



Photosynthetic Light Reactions in Diatoms. II. The Dynamic Regulation of the Various Light Reactions

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Chapter 2: Photosynthetic light reactions in diatoms. II. The dynamic regulation of the various light reactions

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Abstract

Photosynthesis in diatoms is performed using the same basic modules as cyanobacteria and plants. It can be regulated on multiple levels depending on the environmental cues, allowing diatoms to adjust their photosynthetic light reaction towards optimum whilst at the same time minimizing photodamage induced by light. In recent years, tremendous progress has been gained in understanding these acclimation processes, revealing several diatom-specific features. In this chapter, we trace several paths through the photosynthetic electron transport chain to optimize photosynthesis. We review how diatoms repair photoinactivated reaction centers and which mechanisms they have to preempt photodamage. Finally, photoprotection is set in an ecophysiological context, highlighting differences in photoprotection of diatoms from different habitats.

Key words: alternative electron flow, diatoms, Lhcx, NPQ, photoinhibition, photosynthesis, Photosystem II repair, xanthophyll cycle

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66 **Abbreviations**

67	³ Chl: triplet chlorophyll <i>a</i>
68	AEF: alternative electrons flow
69	AOX: Alternative Oxidase
70	ATP: adenosine triphosphate
71	<i>C. meneghiniana</i> : <i>Cyclotella meneghiniana</i>
72	CCM: carbon concentrating mechanisms
73	CEF: cyclic electron flow
74	Chl: chlorophyll
75	cyt <i>b₆f</i> : cytochrome <i>b₆f</i> complex
76	Dd: diadinoxanthin
77	DES: De-epoxidation state
78	Dt: diatoxanthin
79	ECS: electrochromic shift
80	ETR: electron transport rate
81	FCP: fucoxanthin-chlorophyll-binding protein complex
82	Fd: ferredoxin
83	Flv: flavodiiron
84	FNR: ferredoxin-NADP ⁺ reductase
85	H ₂ O ₂ : hydrogen peroxide
86	LEF: linear electron flow
87	LHC: light-harvesting complex
88	NADP ⁺ /NADPH: nicotinamide adenine dinucleotide phosphate
89	NDH: NADPH dehydrogenase
90	NPQ: Non-Photochemical fluorescence Quenching
91	NPQs: sustained NPQ
92	¹ O ₂ : singlet oxygen
93	<i>P. tricornutum</i> : <i>Phaeodactylum tricornutum</i>
94	P680: special chlorophyll pair in the PSII core
95	P700: special chlorophyll pair in the PSI core
96	pmf: proton motive force
97	PQ: plastoquinone
98	PSI: photosystem I
99	PSII: photosystem II
100	PTOX: plastoquinone terminal oxidase
101	qE: energy dependent quenching
102	qI: photoinhibitory quenching
103	qT: quenching based on state transitions
104	qZ: quenching based on conversion of violaxanthin via antheraxanthin to zeaxanthin
105	ROS: reactive oxygen species
106	SOD: superoxide dismutase
107	<i>T. pseudonana</i> : <i>Thalassiosira pseudonana</i>
108	WWC: water-to-water cycle
109	ΔpH: osmotic component of the pmf
110	Δψ: electric component of the pmf
111	σPSII: functional absorption cross section of PSII

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Introduction

As outlined in the previous chapter “*Photosynthetic light reactions in diatoms. I. The lipids and light-harvesting complexes of the thylakoid membrane*”, diatoms share the same elementary photosynthetic modules with other organisms performing oxygenic photosynthesis. The linear photosynthetic electron flow involves two photosystems and results in the transfer of electrons from water, the primary electron donor, to the terminal acceptor, nicotinamide adenine dinucleotide phosphate, NADPH (Fig. 1). Photosystem II (PSII) transfers electrons from the Oxygen Evolving Complex, where water oxidation takes place, to the plastoquinones (PQs) in the thylakoid membrane. Photosystem I (PSI) in diatoms catalyzes the electron transfer from the lumen-soluble electron carrier cytochrome c_6 (Böhme and Kunert 1980) to ferredoxin (Fd). In the stroma, the ferredoxin-NADP⁺ reductase (FNR) mediates the electron transfer from Fd to NADP⁺. The intersystem electron chain, which comprises PQs, the cytochrome b_6f complex (cyt b_6f) and cytochrome c_6 , mediates in-series functioning of the two photosystems. In low iron environments, diatoms can replace the iron containing cytochrome c_6 and Fd by the copper-containing plastocyanin and the flavin-containing flavodoxin, respectively (La Roche et al. 1996; Strzepek and Harrison 2004; Groussman et al. 2015). The coupling of the electron transfer with proton accumulation within the lumen through water splitting and proton pumping across the thylakoid via the cyt b_6f generates an electrochemical proton gradient or proton motive force (pmf), which comprises an osmotic component, ΔpH , and an electric one, $\Delta \psi$. The pmf is used by the chloroplast CF1Fo-ATP synthase to bind a phosphate group to an adenosine diphosphate (ADP) molecule and thus synthesize adenosine triphosphate, ATP. If diatoms share the same elementary bricks with other organisms performing oxygenic photosynthesis, the regulation of their photosynthetic activities and repair processes show several peculiarities, which we will highlight in detail in the following sub chapters.

The other major electron transport route, electron flow in the mitochondrial respiratory chain, is similar in diatoms and the green lineage. It can occur either via the classical electron flow involving complex I, III and IV or via complex I coupled to the Alternative Oxidase (AOX). Both pathways generate a pmf which fuels ATP synthesis thanks to the mitochondrial ATPase. The AOX pathway can behave as a valve to dissipate reducing power under stress conditions in the green lineage (Selinski et al. 2018) which similarly works in diatoms (Murik et al. 2019). Full-chain respiration and AOX pathways are in competition and can compensate each other in diatoms (Bailleul et al. 2015; Schober et al. 2019). Mitochondrial electron transport will not be covered in this chapter, except for its involvement in optimizing photosynthesis (see “1.4 Water-to-water cycles” and “1.5 Chlororespiration, redox state of the plastoquinone pool, and

pmf in the dark”).

1. The regulation of photosynthetic electron flow

1.1 The role of pmf as a master regulator of photosynthesis

The main constraint for the photosynthetic electron transfer is to adjust its activity to the amount of light received and to the metabolic needs in terms of NADPH and ATP, despite a variable environment (Kramer et al. 2003; Peltier et al. 2010). When light absorption exceeds the capacity of the electron transfer chain, the over-reduction of the photosynthetic chain can lead to the photodestruction of both PSII (Nixon et al. 2010) and PSI (Sonoike 2011) (see also “2. *Photosystem II photoinactivation and repair*”). Indeed, when an over-reduction of the acceptor side of PSII and/or PSI occurs, the photochemical yield decreases and the yields of other relaxation pathways increase in a complementary way. The probability of charge recombination between the oxidized special chlorophyll *a* pair of PSII (P680⁺) and reduced phaeophytin in PSII, forming the triplet state of chlorophyll *a* (³Chl), increases when electrons cannot be moved fast enough (Krieger-Liszkay 2005; Vass 2011). There is also the possibility of direct population of ³Chl in the PSII antennae by electron spin flip (Santabarbara et al. 2001; Triantaphylidès and Havaux 2009). When ³Chl interacts with O₂, singlet oxygen (¹O₂) is produced, a very toxic molecule which can degrade lipids, pigments or proteins, like the D1 protein (Krieger-Liszkay 2005; Halliwell 2006; Nixon et al. 2010; Triantaphylidès and Havaux 2009; Vass 2011). PSI acceptor side limitation (and possibly PSII acceptor side limitation as well (Pospíšil 2009)) also favors reduction of O₂ into superoxide anion radicals and hydrogen peroxide (H₂O₂). In the presence of free transition metals such as iron, copper or manganese, H₂O₂ can be converted via the Fenton reaction into the very reactive hydroxyl radical, which e.g. eventually destroys the iron-sulfur centers involved in the electron transfer (Halliwell 2006; Pospíšil 2009; Dietz et al. 2016; Sonoike 2011). The process is almost irreversible because there is no known repair mechanism for PSI (Sonoike 2011). Collectively, ¹O₂, superoxide, H₂O₂ and the hydroxyl radical are called reactive oxygen species (ROS).

The luminal pH regulates photoprotection of the two photosystems through the de-excitation of PSII under excess light conditions (Kramer et al. 2003; Holt et al. 2004, and see “3.4 *The molecular regulation and characteristics of qE*”) and the ‘photosynthetic control’ which is the modulation of the activity of the cyt b₆f by the luminal pH. The photosynthetic control sets the kinetically limiting step of the linear electron flow at cyt b₆f level and by doing so protects PSI by avoiding its acceptor side limitation (Rumberg and Siggel 1969; Laisk et al. 2005; Joliot and Johnson 2011). Moreover, the ATP/NADPH ratio must be adjusted to the metabolic needs of

the carbon fixation and other metabolic pathways fueled by the light phase of photosynthesis (Allen 2002). The ratio of ATP to NADPH produced by the LEF is lower than that required for C fixation in the Calvin-Benson-Bassham cycle (CBB cycle). Based on the stoichiometry of 14 c subunits per ATP synthase from spinach (Hahn et al. 2018), 14 protons are needed to produce 3 ATP, which are, together with 2 NADPH+H⁺, required to reduce one molecule of carbon dioxide in the CBB cycle. With the constitutive Q cycle taking place at the cyt b₆f (Mitchell 1975; Sacksteder et al. 2000), a total of 12 H⁺ are translocated to the lumen for the movement of 4 electrons needed to reduce 2 NADP molecules in LEF. Therefore, the ATP-to-NADPH ratio produced by the LEF is 1.28. However, the ATP-to-NADPH requirement for the CBB cycle is 1.5 and can increase due to carbon concentrating mechanisms (CCM), resulting in an ATP shortfall (Eberhard et al. 2008; Peltier et al. 2010; Curien et al. 2016). Here again, the flexibility of the ATP/NADPH stoichiometry produced by the photosynthetic machinery is modulated by the pmf, which is increased by alternative electron flows (AEFs) fueling the ATP synthase (see “2.2 Alternative electron flows provide photoprotection and flexibility in response to metabolic demand”). In plants and green algae, the flexibility of photosynthesis is therefore largely dependent on the pmf, which plays the dual role of driving ATP and regulating photoprotection mechanisms through its osmotic component, the ΔpH (Kramer et al. 2003). Whether the pmf is a master regulator of the photosynthetic electron transfer in diatoms like in plants is still an open question. In diatoms, the ATP/NADPH produced by the LEF could be different depending on the efficiency of the Q cycle and on the (yet unknown) stoichiometry of c subunits per ATP synthase (Fig. 1). The occurrence of a Q cycle in diatoms seems to be at play based on electrochromic shift (ECS) measurements, i.e. changes in absorption of photosynthetic pigments due to Δψ (Witt 1979; Bailleul et al. 2010a). Like in plants, the increase of ECS concomitant with the cyt b₆f turnover indicates the move of two positive charges (protons) for one electron transferred to cytochrome c₆ (Bailleul et al. 2015). Also, the high ATP demand of the CCM in diatoms (Hopkinson et al. 2011) strongly suggests that mechanisms increasing the pmf are needed (see next section). Clearly, the rapid and reversible, energy dependent regulation of the light harvesting system of PSII (=qE, a major photoprotection mechanism) is regulated by the ΔpH in diatoms (see “3.4 The molecular regulation and characteristics of qE”). So far, there is no clear evidence for a ‘photosynthetic control’ in diatoms but the observation that P700, the special pair of PSI, is oxidized after a pulse of high light could reflect such a control (Shimakawa and Miyake 2018).

1.2 Alternative electron flows provide photoprotection and flexibility in response to metabolic demand

In the green lineage, the ATP shortfall is managed by various AEFs, which are auxiliary routes of electron transfer operating along the photosynthetic chain and sharing part of the components of the LEF (Eberhard et al. 2008; Peltier et al. 2010; Curien et al. 2016). Here, we name AEFs all electron transfer pathways involving PSII and/or cyt b_6f (both generating a pmf), which do not end up in the generation of NADPH. In the green lineage, the AEFs comprise the cyclic electron flow around PSI (Shikanai 2007) and various water-to-water cycles (WWCs), which are electron transfers from water at PSII via O_2 back into water by the means of various oxidases (Eberhard et al. 2008; Curien et al. 2016). These oxidases include the plastoquinone terminal oxidase (PTOX) which reroutes electrons from the plastoquinols, the Mehler reaction and flavodiiron proteins (Flvs) on the acceptor side of PSI, or the rerouting of reducing power towards the mitochondrial oxidases of the oxidative phosphorylation pathway through the malate shuttle (Eberhard et al. 2008; Peltier et al. 2010; Curien et al. 2016).

All those pathways increase the pmf and generate extra ATP, allowing the adjustment of the light phase of photosynthesis with the metabolic requirements (Eberhard et al. 2008; Peltier et al. 2010; Curien et al. 2016). AEFs also protect both photosystems from excess light by three means. First, because they offer supplementary electron sinks, they avoid over-reduction of the photosynthetic chain which otherwise would lead to the creation of ROS. Then, the adjustment of the ATP-to-NADPH ratio by AEFs optimizes the capacity of the CBB cycle to consume photosynthetic electrons and to prevent such over-reduction. Last, because they modulate ΔpH , all AEFs also contribute to the protection of PSII and PSI through ‘photosynthetic control’ and qE (Kramer et al. 2003; Peltier et al. 2010). AEFs are especially important for photoprotection when the substrates of photosynthesis (CO_2 or light) and/or the metabolic demand vary (Kramer et al. 2003; Peltier et al. 2010). We next describe the main AEFs in diatoms.

1.3 Cyclic electron flow around PSI

The existence of cyclic phosphorylation in chloroplasts was first proposed by Arnon and collaborators (Arnon et al. 1954; Arnon and Chain 1975). In plants, genetic analyses have identified two pathways allowing the transfer of electrons from PSI acceptors to the PQ pool, one involving the proteins PGRL1 and PGR5 and the other one passing through the chloroplast NADPH dehydrogenase, NDH (Shikanai 2007). Based on the structure of the cyt b_6f , a third mechanism proposed by Mitchell (1975) was reiterated recently which involves the injection of electrons from Fd to the Q_i site of the cyt b_6f (Iwai et al. 2010; Nawrocki et al. 2019). In

plants, rates of the cyclic electron flow (CEF) rate can reach up to ~ 100 electrons s^{-1} PSI $^{-1}$ (Joliot and Johnson 2011), but which of the three proposed mechanisms dominates is still a matter of debate. The NDH is not found in diatoms (nor in other microalgae with the notable exception of prasinophytes, Oudot-Le Secq et al. 2007). PGRL1 and PGR5 are present in diatoms (Grouneva et al. 2011; Grouneva et al. 2016) and recent reports suggest an involvement of PGRL1 in CEF of *Phaeodactylum tricornutum* (Zhou et al. 2020). The existence of CEF, measured as a PSI activity in conditions of PSII inhibition, was demonstrated in diatoms using both P700 reduction and ECS (Maxwell and Biggins 1976; Bailleul et al. 2015) (Fig. 1). The measured rates, however, correspond to 5 to 10 electrons s^{-1} PSI $^{-1}$ in most diatom species (Maxwell and Biggins 1976; Bailleul et al. 2015), even though higher rates were measured in polar diatoms (~ 25 electrons s^{-1} PSI $^{-1}$, Goldman et al. 2015) or in iron stress conditions (up to 55 electrons s^{-1} PSI $^{-1}$, Thamtrakoln et al. 2013). This suggests that if CEF may not play such a constitutive and ubiquitous role as in plants, it can become a key player of the photosynthetic regulation in some species and conditions.

1.4 Water-to-water cycles

The occurrence of WWCs in diatoms were first tested by comparing oxygen and fluorescence measurements derived photosynthetic electron transport rates (ETR). While there is a strong correlation between O $_2$ production and ETR under low light conditions, discrepancies were measured under higher light intensities (Wagner et al. 2006). Later, direct measurements of photosynthesis-driven oxygen consumption, even in conditions minimizing the photorespiration, confirmed the presence of the WWC (Eisenstadt et al. 2010).

The Mehler reaction reroutes electrons from Fd to reduce O $_2$ into superoxide (Fig. 1) (Mehler 1951; Asada 2000). Superoxide is then reduced by the superoxide dismutase (SOD) into H $_2$ O $_2$, which is further scavenged by the ascorbate peroxidase to form water and oxidized ascorbate (Asada 2000). Such WWC has been hypothesized to contribute to the generation of extra ATP and to protect PSI from over-reduction of its electron acceptors (Ort and Baker 2002). The Mehler reaction has been identified in plants (Asada 2000), green algae (Chen et al. 1996), and cyanobacteria (Asada et al. 1975). In the dinoflagellate genus *Symbiodinium*, the Mehler reaction was proposed as the main alternative electron flow (Roberty et al. 2014). Oxygen photoreduction measured in the diatoms *Nitzschia epithemioides* and *Thalassiosira pseudonana* was ascribed to the Mehler reaction (Waring et al. 2010) but its rate *in vivo* is difficult to estimate because of sources of confusion with other WWCs. Based on the nature of the metal cofactor, Fe-containing SODs and CuZn-containing SODs have been described (Wolfe-Simon

et al. 2005). In diatoms, a MnSOD has been found in the plastid of *T. pseudonana* whereas this enzyme is usually present in mitochondria of other species (Wolfe-Simon et al. 2006). This peculiarity could contribute to the ecological success of diatoms in low iron regions of the ocean. Flv proteins play an important role in photoprotection and ATP/NADPH adjustment in cyanobacteria, green algae, mosses and some plants excluding angiosperms (Yamamoto et al. 2016) but genes encoding Flv are not found in the genomes of diatoms (Zhang et al. 2009).

The electrons downhill PSI can be rerouted to the mitochondria, a transfer of reducing power enabled by malate shuttles with low rates though (Scheibe et al. 2005). Also other observations suggest strong energetic exchanges between organelles in the green lineage (Cardol et al. 2009; Cardol et al. 2010). The reducing power is then converted into ATP through the oxidative phosphorylation pathway, which can occur either via the classical mitochondrial electron flow or via complex I coupled to AOX. The AOX pathway behaves as a valve and dissipates reducing power from the chloroplast under stress conditions in the green lineage (Yoshida et al. 2011; Kaye et al. 2019) but probably also in diatoms (Murik et al. 2019), e.g. under iron stress (Allen et al. 2008). In addition, regardless of the light conditions, there is a strong constitutive coupling between diatom plastids and mitochondria, involving about 10% of photosynthetically generated electrons, which is coupled to the plastidic import of the extra ATP generated in the mitochondrion (Bailleul et al. 2015). Exchanges of ATP between organelles also occur in the green lineage, which is responsible for a pmf across the thylakoids in the dark, resulting from the hydrolysis of ATP of mitochondrial origin (Tanada 1951; Paul and Volcani 1976; Finazzi and Rappaport 1998; Peers and Price 2006; Takizawa et al. 2007). However, the peculiarity of diatom's photosynthesis is the constitutive nature of this energetic interaction. It is unknown how this connection contends with the four membranes surrounding the plastid. One possibility involves an interplay between the CBB cycle and the mitochondrial glycolysis, an unusual metabolic configuration in stramenopiles (Liaud et al. 2000; Smith et al. 2016; Río Bártulos et al. 2018).

All AEFs listed above form a network of inter-connected, flexible and largely interchangeable electron flows. If the energetic interactions between plastid and mitochondrion seem to be the major constitutive AEF in diatoms, it is likely that other modes of electron flows play a crucial role in specific conditions (high light, nutrient stress, low temperature, or CO₂). One should e.g. mention the nitrogen and sulfur assimilation pathways which consume photosynthetic electrons coming from reduced PSI acceptors (Schmidt and Trebst 1969; Foyer and Noctor 2006). Because they generate extra pmf, resulting in ATP synthesis without providing NADPH to the CBB cycle, these pathways can also be considered as AEFs. Nitrogen assimilation has been

proposed to be an important sink for photosynthetic electrons of diatoms under periods of unbalanced light to dark reactions (Lomas & Glibert 1999). Electron cycling around PSII protects PSII and has been described in diatoms, too (Lavaud et al. 2002c; Feikema et al. 2006; Wagner et al. 2016), but it does not participate to pmf and thus does not meet the definition of AEFs of this chapter.

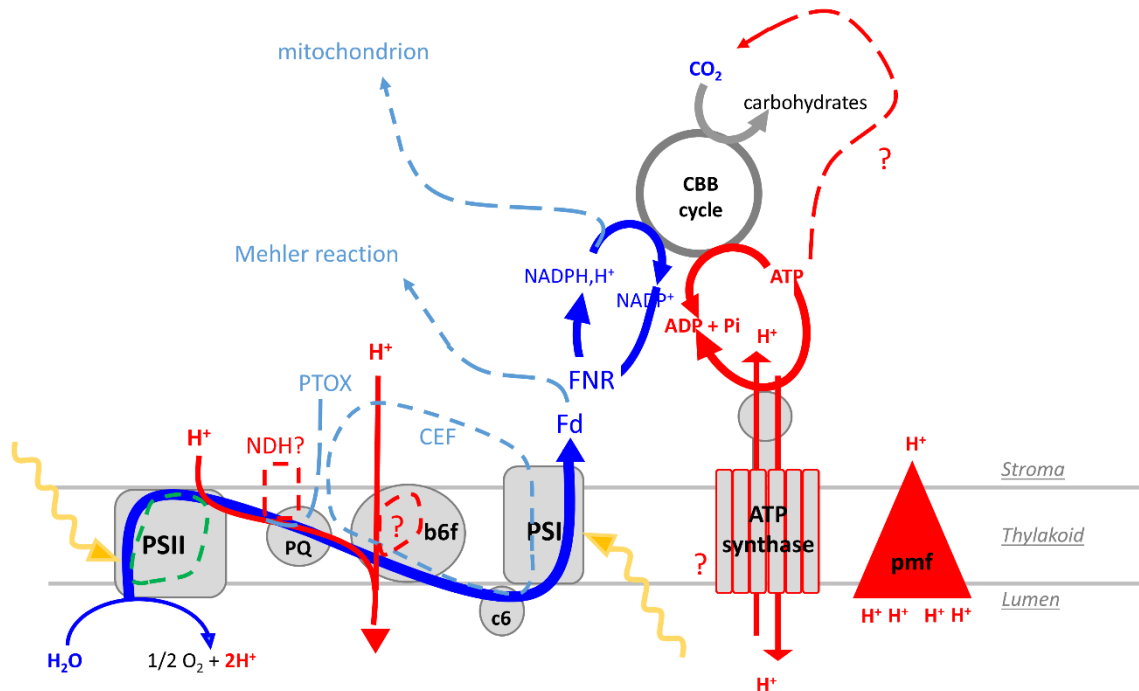


Figure 1

Schematic representation of the photosynthetic electron transfer chains. The linear electron flow is represented as a bold blue arrow. Proton movements are represented by red arrows. The CBB cycle is represented in grey. The unknowns are represented by blue dashed lines (for alternative electron flows), a green dashed line (PSII cyclic electron flow), a red dashed line and red question marks (Q cycle in the cyt b $_6$, ATP demand for CCM and number of c subunits). PSI cyclic electron flow could be mediated via PGRL1/PGR5 or via another yet unknown plastoquinone reducing pathway.

1.5 Chlororespiration, redox state of the plastoquinone pool, and pmf in the dark

Chlororespiration is a respiratory-like electron transport taking place in thylakoids and resulting in the oxidation of stromal reductants (Fd, NADPH). It can occur in the dark and involves two enzymes: NADPH dehydrogenase (type I NDH in plants, type II NDH in green algae, Jans et al. 2008) which transfers electrons from NADPH or Fd towards the (oxidized) PQs, and the thylakoid-bound plastid terminal oxidase (PTOX) which reduces O $_2$ into water thanks to (reduced) plastoquinols (Bennoun 1982) (Fig. 1). Because it combines PQ reducing (NDH) and

oxidizing (PTOX) enzymatic activities, chlororespiration influences the redox state of the PQ pool (Bennoun 1982) which in the green lineage, cyanobacteria but also in diatoms is an important signaling trigger (Pfannschmidt et al. 2009; Lepetit and Dietzel 2015). PTOX is present in two copies in diatom genomes (Burki et al. 2012), it is expressed at least under iron stress conditions (McDonald et al. 2011) and targeted to the plastid (Burki et al. 2012), and there is physiological evidence for chlororespiration taking place in diatoms (Jakob et al. 1999; Dijkman and Kroon 2002). However, no NDH has been found in diatoms so far (Fig. 1) and the importance of chlororespiration for diatoms might have been overestimated in the past. The existence of a pmf in the dark, visualized through the development of Non-Photochemical fluorescence Quenching (NPQ), has long been seen as evidence for an efficient proton pumping chlororespiratory activity in diatom plastids (Jakob et al. 1999, 2001; Grouneva et al. 2009; Cruz et al. 2011; Kennedy et al. 2019). However, the almost complete suppression of the dark pmf in the absence of mitochondrial respiration (via anaerobiosis or pharmacological inhibition) in several diatoms demonstrates that the pmf generated in the dark originates instead rather from the hydrolysis of mitochondrial ATP by the plastidic CF₁F_o-ATP synthase (Bailleul et al. 2015).

When PTOX re-oxidizes the plastoquinols produced by PSII, it generates a peculiar WWC which does not involve the cyt *b₆f* (Nawrocki et al. 2015). The PSII-PTOX pathway can play an important role in the regulation of the ATP/NADPH ratio and photoprotection in stress conditions, e.g. in cyanobacteria and prasinophytes under iron stress (Bailey et al. 2008; Cardol et al. 2008), or in alpine plants (Streb et al. 2005). These cases seem to be exceptions and this pathway is considered to be usually negligible compared to the LEF in the light but plays a crucial role during dark periods (Nawrocki et al. 2015).

2. Photosystem II photoinactivation and repair

PSII is susceptible to photoinactivation through multiple, non-exclusive paths (reviews Oguchi et al. 2011; Vass 2012; Zavafer et al. 2015; Campbell and Serôdio 2020). A direct path likely acts through a low-probability absorbance of a photon by the manganese cluster of the Oxygen Evolving Complex, leading to loss of capacity for photooxidation of water and then to photochemical destruction of PSII by subsequent photon excitations (Tyystjarvi et al. 2005). This path is provoked primarily by UV and blue photons and shows limited sensitivity to the instantaneous physiological state of the cell (Havurinne and Tyystjarvi 2017; Murphy et al. 2017). This direct path occurs across excitation levels at nearly constant probability per photon. Alternately, photons captured by the PSII antennae can provoke formation of ^3Chl within the antennae or reaction center, which can in turn generate destructive $^1\text{O}_2$. This path is thus influenced by the antennae absorbance spectra and cross section and hence likely by qE (see “3.4 The molecular regulation and characteristics of qE”). There is, as yet, no direct evidence that induction of qE actually lowers susceptibility to photoinactivation in diatoms, although such an effect is usually assumed based on investigations on qE in plants (Li et al. 2002). The antenna-dependent photoinactivation path also depends directly upon the degree of PSII closure, which in turn reflects the balance between incoming excitation and the downstream flow of electrons away from PSII, often characterized by the lifetime (τ) for PSII re-opening as measured by Fast Repetition and Relaxation Fluorescence (FRRF) (Kolber et al. 1998). Thirdly, charge recombination within PSII may lead to generation of ^3Chl , and then subsequent $^1\text{O}_2$ generation and damage to PSII. This photoinactivation path may dominate under low light when delivery of sequential excitations to PSII are widely spaced, increasing the probability of recombination within PSII (Ohad et al. 2011; Keren et al. 1997).

Diatoms show low primary susceptibilities to PSII photoinactivation when compared to other phytoplankton lineages, and within diatoms large centric diatoms show lower susceptibilities than do smaller centrics, probably related to optical attenuation by the package effect in larger cells (Key et al. 2010; Wu et al. 2011; Wu et al. 2012; Wu et al. 2015; Campbell and Serôdio 2020). We speculate that the relatively low sensitivity of diatoms to photoinactivation may relate to the photonic crystal nature of the diatom siliceous frustule (Goessling et al. 2018) which modulates the internal light field of diatom cells. We also note that beyond the rather unusual model species *P. tricornutum* (Havurinne and Tyystjarvi 2017) there are fewer mechanistic studies of photoinactivation of PSII from pennate (Petrou et al. 2010; Petrou et al. 2012) than from centric diatoms. It is reasonable to expect different optics in the pennates and

therefore the centric bias of mechanistic studies to date should be kept in mind, in contrast to the ecological dominance of pennates in many habitats.

2.1 Kinetic overlap of photoinactivation and downregulation of PSII

Loss of [PSII]_{active} through either photoinactivation path leads to lowered variable fluorescence from PSII and thus can overlap both phenomenologically and kinetically with reversible downregulation of [PSII]_{active} through induction of qE (Grouneva et al. 2008; Kuzminov and Gorbunov 2016; Buck et al. 2019). From an ecophysiological point of view the suppression of productivity through sustained loss or downregulation of [PSII]_{active}, through whatever mechanism, may be more important than the direct metabolic burden of PSII repair (Raven 2011). Prolonged suppression of PSII activity extending after the end of high light exposure imposes an opportunity cost of loss of potential productivity, but keeps the cell in a state pre-acclimated for a return to higher light, as for example through mixing. Evolution may favor this conservative strategy of prolonged down-regulation over more rapid relaxation of down-regulation to maximize short-term productivity at the risk of oxidative damage to the cell. The kinetic overlap of PSII photoinactivation and repair (also summarized under the term qI, photoinhibitory quenching) with the induction and relaxation of qE can be particularly problematic for mechanistic characterization of the photophysiology of diatoms, where large amplitude inductions of qE-like processes (see “3.3 Non-Photochemical fluorescence Quenching (NPQ)”) can persist in darkness, requiring low light for timely relaxation (Goss et al. 2006), thereby becoming difficult to distinguish from the overlapping influence of PSII repair under low light or even in darkness (Li et al. 2016).

2.2 PSII repair

Photoinactivation of PSII is countered by a PSII repair cycle (Nixon et al. 2010; Komenda et al. 2012; Nishiyama et al. 2014) that proteolytically removes photoinactivated subunit(s), in concert with subunit replacement through translation mediated by chloroplastic ribosomes. It is critical to note that although photoinactivation of PSII may precede recovery through repair, the two processes show distinct kinetics and light responses. PSII photoinactivation rate shows a nearly linear dependence upon instantaneous excitation levels ((Oguchi et al. 2011; Vass 2012; Campbell and Serôdio 2020). In contrast, PSII repair in diatoms reaches saturation under fairly low light (Wu et al. 2012). Under some conditions diatoms can therefore accumulate considerable pools of [PSII]_{inactive} (Wu et al. 2011; Wu et al. 2012; Campbell et al. 2013; Lavaud et al. 2016) representing intermediate stages in the PSII repair cycle (Grouneva et al. 2011).

This temporal offset between photoinactivation and repair can result in a tradeoff between strategies. A 'just-in-time' repair strategy requires cellular investment in sufficient instantaneous PSII repair capacity to counter PSII photoinactivation immediately, with sufficient metabolic capacity allocated to run key proteases and chloroplastic ribosome activity. In contrast, a 'warehouse' strategy involves protein investment into larger pools of [PSII]_{inactive} waiting around for eventual repair. In *T. pseudonana*, the burden of maintaining PSII repair is low under low light, as slow rates of photoinactivation mean that PSII must only be replaced on generational time scales (Li et al. 2015). The low light cells thus follow a 'just-in-time' strategy. As growth light increases, the burden of PSII repair grows, until under light above the growth optima maintenance of PSII repair comes to dominate chloroplastic nitrogen metabolism, thereby restricting capacity for growth and forcing the cells towards a 'warehouse' strategy where [PSII]_{inactive} waits for repair. Behrenfeld et al. (1998) noted that phytoplankton can tolerate a degree of photoinhibitory burn down of the standing pool of [PSII]_{active} without suffering an immediate loss of net photosynthesis, showing that the remaining pool of [PSII]_{active} can accelerate their photochemical turnover to compensate for loss of [PSII]_{active}. This implies a 'warehouse' strategy with an offset between photoinactivation and later repair. Lavaud et al. (2016) found that in *P. tricornutum* a large capacity for NPQ accompanied a 'just-in-time' strategy of repairing [PSII]_{inactive} rapidly. In contrast, *Skeletonema costatum* compensated for limited capacity to induce sustained NPQ with a 'warehouse' strategy by maintaining a large pool of [PSII]_{inactive} awaiting repair. We thus find a compensatory balance between capacity to downregulate PSII through NPQ with capacity to accumulate large pools of [PSII]_{inactive} or excess [PSII]_{active}.

Interestingly, in diatoms the PsbA (D1) & PsbD (D2) subunits both turnover at similar rates (Wu et al. 2011; Wu et al. 2012; Campbell et al. 2013; Li et al. 2016), contrary to text book descriptions which focus on PsbA turnover. We have not pursued the implications as to whether PsbA or PsbD are both subject to direct photoinactivation in parallel, or whether turnover of PsbD simply closely tracks primary photoinactivation of PsbA.

The FtsH protease complex is a membrane associated structure usually comprised of six FtsH isoform subunits, implicated as the primary protease mediating removal of PsbA from thylakoid membranes (Nixon et al. 2010; Komenda et al. 2012), along with roles in turnover of other complexes (Malnoë et al. 2014). Diatom capacity for PsbA turnover is predictable from the FtsH:PsbA ratio which in turn varies depending upon the predicted light dynamics of the original source habitats of strains (Campbell et al. 2013). The 'just-in-time' strategy requires a higher FtsH:PsbA ratio than the 'warehouse' strategy. Furthermore, PSII repair continues in the

dark in diatoms (Li et al. 2016), which we hypothesize is driven by tight integration of chloroplastic and mitochondrial metabolism to fuel the chloroplastic ATP requirements for FtsH, RNA transcription and translation (Prihoda et al. 2012; Bailleul et al. 2015). This capacity for dark repair of previously photoinactivated PSII allows for temporal offsets between episodes of net photoinactivation under high light with transient accumulation of [PSII]_{inactive} and subsequent counteracting repair in low light or darkness, and could thereby contribute to the success of diatoms in environments of fluctuating light. Furthermore, dark turnover of PsbA may contribute to a 'warehouse' strategy where [PSII]_{inactive} is recycled in the dark.

Although large centric diatoms show lower susceptibility to photoinactivation than their smaller cousins, they can also show 'luxury' turnover of PSII subunits beyond the rates predicted by the photoinactivation (Li et al. 2016). This surprising finding suggests that turnover of subunits can use both [PSII]_{active} and [PSII]_{inactive} as substrates, with a repair system only imperfectly discriminating in favor of [PSII]_{inactive}. The three layer organization of diatom thylakoids may alter or restrict the interaction of the FtsH protease complex with PSII, possibly lowering capacity to discriminate in favor of [PSII]_{inactive} (Komenda et al. 2007), and thereby implying a continuous repair process where the lifetime of a PsbA (or PsbD) is determined by lateral delivery to FtsH rather than by the rate of instantaneous photoinactivation. Recently it was shown that photodamaged PSII reaction centers are physically separated from intact PSII complexes and form repair center clusters (Levitan et al. 2019). A particular steric puzzle is how any PSII housed in the central of the three thylakoid layers can interact with ribosomes and membrane associated FtsH complexes, but these repair centers may be located rather at the outer layers or the thylakoid margins. As a final idiosyncrasy Grouneva et al. (2011) found only a single, plastid encoded FtsH protein isoform in diatom thylakoids (Maxwell, Grouneva, Aro & Campbell; unpublished). In contrast, in other eukaryotic photoautotrophs multiple FtsH protein isoforms are encoded by genes in the nucleus and imported into the chloroplast to form a hetero-hexameric FtsH structure. Thus, either diatoms carry an unusual hexamer of a single isoform of FtsH; or additional divergent subunits have not as yet been annotated as contributing to the chloroplastic FtsH complex of diatoms; or PSII repair in diatoms involves alternate paths.

3. Photoprotection in diatoms

When the amount of light absorbed by the light harvesting system exceeds the capacity of the photosynthetic electron transport chain to transfer electrons from the sites of photochemistry to electron acceptors, which also depends on energy consuming pathways such as e.g. the CBB cycle, photorespiration or nitrite reduction, high concentrations of ROS both at PSII and PSI can be produced. On one hand, ROS have various signaling functions well documented in plants and green algae (Dietz et al. 2016) and there is some evidence that ROS may be signaling substances also in diatoms (Lepetit and Dietzel 2015). On the other hand, ROS are strong oxidants and if produced in large amounts and not detoxified, they will eventually kill the cells (Havaux et al. 2005; Petroutsos et al. 2016) (see also “1.1 The role of *pmf* as a master regulator of photosynthesis”). Hence, all photosynthetic organisms have various strategies to cope with excess light. These strategies include mechanisms to preempt the formation of ROS as well as strategies to deal with the consequences of high levels of ROS. The latter strategy involves both antioxidative agents to directly quench ROS and the capacity to remove and replace photodamaged proteins (see “2.2 PSII Repair”).

3.1 Detoxification of reactive oxygen species

Carotenoids, besides their role in light harvesting, are important antioxidants. The classical example is β -carotene in the reaction center of PSII, which quenches $^1\text{O}_2$ generated via energy transfer from ^3Chl (Latowski et al. 2014). Interestingly, diatoms can accumulate huge amounts of xanthophyll cycle (XC) carotenoids (namely diadinoxanthin (Dd) and its de-epoxidized form diatoxanthin (Dt)) in the thylakoid membrane upon prolonged high light acclimation (Lepetit et al. 2010), which is triggered by a reduced PQ pool (Lepetit et al. 2013). For dynamic photoprotection, however, the effective molecule is Dt, whose concentration is depending on XC activity, triggered by the ΔpH (see “3.4 The molecular regulation and characteristics of *qE*”). The larger the ΔpH , the more Dt is synthesized in the XC. Dt fulfills a dual role: When bound to specific light harvesting proteins, Dt mediates thermal dissipation of absorbed energy via *qE*, i.e. this absorbed energy cannot be used to drive photosynthesis. When dissolved in the thylakoid lipid membrane (see “Photosynthetic light reactions in diatoms. I. The lipids and light-harvesting complexes of the thylakoid membrane”), Dt acts as a strong antioxidant (Lepetit et al. 2010). As constitutive thermal dissipation is not desirable for diatom cells especially under fluctuating light conditions and the pH regulated diadinoxanthin de-epoxidase de-epoxidizes both protein bound and membrane dissolved Dd, there is no constitutive antioxidative Dt pool in the thylakoid membrane under low and moderate light conditions.

Tocopherols are potent antioxidants (Demmig-Adams and Adams 2002; Havaux et al. 2005). Diatoms possess a full plastid targeted tocopherol biosynthesis pathway based on KEGG predictions, which is different from other heterokonts/stramenopiles (Nonoyama et al. 2019). Indeed, tocopherol biosynthesis proteins are present in diatom plastid fractions (Schober et al. 2019) and pronounced amounts of tocopherol are found in diatom thylakoid membranes, which increase, similarly to the XC pool, upon acclimation to prolonged high light (Fig. 2). As the antioxidative potential of tocopherols even increases in the presence of carotenoids (Böhm et al. 1997), tocopherols together with the high amounts of membrane dissolved carotenoids provide diatom thylakoids with a strong antioxidative capacity.

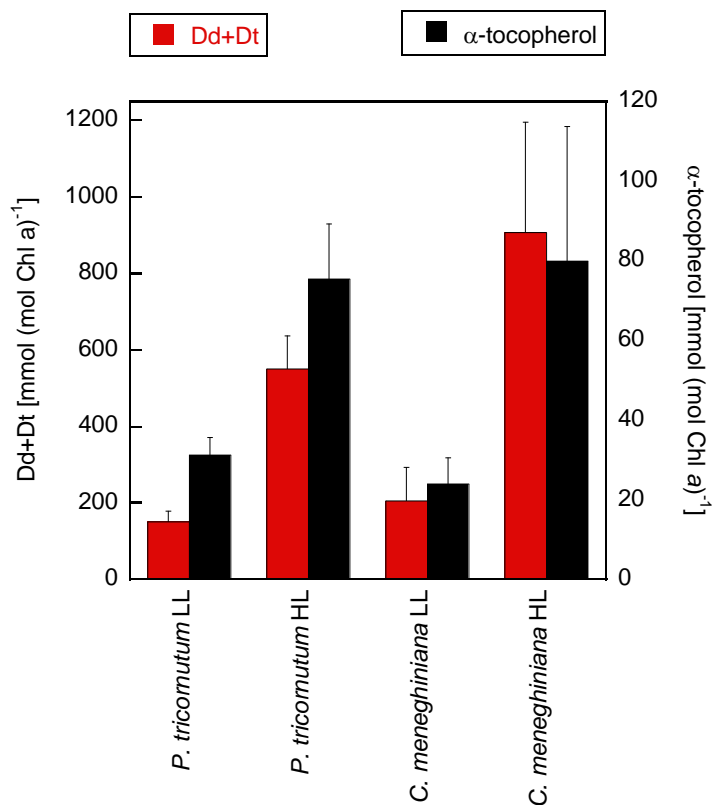


Figure 2

Amount of XC pigments (sum of Dd and Dt) and α-tocopherol, normalized on chlorophyll *a*, in thylakoids of *P. tricornutum* and *Cyclotella meneghiniana*. Diatoms were grown under low light (LL, 40 μmol photons m⁻² s⁻¹) or high light (HL, 180 μmol photons m⁻² s⁻¹) for several generations before thylakoid isolation and pigment quantification was performed as described in Lepetit et al. (2010). α-tocopherol separation and quantification was performed by Kerstin Flieger (University of Leipzig, Germany) using a reversed phase column in an HPLC with a coupled fluorescence detector.

Furthermore, the plastidic levels of superoxide and H₂O₂ can be lowered via superoxide dismutase and ascorbate peroxidase, respectively. While this route exists in diatoms, its respective importance is not clarified yet and species-specific differences do exist (Rijstenbil

2001; Rijstenbil 2003; Roncarati et al. 2008; Waring et al. 2010). Other antioxidants such as ascorbic acid, glutathione and phenolic compounds including flavonoids complement the antioxidative capacity of diatoms, but huge species-specific differences in their concentrations are apparent (Foo et al. 2017; Smerilli et al. 2017; Smerilli et al. 2019).

3.2 Prevention of reactive oxygen species formation

Besides detoxifying ROS and ROS generated products, carotenoids also protect photosynthetic organisms including diatoms before ROS can actually be created. They are involved in NPQ discussed in chapter 3.3, but carotenoids are also very effective quenchers of ^3Chl if orientated closely enough and thereby preempting the formation of $^1\text{O}_2$ (Triantaphyllides and Havaux 2009). Other strategies to avoid the formation of ROS include photorespiration as well as various AEFs (see “1.2 Alternative electron flows provide photoprotection and flexibility in response to metabolic demand”). Interestingly, reversible plastid movement in response to light intensity has been observed in the diatom *Pleurosira laevis*, thus increasing the absorption cross section under low light conditions to maximize light harvesting, but decreasing it under high light conditions due to plastid crowding in the cell center and resulting self-shading (Furukawa et al. 1998). Whether such a phenomenon can contribute to photoprotection in other diatoms remains questionable, as in the diatom *Coscinodiscus granii* plastid movement is also induced after prolonged high light exposure, which is not reversible and is correlated with cell death though (Goessling et al. 2016).

3.3 Non-Photochemical fluorescence Quenching (NPQ)

NPQ is a collective term for different phenomena, which all act to lower photosystem II fluorescence. However, these phenomena are distinct from the suppression of fluorescence caused by the onset of photochemical quenching, i.e. the oxidation of the primary PSII electron acceptor Q_A by a drain of electrons from the ETR due to consumption of NADPH and ATP in the CBB cycle. Importantly, it is by measuring fluorescence that NPQ can be tracked in the lab, but for cellular physiology the amount of fluorescence emission is less relevant than the two other major processes an excited $\text{Chl}^* a$ electron can use to revert to the ground state (heat dissipation, photochemistry). A decrease in fluorescence by NPQ can have different origins, and several distinct NPQ components are described in plants, see e.g. Derks et al. (2015), Malnoë (2018), and Pinnola and Bassi (2018). Often, but not always, an increase in NPQ indicates an increase in photoprotection (Li et al. 2002; Takahashi and Badger 2011).

There are three classical, primarily kinetically defined NPQ components: qE (energy dependent quenching), qI (photoinhibitory quenching), and qT (quenching based on state transitions). qE comprises photoprotection mechanisms which are rapidly induced upon a generation of a $\Delta\phi$ (usually upon exposure to excess light conditions) over time scale of seconds to minutes. qE is also rapidly relaxed upon return to non-saturating light conditions. qI describes processes characterized by a much slower recovery under low light or dark conditions than qE related processes. By virtue of this kinetic definition, qI encompasses drops in fluorescence yield induced by damaged or inactivated PSII reaction centers (see “2.1 Kinetic overlap of photoinactivation and downregulation of PSII”), but also processes induced by a sustained thermal dissipation independent of PSII damage, e.g. in evergreen plants during winter. Therefore, for plants the term qZ was introduced to distinguish some of these slowly recovering processes by their underlying mechanism. qZ describes thermal dissipation processes, which are formed within minutes and exclusively rely on the de-epoxidation of violaxanthin via antheraxanthin to zeaxanthin, independent of the qE providing protein PsbS (Nilkens et al. 2010). Its relaxation also follows strictly the epoxidation of zeaxanthin via antheraxanthin to violaxanthin. In diatoms, recent works start to disentangle the various qI components by introducing the sustained NPQ (NPQs) parameter, which describes within qI those slowly recovering NPQ processes that are independent of PSII damage and repair (Wu et al. 2012; Lacour et al. 2018).

Despite some debates, qT is well understood in the green lineage. qT includes a reversible movement of LHCII antennae between PSII and PSI, where these LHCII antennae modulate the PSII and PSI absorption cross section (Nawrocki et al. 2016; Pan et al. 2018). Also, state transitions are often paralleled by a change in thylakoid macrostructure, with fewer thylakoid stacked regions when LHCII detaches from PSII and shuttles towards PSI (Chuartzman et al. 2008; Nagy et al. 2014). The trigger for state transitions is the redox state of the PQ pool, which is sensed via a thylakoidal kinase, STN7 in plants, STT7 in *Chlamydomonas* (Depege et al. 2003; Bellafiore et al. 2005). A reduced PQ pool activates STN7/STT7, which then phosphorylates LHCII and thus induces its detachment from PSII. Diatoms do not display stacked and non-stacked thylakoidal regions under normal growth conditions, which historically has been used to argue against a possible existence of state transitions. Moreover, in the diatom *P. tricornutum* previous experiments indicated the absence of state transitions (Owens 1986). In this study, a protocol adapted from plants was applied which uses green light as ‘PSII light’ and far-red light as ‘PSI light’. We meanwhile know that there is no strict and stable discrimination of far-red absorption in PSII in *P. tricornutum*, as also PSII can absorb in

the far-red due to the presence of Lhcf15 (Herbstová et al. 2015; Herbstová et al. 2017) (see “*Photosynthetic light reactions in diatoms. I. The lipids and light-harvesting complexes of the thylakoid membrane*”). Interestingly, in *P. tricornutum* there is a putative kinase with strong homology to STT7/STN7, whose function is as yet unclear. Moreover, time resolved fluorescence analyses revealed a spectral component developing under NPQ conditions, which the authors speculated to result from a transfer of some PSII antennae to PSI (Miloslavina et al. 2009). Given the fact that not all aspects of diatom NPQ assigned to qE are fully clarified yet (see next chapter) and that most studies on diatom NPQ characteristics have been performed on only a handful of species while there are ~ 100,000 diatom species to explore (Mann and Vanormelingen 2013), the absence of state transitions in diatoms should not be taken for granted yet.

3.4 The molecular regulation and characteristics of qE

In recent years, major understandings of the molecular regulation of qE in diatoms have been acquired. In addition, there are numerous reports on the ecophysiological distribution and importance of qE in diatoms (see “*4. Variable adjustment of diatom light-response in different ecosystems*”). qE strongly depends on the presence of the xanthophyll pigment Dt (Arsalane et al. 1994; Olaizola et al. 1994; Lavaud et al. 2002b; Goss et al. 2006; Park et al. 2010; Lavaud and Lepetit 2013; Roháček et al. 2014; Blommaert et al. 2017; Lacour et al. 2020). This pigment is produced from Dd via action of a de-epoxidase in the presence of a ΔpH across the thylakoid membrane (Hager and Stransky 1970). Usually, this happens in excess light when the photosynthetic light reactions are limited by what the CBB cycle can metabolize (oxidation of NADPH, hydrolysis of ATP). However, the de-epoxidation also occurs to some extent in dark conditions, likely due to a backwards reaction of the thylakoidal ATP synthase pumping protons into the lumen (Bailleul et al. 2015) or possibly some kind of ‘chlororespiration’ (Jakob et al. 1999) (see also “*1.5 Chlororespiration, redox state of the plastoquinone pool, and pmf in the dark*”).

Dt is converted back to Dd in the absence of a pronounced ΔpH , i.e. under low light and to some extent also dark conditions, catalyzed via an epoxidase which then operates faster than the de-epoxidase (Blommaert et al. 2021). Interestingly, after a switch from high light the epoxidation reaction in diatoms is faster under low light conditions than in darkness (Goss et al. 2006; Blommaert et al. 2017). As the epoxidase requires NADPH as co-substrate, its synthesis through photochemical reactions under low light conditions (not in darkness) in combination with a putatively small NADPH/NADP pool has been proposed to cause this

peculiar feature (Goss et al. 2006), but also another mode of redox control has been postulated recently (Blommaert et al. 2021). The XC of diatoms shows further differences compared to the green lineage: The epoxidation reaction of diatoms is much faster (Goss et al. 2006), but gets downregulated under high light, possibly reflecting its regulation by the stromal pH (Mewes and Richter 2002; Goss et al. 2006) or redox regulation (Blommaert et al. 2021). The de-epoxidase is activated at a much lower ΔpH than in the greens (Jakob et al. 2001), especially when high concentrations of the co-substrate ascorbate are available (Grouneva et al. 2006). Also, the de-epoxidase of diatoms has a considerable higher affinity for ascorbate (Grouneva et al. 2006). Finally, in contrast to the ‘greens’, the abolishment of the ΔpH does not directly remove qE. As long as a Dt is present, it still provides qE (Goss et al. 2006). Hence, the amount of short-term high light induced de-epoxidation of Dd to Dt is usually linearly correlated to the establishment of qE in diatoms, while the epoxidation of Dt back to Dd is linearly correlated to the relaxation of qE (Lavaud et al. 2002a; Goss et al. 2006; Lavaud and Lepetit 2013; Blommaert et al. 2017). In this aspect, the diatom qE rather resembles the qZ mechanism described for plants (see “3.3 Non-Photochemical fluorescence Quenching”), except that diatom qE/qZ operates on a faster timescale. Therefore, the tuning of the XC in diatoms can be best explained in the framework of its utmost importance for induction of qE (Wilhelm et al. 2006): As changes in the pH of the lumen/stroma only indirectly trigger qE via activation/deactivation of the XC enzymes, the enzymatic reactions must proceed very rapidly. In line with this, the kinetic properties of both de-epoxidase and epoxidase reaction can be altered in *P. tricornutum* depending on the long term acclimation to different light intensities (Kuczyńska et al. 2020). We must emphasize that in the diatoms *C. meneghiniana* and *Navicula* sp. there is a component of qE that is independent of the XC, but rather relies on the establishment of the ΔpH alone (Grouneva et al. 2008; Derks and Bruce 2018). So far, mechanistically little is known about this NPQ component, but for *C. meneghiniana*, Grouneva et al. (2008) demonstrated that it requires the initial presence of certain amounts of Dt. In addition to Dt, thylakoid membrane proteins called Lhcx have a key role for qE in diatoms. These proteins belong to the Lhc superfamily and usually are encoded by multiple slightly different copies in the diatom genome (see “Photosynthetic light reactions in diatoms. I. The lipids and light-harvesting complexes of the thylakoid membrane”). When individual Lhcx proteins are lowered or increased by reverse genetics, the capacity for qE is simultaneously either lowered or increased (Bailleul et al. 2010b; Ghazaryan et al. 2016; Taddei et al. 2016; Lepetit et al. 2017; Buck et al. 2019). Moreover, in various diatom species and communities, Lhcx proteins increase in response to light stress conditions (Bailleul et al. 2010b; Park et al.

2010; Zhu and Green 2010; Lepetit et al. 2013; Laviale et al. 2015; Blommaert et al. 2017; Lepetit et al. 2017; Taddei et al. 2018). Other stressors such as iron, copper, phosphorus, or nitrogen limitation increase the amount of some Lhcx, too, also followed by an increase of qE capacity (Zhu et al. 2010; Taddei et al. 2016; Helliwell et al. 2020). Three (Lhcx1,2,3) of the four Lhcx proteins present in *P. tricornutum* can confer qE independently of each other, while also synergistically adding additional qE capacity (Buck et al. 2019). By using multiple functionally complementary *Lhcx* genes whose expression is dependent on different environmental triggers, diatoms tune their qE capacity depending on the environmental constraints. Interestingly, the Lhcx4 protein in *P. tricornutum* cannot induce qE by itself (Buck et al. 2019), although it might do so on top of Lhcx1 mediated NPQ (Taddei et al. 2016). Lhcx4 is also regulated differently, being strongly upregulated under constant darkness (Nymark et al. 2009; Taddei et al. 2016).

Lhcx proteins intimately interact with Dt to provide qE. In *P. tricornutum*, neither Dt nor Lhcx are able to induce any qE individually (Buck et al. 2019), indicating that both components are involved in the same mechanism. Lhcx and Dt induced qE reduces the functional absorption cross section of PSII (σ PSII) (Kuzminov and Gorbunov 2016; Giovagnetti and Ruban 2017; Xu et al. 2018; Buck et al. 2019). Strikingly, when extrapolating the linear relationship between decrease of σ PSII and increase of qE to a thermal dissipation rate of 100%, a σ PSII value remains which is the size of a dimeric PSII core without any peripheral antenna both in *P. tricornutum* (Buck et al. 2019) and in *T. pseudonana* (Xu et al. 2018). Thus, most likely Lhcx and Dt induce a disconnection of the outer antennae from the PSII core, resulting in the strong drop in σ PSII (Buck et al. 2019). Such an antennae detachment is corroborating previous results obtained by time resolved fluorescence spectroscopy (Miloslavina et al. 2009). In this model, the antenna detachment thereby preempts flow of excitation energy from the antenna to the PSII core, lowering excitation pressure on the photosynthetic system.

How the fluorescence in the detached antennae complexes is actually quenched is still a matter of debate. *Lhcx* genes (also termed LhcSR/Li818) are spread throughout the eukaryotic photosynthetic kingdom, being present in most taxa which rely on light harvesting proteins as main antennae, with the major exception of land plants (Dittami et al. 2010; Blommaert et al. 2020). So far, an involvement of Lhcx/LhcSR proteins in qE, besides in diatoms, has been demonstrated in the green alga *C. reinhardtii* (Peers et al. 2009), the eustigmatophyte *Nannochloropsis oceanica* (Park et al. 2019), and the moss *Physcomitrella patens* (Alboresi et al. 2010). Insights from these different organisms may be extrapolated to get clues about the nature of diatom quenching. Based on ultrafast transient absorption and fluorescence

spectroscopy measurements, multiple different quenching mechanisms including chlorophyll-carotenoid excitation energy transfer as well as chlorophyll-chlorophyll and chlorophyll-carotenoid charge transfer states have been suggested to be responsible for qE in plants and green algae (summarized in de la Cruz Valbuena et al. 2019; Bennett et al. 2019). This ambiguity may partly be due to two major facts:

i) In order to avoid scattering artifacts, ultrafast spectroscopy experiments are often recorded on isolated thylakoids or pigment protein complexes which need to be specifically treated to induce NPQ (such as by lowering pH or removing detergent). Whether the so induced quenching complexes actually represent the *in vivo* situation remains questionable (see also Elnour et al. 2018). Also, for interpretation of the different spectroscopic features, one needs to impose several assumptions on them by referring to spectra obtained from other individually measured pigment protein complexes, the latter also not necessarily reflecting the true *in vivo* situation.

ii) These ultrafast spectroscopy experiments are experimentally challenging, with difficulties to find the ‘right’ experimental laser power and exposure time to avoid artefacts due to bleaching and annihilation processes or due to generation of qI phenomena (see Van Oort et al. 2018; Buck et al. 2019).

Because of these technical challenges, Van Oort et al. (2018) argued that many conclusions based on ultrafast spectroscopic experiment are actually experimental artifacts. As even in the green line the nature of the quenching pigments is unclear, in diatoms there is currently no solid idea of the pigments involved in the actual heat dissipation process.

However, several reports indicate the presence of two major qE sites in diatoms. One site is assigned directly dependent on Dt and resides at the PSII core, while the other one is rather induced by Δ pH and located in detached antennae complexes (Miloslavina et al. 2009; Chukhutsina et al. 2014; Giovagnetti and Ruban 2017; Taddei et al. 2018). Such an interpretation is, however, difficult to reconcile with the prime dependency of diatom qE on Dt, with the Δ pH rather having an indirect effect on qE by regulating the XC. We assume that these results may, at least partially, be confounded by the problems described above and may instead rather represent a mixture of qE and qI processes (Kuzminov and Gorbunov 2016; Buck et al. 2019). Also, there may exist diatom species specific differences, with *Cyclotella* possessing a more complex qE behavior than *P. tricornutum* (Grouneva et al. 2008) which could explain the observation of even a third qE site in *Cyclotella* (Chukhutsina et al. 2014). For *P. tricornutum* there is strong evidence that the major qE mechanism is dependent on the presence of Lhcx

proteins and the conversion of Dd into Dt, which detaches the peripheral antennae and thus establishes the major site of qE (Fig. 3) (Kuzminov and Gorbunov 2016; Buck et al. 2019). It remains to be elucidated whether Lhc_x proteins form actual part of these detached quenching complexes or whether, in concert with Dt, they only induce the uncoupling of peripheral antennae and their transformation into the dissipative state. Different biochemical studies do not provide a conclusive picture about localization of Lhc_x proteins yet: Lhc_x have been found in preparations of the peripheral antennae (Beer et al. 2006; Lepetit et al. 2010; Taddei et al. 2018), PSI (Grouneva et al. 2011; Taddei et al. 2018) but also in PSII (Taddei et al. 2018, Kansy et al. 2020). It is clear that LhcSR/Lhc_x proteins can bind pigments including substantial amounts of carotenoids (Bonente et al. 2011), strikingly different to PsbS, the protein mediating qE in plants. Hence, in diatoms Lhc_x proteins may bind XC pigments, which would be the most parsimonious explanation for the intimate connection of the XC and Lhc_x in conferring qE. Unfortunately, recent x-ray structures of diatom antennae do not include Lhc_x proteins (Nagao et al. 2019; Pi et al. 2019) and no *in vitro* Lhc_x protein reconstitution including pigments is available yet. However, it was recently shown that some specific part of the Lhc_x proteins is essential for providing qE (Buck et al. 2021). By modeling this modified Lhc_x sequence on the structure of Lhcf₄, it became clear that especially one prominent tryptophan in this region may most likely coordinate the binding of a Dd/Dt molecule in the second membrane spanning helix, which therefore would provide an explanation for the intimate link of Lhc_x and Dt in conferring qE (Buck et al. 2021).

Given the difficulty of identifying Lhc_x proteins within isolated pigment protein complexes in diatoms, a rather loose association amongst them is likely. We assume that Lhc_x proteins may primarily be located within the PSII supercomplexes, such as in *C. reinhardtii* (Tokutsu and Minagawa 2013; Scholz et al. 2019). As experimental evidence suggests that qE in diatoms involves a disconnection of the peripheral antennae from PSII, we assume a localization of Lhc_x rather in between the peripheral antennae and the PSII core complex. Here, the conversion of Dd into Dt bound to Lhc_x could induce a conformational shift or rearrangement of Lhc_x which leads to a disconnection of the peripheral antennae including a switch into the thermal dissipative state (Fig. 3). The Lhc_x proteins could move together with the peripheral antennae or stay associated with PSII. This model is similar to our earlier model (Lavaud and Goss 2014; Goss and Lepetit 2015), but including only one qE quenching site.

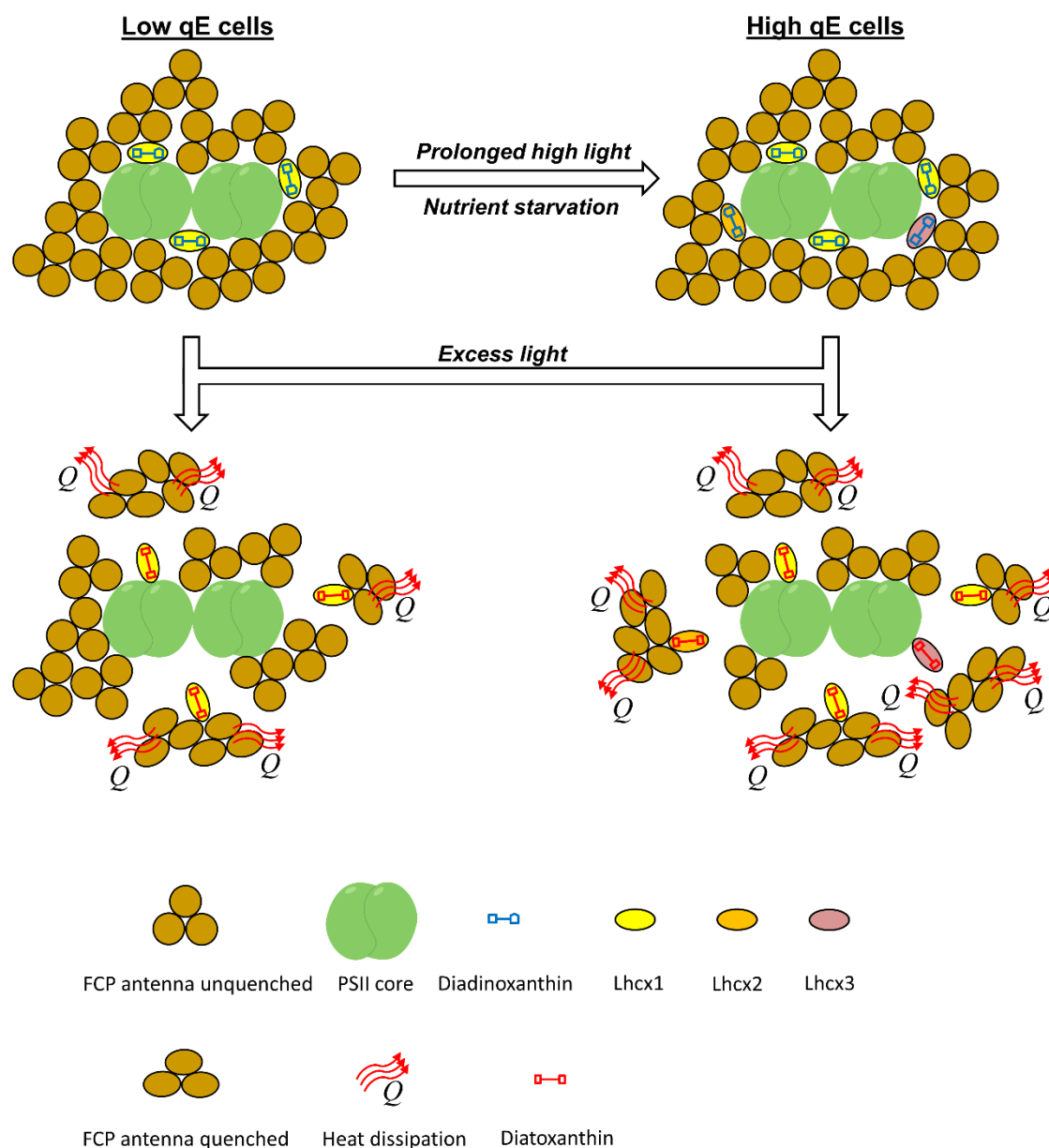


Figure 3

Model of how Lhcx and Dt generate qE in *P. tricornutum*. Depending on their environmental conditions, cells are in a low or high, but yet inactive qE state, which potential qE capacity is determined by the amount of XC pigments and Lhcx proteins present. Upon excess light exposure, the established ΔpH leads to the conversion of Dd into Dt, which induces a reduction in σ_{PSII} by thermal dissipation in the outer, uncoupled FCP antennae (Fucoxanthin chlorophyll binding proteins), shifting the cells into the active qE state.

4. Variable adjustment of diatom light-response in different ecosystems

In the recent years, there has been a significant effort in exploring the light-response diversity among diatoms in relation to their growth form and their specific marine ecosystem and habitat. Diatoms are unique in that they conquered virtually every aquatic habitat, whose characteristics diverge enormously. In that regard, one of the processes that has received the most interest is NPQ and associated XC (see Bertrand 2010; Brunet and Lavaud 2010; Lavaud and Goss 2014; Lacour et al. 2020). Different diatom strains and ecotypes grown under similar conditions in stable culture collection conditions for years and even decades retain differences in effective and potential NPQ and related XC and Lhcx features (Dimier et al. 2007; Lavaud et al. 2007; Bailleul et al. 2010b; Petrou et al. 2011; Barnett et al. 2015; Blommaert et al. 2017; Croteau et al. 2020). Different ecotypes and species can show similar Dd+Dt pool sizes and de-epoxidation states (DES) with completely different XC-mediated NPQ kinetics and capacities. This results possibly from Dd+Dt pools with different functionality and localization and different expression of Lhcx proteins (see “3.4 The molecular regulation and characteristics of qE ”), generating a different overall quenching efficiency of Dt.

The quenching efficiency of Dt has been considered as a solid index of the adaptation of a strain to a given habitat with a specific light climate (Lacour et al. 2020). Diatoms adapt their fast light-response to the light climate of their habitat, in terms of average light dose and light fluctuations, through the molecular control of NPQ by Dt and Lhcx synthesis. Some authors even proposed a classification of Dd-containing microalgae in three distinct ecological groups based on their XC properties vs. irradiance and light fluctuations (Dimier et al. 2007; Dimier et al. 2009). The quenching efficiency and other NPQ features are indeed influenced by ecological niche adaptation with no apparent phylogenetic connection, the most obvious example being benthic forms that inhabit estuarine intertidal flats (Barnett et al. 2015; Blommaert et al. 2017; Blommaert et al. 2018). In turn, NPQ is regarded as a functional trait likely participating in the cost-benefit photoadaptive strategy, the geographical distribution and seasonal dynamics of a species (Irwin and Finkel 2017). NPQ characteristics have been indeed related to i) latitude (Bailleul et al. 2010b; Laviale et al. 2015), ii) different marine (Strzepek and Harrison 2004; Lavaud 2007) and freshwater (Shi et al. 2016) ecosystems, iii) different habitats of the same ecosystem, i.e. seasonal habitat succession in polar systems (Petrou et al. 2011; Croteau et al. 2020) or different intertidal sediment types (Barnett et al. 2015; Blommaert et al. 2017), and iv) seasonal dynamics of phytoplankton in a given ecosystem or habitat (Dimier et al. 2007; Polimene et al. 2014). In the following, we will focus on three ecosystems where diatoms are found abundantly: the water column, the coastal intertidal flats and the polar regions.

4.1 *Diatoms of the phytoplankton*

The light climate of planktonic diatoms shows a depth-dependent attenuation of irradiance and modification of the light spectrum (Stomp et al. 2007; Jaubert et al. 2017). The dynamics of the XC and NPQ, together with other fast-responding photophysiological processes such as the PSII cyclic electron cycle (Lavaud et al. 2002c; Lavaud et al. 2007; Wagner et al. 2016), are relevant for the regulation of the photosynthetic productivity of plankton diatoms in the mixed upper layer of the water column (Brunet and Lavaud 2010; Polimene et al. 2014) and during blooming (Fujiki et al. 2003). Diatoms cope especially well with a fluctuating light climate where they lose less of the absorbed light via alternative electron pathways compared to green algae and thus reach higher growth rates (Wagner et al. 2006). This is achieved by a more balanced and cost-effective qE via a concerted regulation of XC pigments and Lhcx synthesis in a narrow range of irradiance (Wagner et al. 2006; Lavaud et al. 2007; Giovagnetti et al. 2014; Lepetit et al. 2017). Such response is an adaptive advantage in well-mixed habitats where competition for light strongly influences phytoplankton groups and species dynamics (Widdicombe et al. 2010; Polimene et al. 2012; Schofield et al. 2017) and their functional and evolutionary ecology (Tozzi et al. 2004; Benoitson et al. 2017).

The ecophysiological connection between NPQ and XC features and the *in situ* light climate was investigated by comparing strains from different habitats (Lavaud 2007; Lacour et al. 2020). In general, species adapted to higher average light doses or stronger light fluctuations (estuaries and coasts) showed higher Dt quenching efficiencies than counterparts adapted to more stable light environments (semi-enclosed bays and open ocean). Contrastingly, the latter rely more on regulatory processes better suited to cope with more gradual light changes such as a fast turnover of the D1 protein to balance photodamage (Wu et al. 2012; Lavaud et al. 2016) (see also “2.2 PSII repair”). Diatoms that can have both a planktonic and a benthic life (tychoplankton) perform diverse responses, with some representatives showing NPQ features similar to coastal centric diatoms (Perkins et al. 2018; Lacour et al. 2020), while those that inhabit intertidal flats resemble open ocean species (Barnett et al. 2015; Lacour et al. 2020).

4.2 *Diatoms of the microphytobenthos*

Benthic diatoms that inhabit the sediment of intertidal flats experience an extremely complex light environment depending on a multifaceted combination of tidal and diurnal cycles that control the alternation between sharp very low light/darkness periods (during immersion and at night) and open-field like light fluctuations during daytime emersions. They also have to deal with a photic zone condensed to the first hundreds of μm in the sediment (Kühl and Jorgensen

1994). Additionally, other environmental cues such as temperature and salinity can vary rapidly between extremes (Paterson and Hagerthey 2001). Similarly to plankton counterparts, NPQ and related XC pigment dynamics in benthic diatom strongly depend on light as a function of latitude, season, tidal cycle, penetration in the sediment, daily light dose and light fluctuations during emersion (Lavaud and Goss 2014). These temporal NPQ dynamics, together with other photoprotective processes such as the PSII repair cycle (Frankenbach et al. 2018), help benthic diatoms in maintaining their photosynthetic efficiency during emersion (Laviale et al. 2015; Cartaxana et al. 2016). Differences in photoadaptive traits between benthic diatoms are believed to partially explain the differential distribution of growth forms between contrasting sedimentary habitats (i.e. muddy vs. sandy), and they are also claimed to be involved in the hourly species succession within the biofilm during emersion (Underwood et al. 2005).

The two main growth forms of benthic diatoms are the non-motile epipsammon and the motile epipelon. Epipsammon usually dominates in coarser sandy sediment where light penetrates deeper, and it lives in close association with sediment particles. This growth form - similar to plankton counterparts adapted to high average light doses or strong light fluctuations - first relies on XC based NPQ for its photoprotection (Cartaxana et al. 2011; Barnett et al. 2015), and some of them reach some of the highest quenching efficiencies (Lacour et al. 2020). Their high NPQ capacity is based on a large Dd+Dt pool size, high kinetic constants of the XC enzymes, a strong DES and possibly the use of the violaxanthin-antheraxanthin-zeaxanthin cycle under harsh light exposure (Barnett et al. 2015; Blommaert et al. 2017; Blommaert et al. 2018).

Contrastingly, epipelon dominates in fine cohesive muddy sediment where it undergoes active ‘vertical migration’ modelled onto the tidal and diurnal cycles, i.e. it migrates upward the sediment at daytime emersion to form a biofilm at the surface and perform photosynthesis. Epipellic diatoms can also use motility to position themselves along the sediment light gradient and escape from excess light (Consalvey et al. 2004), which generates a strong interplay between behavioral (phototactic motility) and physiological regulation of photosynthesis (Laviale et al. 2016; Blommaert et al. 2018; Frankenbach et al. 2018). Therefore, epipellic diatoms rely less on NPQ and generally show a weaker quenching efficiency (Lacour et al. 2020). Besides, epipellic diatoms rely on a more efficient repair capacity of PSII photodamage than epipsammon (Frankenbach et al. 2018), an ability strikingly similar to their plankton counterparts adapted to a relatively stable light environment (Lavaud et al. 2016). Also, benthic diatoms may contain a higher number of Lhcx proteins (17 in *Seminavis robusta*, Blommaert et al. 2020) to adjust their NPQ capacity to cope with combined environmental stresses (Laviale et al. 2015; Blommaert et al. 2017), but this awaits confirmation by more sequenced benthic

diatoms. Critically, studies regarding the full budget of absorbed light energy and its fate including diverse alternative electron paths, as done in planktonic species (Wagner et al. 2006; Jakob et al. 2007; Bailleul et al. 2015), are not yet available for benthic species.

4.3 Polar diatoms

Diatoms also thrive in polar ecosystems, characterized by very different light climates related to specific, often seasonal, habitats: in sea-ice, underneath the ice, at the marginal ice zone, and in summer free-ice open waters. Furthermore, high latitude habitats are characterized by extreme changes in photoperiods over the year, from complete darkness to 24 h light per day. The combined effects of light with temperature, nutrient availability, and ocean acidification on the regulation of photosynthesis in polar diatoms have been recently extensively considered (Petrou et al. 2016; Trimborn et al. 2017; Hoppe et al. 2018; Lewis et al. 2019; Strzepek et al. 2019; Yan et al. 2019). In general, polar diatoms show photoadaptive features of very low light and temperature acclimation, for instance: i) specific features of Rubisco activity (Valegård et al. 2018) including a high cellular Rubisco content (Young et al. 2015; Gerecht et al. 2019) to compensate for the slow enzymatic rate, ii) very active AEF processes (Alderkamp et al. 2012; Goldman et al. 2015; Schuback et al. 2015; Trimborn et al. 2019), iii) the ability to repair damaged PSII even below 0°C (Petrou et al. 2010), and iv) a strong antioxidant activity (mycosporine-like amino acids and ROS scavengers (Hernando et al. 2002; Janknegt et al. 2008; Ha et al. 2016)).

The pattern of NPQ-related light-response and Dd+Dt pool size is similar to the one of temperate plankton diatoms. It correlates with diurnal and seasonal light dynamics (Schallenberg et al. 2019; Schuback and Tortell 2019), depth (Kashino et al. 2002; Hashihama et al. 2010; Alderkamp et al. 2013) and horizontal light climate heterogeneity, i.e. Dd+Dt pool size is larger in free-ice open waters and at the marginal ice zone than in waters covered with ice. It also depends on the depth of snow covering the floe (Aikawa et al. 2009; Alou-Font et al. 2013; Galindo et al. 2017). Also noteworthy is the high number of FCP and Lhcx proteins (11 isoforms) found in the bipolar strain *Fragilariopsis cylindrus* (Mock et al. 2017). Such as in temperate counterparts, most Lhcx isoforms are downregulated in darkness (Kennedy et al. 2019) and some are upregulated under high light exposure (Park et al. 2010; Kvernvik et al. 2020).

Although they are adapted to very low light, bottom sea-ice diatom communities possess the physiological panoply for responding to sudden and relatively prolonged irradiance increase, e.g. in spring, due to snow flash melt (Griffith et al. 2009; Katayama and Taguchi 2013; Arrigo

et al. 2014). Alderkamp and colleagues (Alderkamp et al. 2010; Alderkamp et al. 2011; Alderkamp et al. 2013; Joy-Warren et al. 2019) demonstrated how NPQ, XC pigments and PSII repair mitigate photoinhibition in polar diatom communities, and how this controls their productivity by strongly modulating the coupling between ETR and carbon fixation (Schuback et al. 2017; Ryan-Keogh et al. 2018).

Polar diatoms are able to sustain a functional photosynthetic machinery during winter polar night at least for 1.5 months and to reactivate photosynthesis upon the spring onset of light within less than 24 h (Kvernvik et al. 2018). While this involves many concerted physiological and metabolic adjustments (Kennedy et al. 2019; Morin et al. 2020), NPQ and XC pigments (and likely AEFs) are of primary importance especially during re-illumination to reactivate photosynthesis (Lacour et al. 2019; Morin et al. 2020). In these conditions, even a low photon flux is dramatically in excess of photosynthetic capacity, and light onset is anticipated in some species via Dt synthesis in the dark, switching PSII in the dissipative state (=‘dark NPQ’) (Kennedy et al. 2019; Lacour et al. 2019). Dt synthesis in darkness occurs possibly through the build-up of a transthylakoidal Δ pH via chlororespiration and/or plastid-mitochondria coupling (see “1.5 Chlororespiration, redox state of the plastoquinone pool, and pmf in the dark”). Upon re-illumination, dark NPQ provides immediate protection (Lacour et al. 2019), onto which light-driven Dt accumulation based NPQ is added (Morin et al. 2020), which supports the rapid transition towards fully operational photosynthesis (Kvernvik et al. 2018; Morin et al. 2020).

Outlook

A wealth of knowledge about photosynthesis in diatoms has been gathered in the last decades, but most of these data have been acquired using only a handful of model species. Considering the ecophysiological diversity of diatoms, these data can only represent a small part of the puzzle. The remarkable flexibility of photosynthetic electron flows and especially the tight interplay with mitochondrial respiration needs to be addressed under various stress conditions and in different diatom species to understand how diatoms optimize electron flows. In this regard, a closer look into mitochondrial respiration may help dissecting further peculiarities of diatoms compared to the green lineage. We also need a first highly resolved image of the diatom ATP synthase to get an idea of the proton requirement per ATP synthesis. In addition, the identity of the actual fluorescence quenching pigments involved in thermal dissipation is unclear so far, and the molecular details of the photosynthetic repair machinery are not known yet. For all these questions, the application of modern genome editing tools such as CRISPR-Cas will be essential. Moreover, the development of heterotrophic diatom model systems, as

proposed for *Cyclotella cryptica* and *Cylindrotheca fusiformis* (Falciatore et al. 2020), could enable for the first time studying processes in heterotrophic mutants (lethal in autotrophic diatoms) which include plastid division and development, but also thylakoid (protein complex) and pigment synthesis. Finally, the further exploration of the functional and ecological diversity of different growth forms and species isolated from different marine habitats will help better understanding how the specificities of diatom photosynthesis support their worldwide ecological success.

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