

Introduction



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The peculiar carbon metabolism in diatoms

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Diatoms are microalgae that arose over the last 100 Myr, thus *phylogenetically* constituting a relatively recent group of organisms. Analysis of microfossils that can be traced through geological time, as well as their contributions to sea-floor sediments and fossil fuel reserves, demonstrates that diatoms have played a crucial role during this time. The review by Benoiston *et al.* [1] in this issue combines the current information on the evolution and biogeochemical functions of diatoms over time. Paleocological data contain information for evaluating genetic variation through past climate changes, going back thousands of years in time [2]. In their review, Godhe & Reynardson [3] suggest the adoption of multiple strains of individual species for refining our understanding of the carbon metabolism and its variation within and between species.

Diatoms are photosynthetic organisms using the energy of the Sun to build up organic molecules via CO₂ fixation (primary production). For a long time, land plants have been supposed to be the main primary producers, however, recent estimations consider the contribution of algae to be as high as that of land plants [4]. The key process of the photosynthetic Calvin–Benson–Bassham cycle is the fixation of CO₂ onto ribulose-1,5-bisphosphate, mediated by the catalytic enzyme activity of RuBisCO. This reaction yields 3-phosphoglycerates, which immediately are converted to triose phosphates that are required to regenerate ribulose-1,5-bisphosphate. The contribution by Jensen *et al.* [5] reviews the regulation of the Calvin–Benson–Bassham cycle in diatoms, presenting a regulation process that is based on transcriptional regulation. This finding contrasts with land plants, in which the Calvin–Benson–Bassham is mostly regulated at the enzymatic level. Because a high local CO₂ partial pressure in the close vicinity of the RuBisCO is vital to avoid photorespiration, an adequate delivery of CO₂ to RuBisCO is of crucial importance. In waters, the concentration of CO₂ is limited, because at usual pH values the dissolved inorganic carbon is mostly present as bicarbonate (HCO₃[−]). To challenge this, algae have evolved carbon concentration mechanisms (CCMs). These mechanisms have been critically reviewed by Matsuda *et al.* [6], focusing on the question of whether these mechanisms are shared among different classes other than diatoms within the Ochrophyta phylum. The biochemical, physiological and genomic data reviewed by Raven & Giordano [7] speak in favour of the presence of CCMs in Eustigmatophyceae and Phaeophyceae, whereas in the Chrysophyceae and Synurophyceae, CO₂ might be acquired simply via diffusion.

Some of the triose phosphates generated by the Calvin–Benson–Bassham cycle are exported out of the chloroplast, becoming building blocks for the generation of more complex molecules. The efficiency of this process, which starts with photons and ends with organic compounds, is under debate; therefore, in their review, Wagner *et al.* [8] describe the general pathways of cellular energy distribution from light absorbance towards the final carbon allocation. They summarize the current knowledge of diatom-specific allocation patterns and describe regulatory mechanisms of carbon partitioning between lipids, carbohydrates and proteins in diatoms. Heydarizadeh *et al.* [9] in their research paper describe the molecular, biochemical and physiological effects of a sudden light shift to high- or low-light

conditions in CO₂-starved *Phaeodactylum tricornutum*, acclimated to an optimal photon flux density. Their data indicate a rearrangement of the carbon metabolism towards the production of phosphoenolpyruvate (PEP) and/or pyruvate. These intermediates are converted differently by the cell as a function of the photon flux density: under low-light conditions, PEP/pyruvate was used for respiration, whereas under high-light conditions, lipids and proteins were accumulating slightly. In addition, the genes coding for enzymes involved in the synthesis of aromatic amino acids and phenolic compounds were upregulated, suggesting that the shikimate pathway was activated.

Given the ecological importance of diatoms, still little is known about their physiology and their biochemistry. The recent attempts to generate metabolic maps using genomic data revealed that a core set of biochemical reactions is common with land plants, while at the same time unexpected pathways such as a urea cycle [10] or the Entner–Doudoroff pathway have been detected [11]. An important redundancy and diversity of metabolic isoenzymes in diatoms also emerged from genome sequencing [12]. Undoubtedly, the origin of this redundancy is the evolutionary history of diatom plastids by a eukaryote–eukaryote endosymbiosis, a process that implies temporary redundancy of functionally complete eukaryotic genomes. During the establishment of the plastids, this redundancy was partially reduced via gene losses, and was partially retained via gene transfer to the nucleus of the respective host cell. These gene transfers required re-assignment of intracellular targeting signals, a process that simultaneously altered the intracellular distribution of metabolic enzymes compared to the ancestral cells. Genome annotation, the correct assignment of the gene products and the prediction of putative function, strongly depends on the correct prediction of the intracellular targeting of a gene product. Understanding the carbon metabolism relies on understanding the targeting systems for organelle import, which are partially different to those in land plants. The review by Gruber & Kroth [13] describes methods of predicting intracellular enzyme locations, highlights findings of metabolic peculiarities in diatoms and presents genome-enabled approaches to study their metabolism. An example of the potential of these methods is provided in the paper by Pan *et al.* [14]. In their study, propionyl-CoA carboxylase RNAi silenced strains and 3-hydroxyisobutyryl-CoA hydrolase overexpression strains have been constructed to elucidate the isoleucine degradation pathway and its influence on lipid accumulation in *P. tricornutum*.

Today, diatoms have colonized all kinds of biotopes [15], including demanding areas such as the intertidal zone. The tidal regime exposes diatoms in this zone to particularly harsh conditions, including the reduced availability of dissolved inorganic carbon. Marques da Silva *et al.* [16] review the effects of dissolved inorganic carbon availability on photosynthesis and productivity of a diatom-dominated microphytobenthos. The changes in the dissolved carbon availability induces an active vertical migration of epipelagic

motile diatoms, allowing cells to be alternately exposed to light and inorganic carbon supply. To resist these harsh conditions including high light, high temperatures, high salinities, desiccation, as well as nutrient stress, diatoms have developed the capacity to acclimate or adapt. Long-term acclimation to stress conditions is often dependent on the capacity to re-program their carbon metabolism towards the production of molecules with a higher energy density than carbohydrates, i.e. lipids or carotenoids. Brembu *et al.* [17] here review the effect of phosphorus limitation on carbon metabolism in diatoms, and propose a model for the carbon flow in phosphorus-replete and phosphorus-limited diatom cells. Sayanova *et al.* [18] present original results on the effects of a low-temperature stress on the synthesis of lipids and Ω -3 long-chain polyunsaturated fatty acids. This contribution also reviews the recent advances in bioengineering lipid production in diatoms and discusses new perspectives for designing strains for sustainable production of high-value lipids. These lipids accumulate in spherical organelles called oil bodies. The mechanism involved in oil body formation has attracted attention because these oil bodies could facilitate the harvesting of biofuel. The review by Maeda *et al.* [19] describes the recent progress in studies of the structure and properties of diatom oil bodies.

The papers published in this thematic issue summarize the considerable attention that has been paid to diatom carbon metabolism in recent years. Altogether, the amazing acclimation and adaptation capacity of diatoms to diverse environmental conditions, their incredible evolutionary history and their unique metabolism, demonstrate the enormous potential of diatoms for biotechnology. The development of this field is even accelerating thanks to the fact that diatoms are genetically amenable. Huang & Daboussi [20] here provide an overview of recent advances in methods for genetic engineering of diatoms, from the development of gene expression cassettes and gene delivery methods, to cutting-edge genome-editing technologies. The popularization of these techniques will be helpful to both basic and applied research. Light often is strongly attenuated in photobioreactors when the cell cultures become dense, and obtaining biomass efficiently often is a limiting step in classical biotechnological processes that are based on photoautotrophic organisms. This difficulty can be overcome by using taxons that are able to grow heterotrophically or mixotrophically. However, very little is known about the biology of such taxons. Villanova *et al.* [21], therefore, present the results of a multidisciplinary study on the consequences of mixotrophy on the growth and metabolism of the pennate diatom *P. tricornutum*, using glycerol as a source of reduced carbon.

Data accessibility. This article has no additional data.

Competing interests. We have no competing interests.

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