Volume 4 Issue 1 January 2020

Ratios Matter

Does excess carbon dioxide make my ecosystem fat?

Justus von Liebig is a revered figure in ecology and agriculture because of his important contribution of the Law of the Minimum. The image of a barrel with the lowest stave representing the most limiting nutrient, often N or P, is pretty much scorched into every ecologist's brain. However, the simplicity of this concept is increasingly inconsistent with recent evidence that plants and microbes regulate internal nutrient and carbon concentrations non-homeostatically. In fact, we have observed that strains of heterotrophic bacteria can change their biomass C:P ratios over 1000% when moved from high into low P media. The fact that microbes can be extremely flexible in their biomass composition is also consistent with increasing evidence from natural systems showing limitation of two or more nutrients.

But what does this have to do with an obese environment? In Cotner (2019), I argue that one of the manifestations of an environment bathed in excess CO_2 is increasing C:nutrient stoichiometry in natural systems. Free-air CO_2 enrichment experiments have demonstrated that not only does carbon increase in plants with increasing CO_2, but also that micronutrients are essentially diluted out of biomass, with important implications for the food we eat as well as natural ecosystems. Excess energy in our food makes us obese and excess carbon may be doing the same thing in ecosystems. So, while as ecologists we focus a lot of our studies on climate change as an important manifestation of the 'CO_2 problem', there is also a stoichiometric manifestation that we need to pay more attention to, with implications for our health, food webs and biogeochemical cycles.

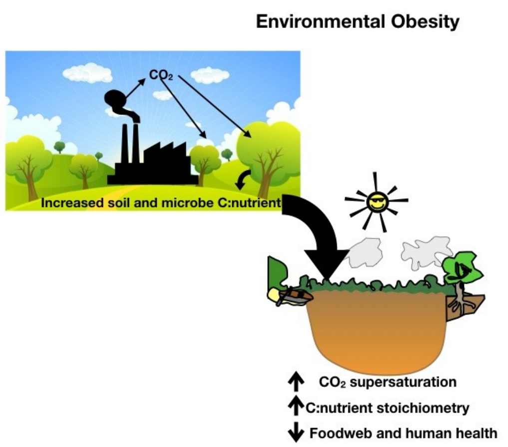


Figure 1 from Cotner (2019). Hypothesized effects of increased CO_2 on ecosystems.

Contributed by Jim Cotner

Cotner, J.B. 2019. How increased atmospheric carbon dioxide and 'The Law of the Minimum' are contributing to environmental obesity. Acta Limnol. Bras. 31. doi:10.1590/s2179-975x6519

ASLO's Yentsh-Schindler Early Career Award

Ratios Matter is proud to report that its own Dedmer van de Waal has won another award: ASLO's 2020 Yentsh-Schindler Early Career Award. This award is given out annually to an early career member who significantly contributes to research, education, and broader societal issues. Dedmer won this award, in part, for his work in describing the mechanisms of phytoplankton toxin production using ecological stoichiometry. He has identified that concentrations of supply nitrogen (N) correlated positively with the production of low C:N toxin molecules (i.e., microcystin and saxitoxin). Congratulations on this well-deserved award Dedmer!

Help Wanted: "Nutrient Stoichiometry in Aquatic Ecosystems" in the *Encyclopedia of Inland Waters* needs updating

I was recently contacted by an editor of the forthcoming revised edition of the *Encyclopedia of Inland Waters* about the ~6800-word article entitled "Nutrient Stoichiometry in Aquatic Ecosystems". They are looking for updates to that article, so now I'm looking for some help.

I'm requesting two kinds of help from the *Ratios Matter* community. First, if you wish to suggest new topics or updated references that should be part of this relatively compact but topically broad overview of the field, please send those to me. Sending me your own work is fine and I'll be happy to receive it, but even more impressive would be sending me work by others that you feel merits inclusion.

Second, if a relatively small number of persons want to roll up their proverbial sleeves and do some of the writing of the revision with me, I'd be happy to include 2-3 coauthors, especially early career researchers. If interested, please send me an email saying what you think you can contribute. I'll be most interested in including fresh perspectives and shoring up areas where the original article was lacking, recognizing we still have to meet some stringent space limitations with the whole thing.

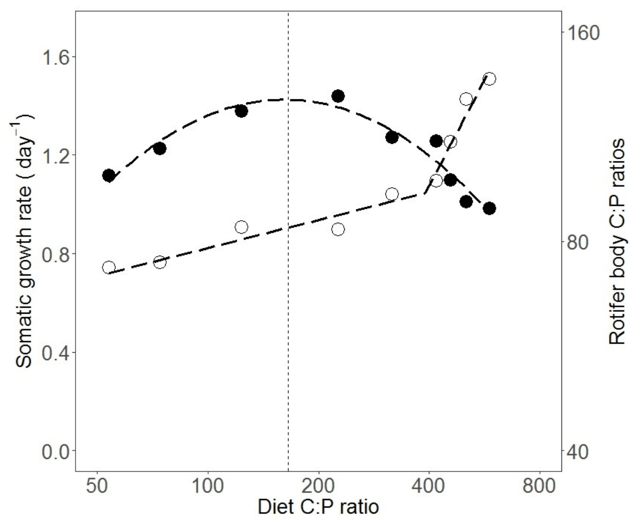
I'm told the deadline is "mid-2020". If you have questions or if you don't have institutional access to the original article linked to above let me know.

Bob Sterner, stern007@d.umn.edu
Large Lakes Observatory, University of Minnesota Duluth

Plankton consumer responses to a 10-fold food C:P gradient

Stoichiometric mismatch occurs when the elemental composition of resources deviates from that of the consumers' demand. Although most research has focused on the effects of food P-limitation, some studies have suggested that consumers may be living on a 'stoichiometric knife-edge' and that high concentrations of P in their food may reduce consumer performance as well. However, the underlying mechanisms of the knife-edge are still poorly documented and understood.

In this study, we exposed the planktonic rotifer *Brachionus calyciflorus* to a ten-fold gradient of food C:P ratios. We indeed found a unimodal response of both somatic and population growth along the gradient, with a growth optimum at a food C:P level of about 170. Above this optimum, growth rate reductions coincided with increased food ingestion rates and decreased P loss rates, while the opposite pattern was found with decreasing food C:P. Interestingly, along with strong performance reductions, we observed a complete homeostatic breakdown of rotifers when food C:P exceeded 391. Rather than adaptive plasticity, the latter suggests an inability of animals to cope with strong stoichiometric imbalance.



Response of rotifer specific somatic growth rate (solid symbols) and body stoichiometry (open symbols) to the experimental food C:P gradient. The dashed lines represent the expected values according to the respective regression models; the vertical dotted line represents the food C:P ratio corresponding to the maximal somatic growth rate as calculated by a quadratic regression model. (Modified from Figure 1b and Figure 2a in Zhou and Declerck 2019).

Our results thus confirm the existence of a stoichiometric knife-edge. Furthermore, they suggest that consumers face different challenges along opposite sides of the C:P gradient (i.e., animals experience excess C at high food C:P and excess P under low C:P conditions).

From the paper, "*Our results suggest that the mechanisms underlying adverse effects of stoichiometric imbalance are determined by both the identity of elements that are limiting and those that are present in excess. Negative effects of excess P reveal an additional way of how eutrophication may affect consumers.*"

Contributed by Libin Zhou and Steven Declerck

Zhou, L. and S.A.J. Declerck. (2019). Herbivore consumers face different challenges along opposite sides of the stoichiometric knife edge. Ecology Letters. 22, 2018-2027. https://doi.org/10.1111/ele.13386

Profiles in Stoichiometry

Nine Questions for Vanessa Minden

Tell us about yourself and how you became interested in ecology. I am a German researcher currently working at the Vrije Universiteit Brussel, Belgium. I started studying biology with the idea of becoming a marine ecologist (but now I forget why!). However, I soon realized that plants are pretty cool and that I prefer terrestrial plant ecology. This was confirmed when I began studying the effects of an invasive plant on the native community in Hawaiian rain forests. After that, I worked on plant responses to environmental gradients in salt marshes in Northwest Germany for my PhD research. Most recently, I have been working in greenhouses, which I somewhat blame on the bad weather on the North Sea coast. The questions I am interested in (plant responses to different types of stressors) are nonetheless more suited to greenhouse experiments. For example, we are testing the effects of veterinary antibiotics on plant performance. It turns out that antibiotic concentrations as we find them now in our agricultural fields already affect plant performance and also affect plant element concentrations.

Do you remember when you first heard about ecological stoichiometry? This was during my PhD project. We were measuring C, N and P in plant tissues along with other plant traits like SLA or canopy height. I remember that it took me a while to get into the topic, as it went deeper into plant biochemistry than the 'ordinary' plant traits. After my PhD, I continued on with plant stoichiometry. For me, matching plant stoichiometry with other traits (e.g. light interception through leaf area) is a perfect combination to understand plant responses to environmental drivers.

What is your current research in ecological stoichiometry? My current research is on plant responses to variation in N, P and K availability, (transgenerational) plasticity in plants, and the substitution of C by silicon (Si) as a response to nutrient stress. To use the words of Julia Cooke: 'Plant ecology [is] more silicious than we realise.' ☺

What is your favourite stoichiometry paper and why? That is an easy one! It is Güsewell's (2004) paper, "N:P ratios in terrestrial plants: variation and functional significance", *New Phytologist* 164: 243-266. I first read it during my PhD and it is so rich in information. I particularly like the parts on ontogenesis and on the regulatory coefficient H.

Do you view ecological stoichiometry as its own research field? Why or why not? In part, ES is seen as its own research field, although it should not be. For example, my field of research is on plant elements, or ratios of plant elements, which I see as plant traits, in the sense of the definition. Some of them are functional traits, like N or P, others not, like iodine. I think we are still in the process of distinguishing the 'functional' elements from the 'non-functional' elements, or in other words, we still do not fully understand their role in plant functioning.

Where do you see ecological stoichiometry progressing in the next 10 years? Given the increasing inputs of nutrients into our natural environments, ES is certainly an important tool to better understand the effects of changes on nutrient availabilities. As such, continuing research in ES is timely and important. Getting ES-research more in the spotlight of applied sciences would certainly be progress. For example, potassium (K) is very important in drought stress, which is a key component of climate change. Also, promoting a stronger link between plant ecology and ES-research with (epi)genetics would be a major advantage as these fields currently work rather separately.

Do you see elements beyond CNP becoming more of a focus? Other elements: as I said K is very important, especially in the context of drought resistance. There is a very nice review by Sardans & Penuelas (2015), and in Brussels, we conducted a study on K availability in comparison to N and P (Minden & Olde Venterink 2019). Also, certainly silicon! This is a very interesting element, I just submitted a first study to a journal (fingers crossed!), examining to which extent plants substitute C with Si under nutrient stress. It is much 'cheaper' for the plants to take up Si than to assimilate C and this may be important as plant strategy under various environmental conditions.

What is your favourite element? Right now silicon, but I like potassium a lot too. Who knows what it will be in a few years.

Do you use your stoichiometric knowledge in your personal life? Some time ago, I was growing tomatoes in my garden. I wanted to do them some good, so I buried biomass of the nettle, *Urtica dioica,* in their pots as fertilizer. *U. dioica* grows in nutrient rich environments and has an Ellenberg N value of 8. The tomatoes turned out to be giants. Super huge plants, but with no flowers at all. I realized that I had created P-limitation by providing so much N, and with that comes a suppression of the generative stage. I had no tomatoes that year, but at least I knew why…

Sardans, J. and J. Peñuelas. 2015. Potassium: a neglected nutrient in global change. Global Ecology and Biogeography 24: 261-275.

Minden, V. and H. Olde Venterink. 2019. Plant traits and species interactions along gradients of N, P and K availabilities. Functional Ecology 33: 1611-1626.

Extreme Stoichiometry at its Limits

For ecological stoichiometry, extreme stoichiometry is usually thought of in terms of elevated C:N or C:P ratios seen in especially nutrient-limited ecosystems or plants. Humans have pushed the stoichiometry of engineered materials far past these natural boundaries. One example of this is refined silicon (Si) that, at metallurgical grades, contains other elements such as Al, P, Ca, and Fe[1]. These elemental impurities can be at concentrations in hundreds to thousands of parts per million, which would mean a Si:other element of ~1 x 10^3 or 1000 to 1 or less[1]. This metallurgical grade Si is not pure enough for use in semiconductors[2] as small amounts of other elements can affect their electrical characteristics[3]. To address this, humans have pushed this Si:other element ratio by purifying Si in semiconductors, which can have up to “eleven nines” purity[4]. Eleven nines means 99.999999999% Si content (by mols) or eleven nines past the decimal point in the proportional ratio. This is equivalent to a Si:other element ratio of approximately 1 x 10^{11} or 100 billion to 1 or an increased purity of 8 orders of magnitude over the metallurgical grade Si. While important for engineered materials, this level of extreme stoichiometry is highly unlikely in biological materials given the diversity of elements needed to sustain life and the varied elemental composition of different biochemical constituents. Nevertheless, maybe now it makes sense why computers have been so useful in the study of extreme biological stoichiometry.

[1]https://en.wikichip.org/wiki/electronic-grade_silicon
[2]As in, silicon semiconductors which are used in most computerized electronic devices.
[3]Somiya, Shigeyuki. 2013. *Handbook of advanced ceramics: materials, applications, processing, and properties*. Academic press.
[4]Shimura, Fumio, ed. 2012. *Semiconductor silicon crystal technology*. Elsevier.

Going to ASLO-SFS 2020?

As always, **ecological stoichiometry** is on the agenda. Submit an abstract and/or be sure to check out these special sessions:

SS41 Showering the Earth with carbon: The implications of CO_2 as an unbalanced stoichiometric driver to organism, ecosystem and human health
SS65 Macroscale stoichiometry: assessing elemental ratios from ecosystems to the globe
SS43 Physiological and Environmental Drivers of HAB Formation and Toxicity

Abstract submission deadline is March, 9, 2020. We hope to see you and your stoichiometry at ASLO-SFS 2020 this coming summer.

ASLO-SFS 2020
JOINT SUMMER MEETING
7–12 June 2020 · Madison, Wisconsin

Contact us by email:
ratiosmatter@gmail.com

Find us on the web:
ratiosmatter.wordpress.com

Follow us on Twitter:
@ratios_matter

Ratios Matter is a non-profit, informational newsletter that is independently published primarily for news and educational purposes. We will automatically send you each new issue; just send us an email requesting your free subscription. Comments, suggestions, and submissions including photos, graphics, and paper summaries are always welcome. Contact us at ratiosmatter@gmail.com with your submission ideas.

Selected Recent Stoichiometry Publications

Bertrand, I., V. Viaud T. Daufresne and others. 2019. Stoichiometry constraints challenge the potential of agroecological practices for the soil C storage. A review. Agron. Sustain. Dev. 39: 54 doi:10.1007/s13593-019-0599-6

Buchkowski, R.W., A.N. Shaw, D. Sihi, G.R. Smith and A.D. Keiser. 2019. Constraining carbon and nutrient flows in soil with ecological stoichiometry. Front. Ecol. Evol. 7: 382. doi:10.3389/fevo.2019.00382

Butler, O.M., J.J. Elser, T. Lewis and others. 2019. The multi-element stoichiometry of wet eucalypt forest is transformed by recent, frequent fire. Plant Soil In Press: 1–15. doi:10.1007/s11104-019-04397-z

DeGasparro, S.D., D.V. Beresford, C. Prater and P.C. Frost. 2019. Leaf litter decomposition in boreal lakes: variable mass loss and nutrient release ratios across a geographic gradient. Hydrobiologia In Press: 1–12. doi:10.1007/s10750-019-04140-w

Fernández-Martínez, M., I. Pearse, J. Sardans and others. 2019. Nutrient scarcity as a selective pressure for mast seeding. Nat. Plants 5: 1222–1228. doi:10.1038/s41477-019-0549-y

Grover, J.P., J.T. Scott, D.L. Roelke and B.W. Brooks. 2019. Dynamics of nitrogen-fixing cyanobacteria with heterocysts: A stoichiometric model. Mar. Freshw. Res. In Press: 1–15. doi:10.1071/MF18361

Hofmann, P., A. Chatzinotas, W.S. Harpole and S. Dunker. 2019. Temperature and stoichiometric dependence of phytoplankton traits. Ecology 100: e02875. doi:10.1002/ecy.2875

Holland, A.T., C.J. Williamson, F. Sgouridis and others. 2019. Dissolved organic nutrients dominate melting surface ice of the Dark Zone (Greenland Ice Sheet). Biogeosciences 16: 3283–3296. doi:10.5194/bg-16-3283-2019

Ji, H., B. Du, J. Wen, N. Sun, M. Peng, H. Du and C. Liu. 2019. Metabolome and ionome analyses reveal the stoichiometric effects of contrasting geological phosphorus soils on seed-parasitic insects in subtropical oak forests. Chemoecology 29: 199–210. doi:10.1007/s00049-019-00290-4

Lemmen, K.D., O.M. Butler, T. Koffel, S.M. Rudman and C.C. Symons. 2019. Stoichiometric traits vary widely within species: A meta-analysis of common garden experiments. Front. Ecol. Evol. 7: 339. doi:10.3389/fevo.2019.00339

Paseka, R.E., A.R. Bratt, K.L. MacNeill, A. Burian and C.R. See. 2019. Elemental ratios link environmental change and human health. Front. Ecol. Evol. 7: 378. doi:10.3389/fevo.2019.00378

Peace, A. and H. Wang. 2019. Compensatory foraging in stoichiometric producer–grazer models. Bull. Math. Biol. 81: 4932–4950. doi:10.1007/s11538-019-00665-2

Plum, C. and H. Hillebrand. 2019. Multiple zooplankton species alter the stoichiometric interactions between producer and consumer levels. Mar. Biol. 166: 163. doi:10.1007/s00227-019-3609-y

Ren, Z., N. Martyniuk, I. A. Oleksy, A. Swain and S. Hotaling. 2019. Ecological stoichiometry of the mountain cryosphere. Front. Ecol. Evol. 7: 1–16. doi:10.3389/fevo.2019.00360

Van Dievel, M., N. Tüzün and R. Stoks. 2019. Latitude-associated evolution and drivers of thermal response curves in body stoichiometry. J. Anim. Ecol. 88: 1961–1972. doi:10.1111/1365-2656.13088

Wagner, N.D., F.S. Osburn, J. Wang, R.B. Taylor, A.R. Boedecker, C.K. Chambliss, B.W. Brooks and J. T. Scott. 2019. Biological Stoichiometry regulates toxin production in Microcystis aeruginosa (UTEX 2385). Toxins (Basel). 11: 601. doi:10.3390/toxins11100601

Wang, J., J. Wang, L. Wang, H. Zhang, Z. Guo, G. Geoff Wang, W. K. Smith and T. Wu. 2019. Does stoichiometric homeostasis differ among tree organs and with tree age? For. Ecol. Manage. 453: 117637. doi:10.1016/j.foreco.2019.117637