BIOLOGICAL OCEANOGRAPHY

The CO_2 switch in diatoms

Diatoms are important primary producers in the ocean, however their response to rising CO_2 is uncertain. Now research shows how diatoms regulate their metabolism in response to changing CO_2.

Jodi N. Young and François M. M. Morel

Diatoms are unicellular algae that account for ~20% of global primary production[1]. Some of the carbon fixed is exported to the deep ocean, leading to a carbon sink. How carbon fixation by diatoms will respond to rising CO_2 is unclear as most experiments so far have measured only the net carbon fixation and found conflicting results[2]. There is a need to understand the physiological and metabolic processes that underpin the diatom response to changes in CO_2. Writing in *Nature Climate Change*, Gwenn Hennon and colleagues[3] measure the expression of genes in diatoms that are acclimated to various CO_2 concentrations, and use these data to elucidate the mechanism behind the physiological changes observed in their N-limited continuous cultures. They also probe a compilation of gene expression data from previous CO_2 manipulation experiments and show that the same signalling pathway controls the regulation of genes that code proteins involved in the carbon concentrating mechanism (CCM) and photorespiration.

Photosynthesis is rarely limited by CO_2 in in the surface ocean, despite the concentration being well below that needed to saturate the photosynthetic CO_2-fixing enzyme, Rubisco (Ribulose 1,5 bisphosphate carboxylase oxygenase). This is because diatoms and most other phytoplankton possess CCMs. These CCMs pump carbon — either in the form of CO_2 or in the much more abundant form of bicarbonate — into the cell, elevating intracellular CO_2 levels to a concentration that nearly saturates Rubisco. The use of CCMs by phytoplankton raises the question of whether they will show any response to rising CO_2 emissions.

CCMs are energy- and nutrient-intensive processes that require transporters and enzymes to pump carbon against a concentration gradient. Most of the surface ocean is nutrient limited, with nitrogen a common limiting factor, thus phytoplankton need to optimize the partitioning of energy and nutrients between a multitude of metabolic processes. Because of this optimization, it has been speculated that rising CO_2 concentrations will alleviate some of the requirement for a CCM and thus free up resources for other processes, such as faster growth[4].

Hennon and colleagues[3] attempt to uncover how diatom metabolism responds to long-term (>15 generations) growth at high CO_2 by measuring the expression of genes in continuous cultures of the model diatom, *Thalassiosira pseudonana*, grown under nitrate limitation. The physiological response, which has been previously published[5], showed that at constant growth rate (as set by the dilution rate of the continuous culture), there was a decrease in both gross photosynthesis and respiration when CO_2 was increased from 350 μatm to 800 μatm, suggesting an overall reduction in general metabolism (Fig. 1). In the current study, the authors demonstrate an overall reduction in the expression of respiratory and photosynthetic genes, along with genes involved in general metabolism, for example, in transcription regulation and production of kinases. Interestingly, the expression of ribosomal components (structures that facilitate protein synthesis) was upregulated but the reason for this remains unknown.

To understand the mechanism by which *T. pseudonana* regulates gene expression in response to elevated CO_2, Hennon and colleagues[3] probed a compiled dataset that included their results combined with data from 98 previously published CO_2 manipulation experiments. They found that genes involved in the CCM and photorespiration (accidental fixation of O_2 by Rubisco and the subsequent removal of the toxic product[6]) showed similar downregulation under elevated CO_2. Analysis of the genetic sequence upstream of these genes and further experimentation in nitrate-replete cultures identified that expression of these genes was repressed by a transcription factor called cyclic AMP (cAMP), which is produced under high CO_2 (Fig. 1). cAMP-mediated gene expression is widespread, found in a variety of organisms, and regulates a number of different functions. The sensing of CO_2 via cAMP has been reported in

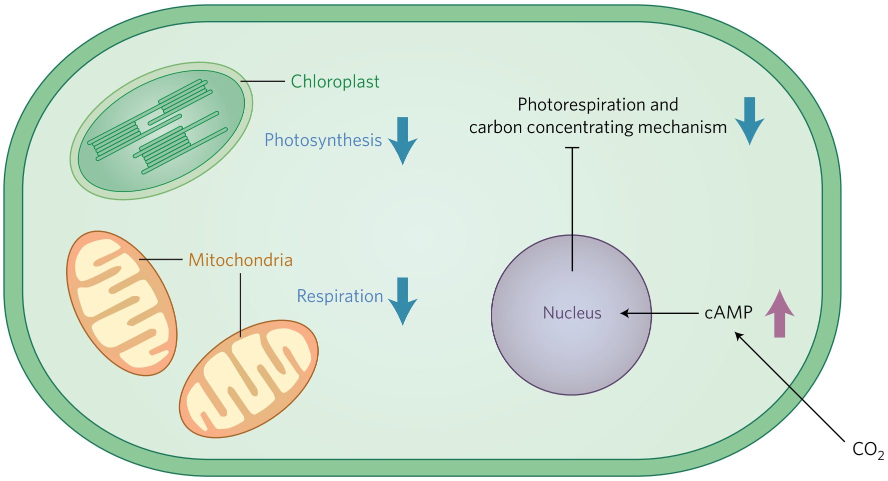

Figure 1 | Metabolic response of *T. pseudonana*, acclimated to high CO_2 in N-limited continuous cultures with constant growth rate. Photosynthesis in the chloroplast and respiration in the mitochondria are reduced. Hennon and colleagues[3] also identified increased production of the signalling molecule, cAMP, which represses the expression of genes involved in photorespiration and the carbon concentrating mechanisms. Coloured arrows indicate up- and downregulation (in purple and blue, respectively).

cyanobacteria, fungi and mammals, and has been demonstrated to regulate the expression of a CCM gene in another diatom, *Phaeodactylum tricornutum*[7].

It is not immediately obvious why genes involved in the CCM and photorespiration are co-regulated. Cells regulate their CCM to maintain an intracellular concentration of CO_2 that saturates Rubisco by ~80%[8,9]. Correspondingly, downregulation of the CCM in response to high CO_2 should have little effect on the intracellular CO_2 to O_2 ratio, resulting in no change in the rate of photorespiration. The reduction of photosynthesis might possibly lower the rate of photorespiration, either through a lower production of O_2 or because of a lower Rubisco concentration. However, lower rates of photosynthesis are only observed in acclimated cells whereas photorespiratory and CCM genes respond both in the short and long-term CO_2 response.

Downregulation of the CCM at elevated CO_2 has commonly been observed[10] and is speculated to be an energy-saving strategy[4], though the mechanism of regulation has previously been uncertain. As growth was kept constant in this experiment, the energy saved by downregulation of the CCM may partly explain the lower rate of respiration observed, although high CO_2 may also decrease respiration due to other reasons, such changing pH[11].

According to this interpretation it may be respiration, not photosynthesis, that directly responds to CO_2, and photosynthesis is thus reduced as cells cannot grow any faster in nitrogen-limited continuous cultures. In the field, growth rates are not fixed and net photosynthesis and growth could actually increase. A reduction of respiration at high CO_2 has been observed in the field, along with increased growth[11]. Hence in the future increasing CO_2 concentrations could result in either increased growth or constant growth but at a lower metabolic cost, depending on nutrient limitation.

The research by Hennon and colleagues[3] highlights the need to gain a fundamental understanding of the metabolic response of phytoplankton to changing CO_2 concentrations. This will allow us to tease apart the complex and often contradictory physiological results observed in the field and in the laboratory. Furthermore, Hennon and colleagues[3] have identified key CO_2 signalling pathways and components controlling the expression of CCM and photorespiratory genes, which can now be looked for in other, less well understood phytoplankton species. ❐

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Published online: 15 June 2015

ARCTIC PERMAFROST

Microbial lid on subsea methane

Submarine permafrost thaw in the Arctic has been suggested as a trigger for the release of large quantities of methane to the water column, and subsequently the atmosphere — with important implications for global warming. Now research shows that microbial oxidation of methane at the thaw front can effectively prevent its release.

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Methane gas has a high global warming potential on sub-century timescales, and release of currently trapped methane could drive rapid climate change[1]. Thus the possibility of substantial amounts of this greenhouse gas reaching the atmosphere has attracted attention — both in scientific and policy discussions. A potentially important source could be methane trapped within permafrost, including subsea sources that may be extensive and unstable. Staggering amounts of methane are thought to exist below the Russian Arctic shelf seas, mostly associated with shallow gas hydrates (solid ice-like structures encapsulating gas molecules) beneath and within the permafrost. Writing in the *Journal of Geophysical Research: Biogeosciences*, Pier Paul Overduin and colleagues report on a sediment core retrieved from beneath the shallow waters (4 m depth) of the southern Laptev Sea, a location inundated only 540 years ago, thus offering insight into sedimentation, thawing, and other processes that affect the inner shelf since sea levels began to rise at the end of the last glaciation. A suite of biogeochemical data directly related to methane dynamics in this setting is presented for the first time, showing methane gas is consumed by microbes before it can reach the overlying ocean[2].

The effects of the thawing of long-submerged permafrost on marine methane are manifold. Freeze-locked organic carbon becomes available to microbes as permafrost thaws, and the resulting greenhouse gases may be released to overlying sediments. The permafrost itself may act as a low-permeability physical barrier to upward migration of gases from deeper sources. Alternatively, methane may be frozen into the permafrost as gas hydrates and is released at the moment of permafrost thaw. (For the study considered here[2], pressures at the depth limit of the core (52 m) are too low for gas hydrate stability, although they could exist at greater depths[3]).

In recent years, interest has focused on the wide, shallow Siberian continental shelf seas, which were inundated after the end of the Last Glacial Maximum resulting in preservation of relict terrestrial permafrost under portions of these shelves[4]. Shallow areas such as those investigated by Overduin *et al.* are a prime location for