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SOURCE (OR PART OF THE FOLLOWING SOURCE):

Type	Dissertation
Title	Out of balance: implications of climate change for the ecological stoichiometry of harmful cyanobacteria
Author	D.B. van de Waal
Faculty	Faculty of Science
Year	2010
Pages	144
ISBN	978-94-61080-45-5

FULL BIBLIOGRAPHIC DETAILS:
http://dare.uva.nl/record/341589

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Summary

All life on Earth consists of a set of chemical elements such as carbon (C), nitrogen (N) and phosphorus (P). Primary producers stand at the very base of aquatic and terrestrial food webs due to their ability to transform inorganic elements into organic compounds such as carbohydrates and proteins. These organic compounds provide the food source for animals, transferring carbon, nitrogen, phosphorus and other elements to higher levels in the food web. The field of 'Ecological Stoichiometry' studies the balance of these chemical elements to describe the complex relationships between organisms and their environment.

In this thesis, I address the following three main questions:

1) What are the implications of climate-driven changes in resource availability on the ecological stoichiometry of aquatic ecosystems (Chapter 2)?
2) How will changes in resource availability alter the nitrogen:carbon stoichiometry and toxin production of harmful cyanobacteria (Chapter 3-5)?
3) What are the implications of rising CO_2 concentrations for the competitive interactions between phytoplankton species (Chapter 6)?

To address the first question, we performed a detailed literature review (Chapter 2). Increasing global temperatures tend to strengthen the thermal stratification of aquatic ecosystems, suppressing vertical mixing and thereby reducing the upward flux of nutrients into the surface layer. Rising CO_2 concentrations but reduced nutrient availability will decrease the nutrient:carbon stoichiometry of phytoplankton. Phytoplankton with a low nutrient:carbon content provide poor-quality food for most zooplankton species, which may shift the species composition of zooplankton and higher trophic levels to less nutrient-demanding species. As a consequence, climate-driven changes in plankton stoichiometry may alter the structure and functioning of entire aquatic food webs.

To address the second question, we performed a series of laboratory experiments with the cyanobacterium *Microcystis aeruginosa* producing the hepatotoxin microcystin (Chapter 3). *Microcystis* increased its cellular nitrogen:carbon ratio under excess CO_2 and nitrate supply. Its high nitrogen:carbon ratio was accompanied by high cellular contents of total microcystin, and in particular the nitrogen-rich variant microcystin-RR. Conversely, under nitrogen-limited conditions, *Microcystis* had a low cellular nitrogen:carbon ratio and low cellular content of microcystin-RR. Comparable patterns were found in *Microcystis*-dominated lakes, where the relative microcystin-RR content increased with the seston nitrogen:carbon ratio. To the best of my knowledge, this is the first time that the carbon-

nutrient balance hypothesis, originally developed to describe secondary metabolite production in terrestrial plants has been applied to toxic cyanobacteria.

Hence, the cellular nitrogen:carbon stoichiometry influences the toxin production and toxin composition of harmful cyanobacteria. But what are the underlying physiological mechanisms? Because microcystins consist of amino acids, we investigated whether amino acids supplied in the growth medium affected the microcystin composition in the harmful cyanobacterium *Planktothrix agardhii* (Chapter 4). Addition of leucine resulted in a strong increase of the microcystin-LR/microcystin-RR ratio, while addition of arginine resulted in a decrease of this ratio. In addition, we grew the same *P. agardhii* strain under nitrogen-depleted conditions and added a nitrate pulse (Chapter 5). This caused a rapid increase of the cellular nitrogen:carbon stoichiometry, which was accompanied by a transient increase in the amino acids aspartic acid and arginine, indicative for cyanophycin synthesis, and by a more gradual increase of the total amino acid content. As expected, the nitrogen-rich microcystin-RR variant (which contains two arginine molecules) increased strongly after the nitrate pulse, while microcystin-LR increased to a much lesser extent (Chapter 5). These results show that the effect of nitrogen:carbon stoichiometry on microcystin production and composition in harmful cyanobacteria is mediated by their amino acid synthesis.

To address the third question, we developed a new model that describes phytoplankton competition for inorganic carbon. We performed monoculture and competition experiments in chemostats with a toxic and a nontoxic *Microcystis aeruginosa* strain under carbon-limited conditions. In addition, we tested our model on earlier experiments (Kardinaal *et al.* 2007b) in which the same two strains were used, but grown under light-limited conditions. The model could qualitatively and quantitatively predict the outcome of competition. The low CO_2 concentration in the carbon-limited chemostats led to dominance of the toxic strain. In contrast, the high CO_2 but low light conditions in the light-limited chemostat led to dominance of the nontoxic strain. Thus, the toxic strain was a better competitor for CO_2, whereas the nontoxic strain was a better competitor for light. These results show both theoretically and experimentally that changes in CO_2 and light availability may result in a complete reversal of the outcome of competition in harmful algal blooms.

The work in this thesis demonstrates that the toxin composition of harmful cyanobacteria is sensitive to changes in inorganic carbon and nitrogen availability. In addition, the competitive dominance of toxic versus nontoxic strains can shift with changes in CO_2 availability. Rising CO_2 concentrations and associated global warming are likely to alter the carbon and nitrogen availability in many aquatic ecosystems, and may thereby affect the elemental stoichiometry and species composition of phytoplankton communities as well as the nature of the toxins that they produce.