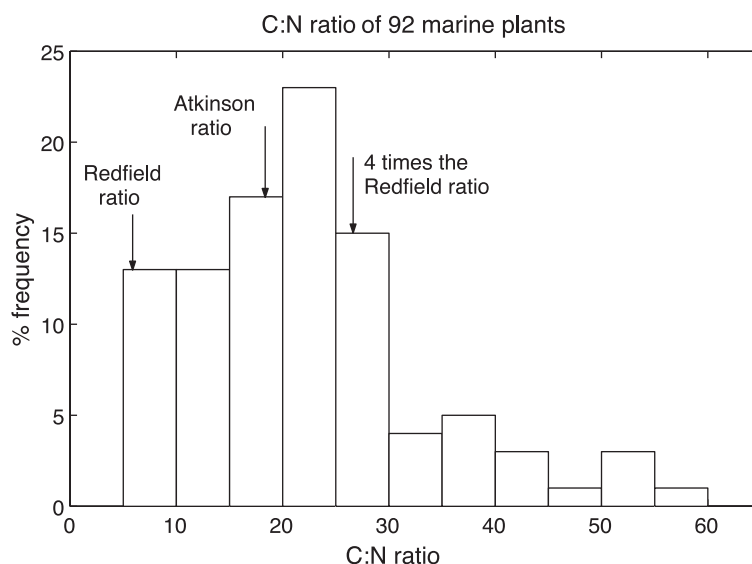


Fig. 1. Percent frequency of C/N ratios for 92 benthic plants collected from a variety of habitats (Atkinson and Smith, 1983). The Redfield ratio (C/N=6.625), the Atkinson ratio (C/N=18.3) and the Redfield ratio times the geometric factor of four (C/N=26.5) are indicated.

To consider the potential effects of the ratio of light absorption to nutrient uptake on C/N ratios, the following calculations rely on the assumption of a biological constraint of a relatively fixed C/N ratio. The C/N ratio of both unicellular algae and benthic plants can change quickly in response to environmental conditions. Environmental conditions can alter the ratio of light absorption to nutrient uptake by many orders of magnitude, but the cellular C/N ratios typically vary by just a few factors or less, and never by orders of magnitude. Even after many generations, autotrophs will respond to a particular set of environmental conditions by returning to the same C/N ratios as previous generations had under those conditions, as demonstrated by the repeatability of chemostat experiments on unicellular algae (Caperon, 1969; Droop, 1974). This paper attempts to explain aspects of the inter-generational component of C/N ratios, as quantified by the Redfield and Atkinson ratios, which are presumably influenced by evolutionary pressures.

In particular, this paper explores whether the biological constraint of a relatively fixed stoichiometry and the effects of physical limits of the rates of nutrient uptake and light absorption may be evident in the C/N ratios of unicellular algae and benthic plants.

2. Theory

Simple calculations of the physically limited maximum rates of light absorption and nutrient uptake can be made using geometric approximations. The approximation of rates of nutrient uptake and light absorption as the physical, shape-dependent limits is most applicable under environmental conditions in which physically limited rates are slower than physiological processes (Sanford and Crawford, 2000).

The calculations of three ratios are undertaken in this paper: (1) the ratio of light absorption to nutrient uptake in unicellular algae; (2) the ratio of light absorption to nutrient uptake in benthic plants; and (3) the ratio of light absorption to nutrient uptake of unicellular algae relative to benthic plants. The three cases considered are not intended to be applicable under all environmental conditions, and are to some extent mutually exclusive. For example, under case 1, nutrient uptake to unicellular algae is assumed to be a function of surface area, while in case 3 both a surface area and radial dependence is considered. Nonetheless, each case represents a feasible implication of shape-dependent physical limits and a fixed stoichiometry.

2.1. Case 1: unicellular algae

In this paper, unicellular algae are taken to include both those suspended in the water column (phytoplankton), and those suspended in sediments (microphytobenthos). Nutrient uptake to unicellular algae may be limited by transport through a diffusive boundary layer (Munk and Riley, 1952), by uptake kinetics on the cell surface, or a combination of the two (Pasciak and Gavis, 1975). The diffusive limit is proportional to radius, r , while a process on a cell surface is likely to be proportional to surface area, $4\pi r^2$. At smaller radii, surface processes are more likely to be limiting (since their rates scale with r^2 , compared to the diffusive limit, which is a function of r).

Light absorption by unicellular algae is a function of the size, shape and pigment concentration (Kirk, 1994). At low light levels, the initial slope of the photosynthesis against irradiance curve approaches the absorption cross-section of the cell. For a strongly pigmented cell with a high absorption coefficient, the absorption cross-section approaches the average (over the cell's orientation to the light) projected area. Using the general relationship of intracellular chlorophyll a concentration as a function of cell volume for marine diatoms cultured at $25 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (Finkel, 2001), and the Mie theory of absorption of light by spherical particles (Finkel and Irwin, 2000), unicellular algae cells have an absorption cross-section between 54% (volume= $524 \mu\text{m}^3$) and 75% (volume= $3.8 \times 10^6 \mu\text{m}^3$) of the projected area of a sphere of the same volume. For the following calculations, the absorption cross-section is approximated as the projected area. Other limitations on photosynthesis, such as diffusive transport of dissolved CO_2 , which may be important under particular environmental conditions (Smith and Walker, 1980), have not been considered.

For a spherical cell of radius r , the surface area is $4\pi r^2$ and the projected area is πr^2 —a factor of four different. In fact, the surface area of all randomly oriented convex shapes of any size is given by four times the projected area. This geometric property was discovered by Augustin Cauchy (Vickers and Brown, 2001). The result was first presented in 1832 and is documented in a compilation of his work (Cauchy, 1908). In general, suspended unicellular algae are

convex. Of the 850+ genera of unicellular algae listed in Hillebrand et al. (1999), only 5 are considered concave for the purposes of biovolume calculations. Unicellular algae are typically much smaller than the smallest scale of motions of fluid in the natural environment, and as a result are unable to orient themselves towards light (Kirk, 1976). A possible exception are dinoflagellates, which can have a time scale for reorientation which is shorter than the time scale of the smallest fluctuations in natural turbulent flows (Karp-Boss et al., 2000). Whether this swimming ability is utilised just for migratory purposes, or whether it is utilised to orient a cell favourably towards sunlight over a significant portion of the daylight hours is not known. In any case, looking broadly at unicellular algae, a random distribution of orientation is a reasonable assumption. Assuming (1) nutrient uptake is a linear function of surface area and (2) light capture is a linear function of projected area, the ratio of physically limited light absorption to nutrient uptake of *all* convex randomly oriented unicellular algae cells is *identical* (a simplification surprising to the authors).

The evolutionary pressures on unicellular algae to take a particular shape to maximise either (1) nutrient uptake by maximising surface area or (2) light absorption by maximising projected area may to some extent be reduced by the biological constraint of a relatively fixed stoichiometry and the physical constraint of a constant ratio of surface area to projected area characteristic of all randomly oriented convex shapes. Since the evolutionary pressure for unicellular algae to take a particular C/N ratio, as exerted by processes with shape-dependent physical limits, is equal for all cells, the Redfield ratio may be a result of biological factors alone, as suggested by Falkowski (2000). The variety of unicellular algal shapes is consistent with a range of shapes bestowing similar fitness.

2.2. Case 2: benthic plants

The calculations of light absorption and nutrient uptake rates to unicellular algae in case 1 are undertaken per individual cell (or per unit biomass). For benthic plants such as macroalgae and seagrass, it is simpler to apply physical limits to the whole community. In particular, the boundary layer that surrounds a

benthic plant is set up by the roughness of the whole community (Baird and Atkinson, 1997). This suggests a fundamental difference between the unicellular algae and benthic plant communities. The nutrient field that surrounds a unicellular alga varies away from the cell surface in three dimensions, while that of a benthic plant community can be assumed to vary only normal to the surface. In this paper, the fundamental difference in nutrient fields surrounding unicellular algae and benthic plant communities will be described as part of the three- and two-dimensional environment that the autotrophs respectively experience. That is, as a result of extending along a two-dimensional surface, the benthic plant communities experience an environment similar to that of two-dimensional surface. Naturally, it is recognised that benthic plant communities still have many three-dimensional properties. The contrast between a two- and a three-dimensional experience will be become clear in case 3 below.

The maximum light received by a benthic plant community per unit area is simply given by the irradiance (which is the flux per unit area). The ability of the benthic plants to capture this light depends primarily on the thickness of the canopy and the absorption cross-section of the leaves (Enriquez et al., 1994). To estimate how thick a benthic plant canopy needs to be, consider a community with an average carbon-specific absorption cross-section of $0.054 \text{ m}^2 \text{ g C}^{-1}$, the value Enriquez et al. (1994) uses for macrophyte leaves. To capture $1/e^2$ or 86% of the light, a benthic community with an average absorption cross-section of $0.054 \text{ m}^2 \text{ g C}^{-1}$ would require 37 g C m^{-2} spread evenly over the bottom. A biomass of 37 g C m^{-2} is not particularly dense for a benthic community. A well-established benthic community can reasonably be approximated to have most of the light that reaches it available for photosynthesis.

Like nutrient uptake by unicellular algae, benthic communities may be limited by transport through a diffusive boundary layer (Baird and Atkinson, 1997), by uptake kinetics on the plant surface, or by a combination of the two (Bilger and Atkinson, 1995). When limited by transport through a diffusive boundary layer, nutrient uptake is best thought of as a flux per unit projected area, while the rate remains a function of surface roughness and water velocity. In the case of benthic communities, limitation of nutrient

uptake by a diffusive boundary layer is common (Hurd, 2000).

It is unresolved as to how best to quantify the effect of irregular roughness on mass transfer processes such as nutrient uptake (Baird and Atkinson, 1997). Hearn et al. (2001) used the rate of dissipation of turbulent kinetic energy in the water column above the surface, ε_{BP} , to determine the rate of nutrient uptake to a benthic community, J_{BP} :

$$J_{\text{BP}} = \left(\frac{D^2}{\nu} \right)^{1/4} \varepsilon_{\text{BP}}^{1/4} (N - N_0) \quad (1)$$

where D is the molecular diffusivity of the nutrient, ν is the molecular diffusivity of momentum, N is the nutrient concentration outside the boundary layer and N_0 is the nutrient concentration at the surface of the benthic community. At the physical limit for nutrient uptake, N_0 approaches zero. The dissipation rate of turbulent kinetic energy ranges from 10^{-9} to $10^{-6} \text{ m}^2 \text{ s}^{-3}$ in the pelagic ocean (Mann and Lazier, 1991). Near a surface, such as a coral reef or other benthic community, ε_{BP} can take values as high as $10^{-2} \text{ m}^2 \text{ s}^{-3}$ (Hearn et al., 2001).

In contrast to unicellular algae, the dependence of nutrient uptake on ε_{BP} implies that the ratio of light absorption to nutrient uptake for a given benthic plant in a near shore environment will vary widely depending on prevailing environmental conditions and plant morphology. Given the wide range of benthic environmental conditions and benthic plant morphology, it is not surprising that there is a greater variability in the C/N ratio of benthic plants than is the case for unicellular algae.

2.3. Case 3: unicellular algae compared to benthic plants

Cases 1 and 2 consider the effects of the ratio of light absorption to nutrient uptake on the variability of C/N ratios in unicellular algae and benthic plants. This third case considers whether there may be a physical origin to the significantly different C/N ratios of benthic plants and unicellular algae.

In order to illustrate a fundamental difference between the three-dimensional environment that unicellular algae experience and the two-dimensional experience of the benthic plant communities, a num-

ber of assumptions are made, some of which are later removed. As a first approximation, assume the nutrient uptake rate to both unicellular algae and benthic plants is limited by diffusion through a diffusive boundary layer of thickness δ_{BP} for a benthic plant and δ_{UA} for an algal cell. As in cases 1 and 2, it is assumed that all light reaching the phototroph is absorbed and that this rate of light absorption is directly related to the rate at which the phototroph incorporates carbon.

For a benthic plant community, light absorption and nutrient uptake rates are considered as per unit projected area of the benthos. The physically limited N uptake rate is given by Fick's law of diffusion as DN/δ_{BP} where D is the molecular diffusivity of the nitrogen species and N is the concentration of the nitrogen species. The concentration at the surface of the plant, N_0 , is assumed to be zero. The diffusive boundary layer thickness surrounding a benthic plant, δ_{BP} , will be a function of plant morphology and hydrodynamic conditions (Crawford and Sanford, 2001). As in case 2, the maximum light capture by a benthic plant community is assumed to be given by the irradiance, I , which is specified as a flux per unit projected area.

For unicellular algae, light absorption and nutrient uptake rates are evaluated per cell. A spherical cell of radius r has a surface area of $4\pi r^2$. The nutrient uptake to the cell across a boundary layer of thickness δ_{UA} is assumed to be given by Fick's law (as above), this time multiplied by the surface area to give a flux per cell, $4\pi r^2 DN/\delta_{UA}$. As in case 1, the maximum light absorption by the cell is assumed to be given by the projected area, πr^2 , multiplied by the irradiance, I , or $\pi r^2 I$.

Under the above assumptions, the ratio of the physically-limited light absorption to nutrient uptake rates of a benthic plant community compared to that of the unicellular algal cells becomes:

$$\left[\frac{(\text{light} : N)_{BP}}{(\text{light} : N)_{UA}} \right] = \frac{\frac{I}{DN/\delta_{BP}}}{\frac{I\pi r^2}{4\pi r^2 DN/\delta_{UA}}} = \frac{4\delta_{BP}}{\delta_{UA}} \quad (2)$$

Assuming that the diffusive boundary layer thicknesses are similar ($\delta_{BP} \approx \delta_{UA}$), the two-dimensional experience of the benthic plant results in a light

absorption rate relative to nutrient uptake rate of four times that of the three-dimensional algal cell.

While the above analysis illustrates that the ratio of light absorption and nutrient uptake differs by a factor of four due to dimensionality considerations, δ_{BP} and δ_{UA} are not necessarily equal. The boundary layer thicknesses δ_{BP} and δ_{UA} will be affected by the autotroph geometry and the turbulence in the environment. In particular, the curvature of the unicellular algae reduces the dependence of diffusion limited uptake to a radial dependence, as noted in case 1.

Instead of quantifying the uptake in terms of surface area and boundary layer thickness, it is more convenient to quantify diffusion limited nutrient uptake as a function of the dissipation rate of turbulent kinetic energy, ε . Eq. (1) gives the nutrient uptake rate for a benthic surface as a function of ε . For a small spherical particle of radius r , the diffusion limited nutrient uptake rate is given by (Batchelor, 1980):

$$J_{\text{cell}} = 4\pi r D \left(1 + 0.55 \left(\frac{r^2}{D} \sqrt{\frac{\varepsilon_{UA}}{\nu}} \right)^{1/3} \right) (N - N_0) \quad (3)$$

where ε_{UA} is the rate of dissipation of turbulent kinetic energy in the vicinity of the unicellular algae and D , ν , N and N_0 have their previous meanings (and noting that this is essentially a linear radial dependence of nutrient uptake, with an additional weak radial dependence due to fluid motion through ε_{UA}).

The ratio of light absorption to nutrient uptake, Eq. (3), can then be re-written:

$$\left[\frac{(\text{light} : N)_{BP}}{(\text{light} : N)_{UA}} \right] = \frac{4\nu^{0.25} D^{0.5} \left(1 + 0.55 \left(\frac{r^2}{D} \sqrt{\frac{\varepsilon_{UA}}{\nu}} \right)^{1/3} \right)}{\varepsilon_{BP}^{0.25} r} \quad (4)$$

Applying ranges of $10^{-9} < \varepsilon_{UA} < 10^{-5} \text{ m}^2 \text{ s}^{-3}$, $10^{-6} < \varepsilon_{BP} < 10^{-3} \text{ m}^2 \text{ s}^{-3}$ and $r < 30 \text{ } \mu\text{m}$, generally, it can be said that benthic plant communities receive 1–40 times more light than N, relative to unicellular algae. A factor of four can be attributed to the difference in dimensionality of unicellular algae and benthic plant community experience. The actual C/N ratio of ben-

thic plants is some three times that of unicellular algae (Fig. 1).

Only for large cells ($r > 30 \mu\text{m}$) in low turbulent conditions ($\varepsilon_{\text{UA}} = 10^{-9} - 10^{-7} \text{ m}^2 \text{ s}^{-3}$), compared to highly turbulent flows over benthic plants ($\varepsilon_{\text{BP}} = 0.001 \text{ m}^2 \text{ s}^{-3}$) do benthic communities have the physical limits with greater nutrient uptake than light absorption, relative to unicellular algae.

3. Discussion

There are a large number of factors that will exert an evolutionary pressure on the C/N ratio of aquatic phototrophs. Falkowski (2000) proposed that the origin of the constant Redfield ratio is a result of a limitation intrinsic to protein synthesis. Atkinson and Smith (1983) proposed the higher C/N ratio of benthic plants was due to a requirement of structural strength. This paper adds the physical limits of nutrient uptake and light absorption to this list. In common with Falkowski's and Atkinson's proposals, the physical constraints described here will apply to the extremely broad range of aquatic phototrophs.

The essence of autotrophic growth is the combination, at a relatively fixed ratio, of elements such as C and N. An autotroph's ability to grow will depend on its requirement of light (to fix C) and N, as determined by the C/N ratio, and the rate at which it receives light and N from the environment. To be ideally suited to a particular environment, it would therefore not be surprising to observe different C/N ratios for autotrophs in different environments. This paper has attempted to link physical factors characteristic of two types of autotrophs, unicellular algae and benthic plants, to their observed C/N ratios.

The significantly different and more variable C/N ratios of benthic plants relative to unicellular algae stimulated the three cases investigated in this paper. The grouping of autotrophs into just two categories, unicellular algae and benthic plants, instead of a further breakdown into taxonomic, size or morphological categories, allows broad assumptions of light absorption and nutrient uptake rates which should be kept in mind when interpreting the outcome of the calculations. In particular, the shift that can occur, especially in unicellular algae, between nutrient uptake limitation by diffusive transport and limitation by

cell surface reactions complicates any conclusions that can be drawn. It may turn out that only one of the case 1 and case 3 calculations is relevant to the C/N ratios in autotrophs.

Of the calculations undertaken, perhaps the most surprising is case 3. At first glance, it might appear a significant disadvantage to benthic plants that, as a result of their higher C/N ratios, they require approximately four times the light, relative to nitrogen, compared to the unicellular algae suspended in the water column. Such a perception is further encouraged by the fact that unicellular algae, which are suspended in the water column, have a chance to absorb light before it reaches the benthos. Case 3 suggests, contrary to this perception, that the two-dimensional experience of benthic communities results in a greater potential light absorption relative to nutrient uptake than the three-dimensional experience of unicellular algae. Given this greater potential of light absorption, it is therefore not surprising to note that benthic communities are commonly limited by nutrient uptake (Hurd, 2000), and can have greater C/N ratios than unicellular algae.

In conclusion, calculations based on physically limited rates of light absorption and nutrient uptake provide an interesting viewpoint to comment on observed C/N ratios. The constant ratio of physically limited light absorption and nutrient uptake in convex-shaped randomly oriented unicellular algae is consistent with the observed Redfield ratio. The more variable C/N ratio of benthic plants is consistent with light absorption and nutrient uptake rates that vary with plant morphology and environment. The C/N ratios of benthic plants are significantly greater than unicellular algae, in accordance with the greater potential light absorption relative to nutrient uptake of benthic communities relative to unicellular algae. These calculations suggest that, whether by selection or coincidence, benthic plants are generally as well suited to phototrophic processes in the two-dimensional environment they experience as algal cells are to a random orientation in a three-dimensional environment.

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