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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

112

113 **Introduction**

114 As outlined in the previous chapter “*Photosynthetic light reactions in diatoms. I. The lipids and*
115 *light-harvesting complexes of the thylakoid membrane*”, diatoms share the same elementary
116 photosynthetic modules with other organisms performing oxygenic photosynthesis. The linear
117 photosynthetic electron flow involves two photosystems and results in the transfer of electrons
118 from water, the primary electron donor, to the terminal acceptor, nicotinamide adenine
119 dinucleotide phosphate, NADPH (Fig. 1). Photosystem II (PSII) transfers electrons from the
120 Oxygen Evolving Complex, where water oxidation takes place, to the plastoquinones (PQs) in
121 the thylakoid membrane. Photosystem I (PSI) in diatoms catalyzes the electron transfer from
122 the lumen-soluble electron carrier cytochrome c_6 (Böhme and Kunert 1980) to ferredoxin (Fd).
123 In the stroma, the ferredoxin-NADP⁺ reductase (FNR) mediates the electron transfer from Fd
124 to NADP⁺. The intersystem electron chain, which comprises PQs, the cytochrome b_6f complex
125 (cyt b_6f) and cytochrome c_6 , mediates in-series functioning of the two photosystems. In low iron
126 environments, diatoms can replace the iron containing cytochrome c_6 and Fd by the copper-
127 containing plastocyanin and the flavin-containing flavodoxin, respectively (La Roche et al.
128 1996; Strzepek and Harrison 2004; Groussman et al. 2015). The coupling of the electron
129 transfer with proton accumulation within the lumen through water splitting and proton pumping
130 across the thylakoid via the cyt b_6f generates an electrochemical proton gradient or proton
131 motive force (pmf), which comprises an osmotic component, ΔpH , and an electric one, $\Delta\psi$. The
132 pmf is used by the chloroplast CF1Fo-ATP synthase to bind a phosphate group to an adenosine
133 diphosphate (ADP) molecule and thus synthesize adenosine triphosphate, ATP. If diatoms share
134 the same elementary bricks with other organisms performing oxygenic photosynthesis, the
135 regulation of their photosynthetic activities and repair processes show several peculiarities,
136 which we will highlight in detail in the following sub chapters.

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

147 *pmf in the dark*”).

148

149 **1. The regulation of photosynthetic electron flow**

150 ***1.1 The role of pmf as a master regulator of photosynthesis***

151 The main constraint for the photosynthetic electron transfer is to adjust its activity to the amount
152 of light received and to the metabolic needs in terms of NADPH and ATP, despite a variable
153 environment (Kramer et al. 2003; Peltier et al. 2010). When light absorption exceeds the
154 capacity of the electron transfer chain, the over-reduction of the photosynthetic chain can lead
155 to the photodestruction of both PSII (Nixon et al. 2010) and PSI (Sonoike 2011) (see also “2.
156 *Photosystem II photoinactivation and repair*”). Indeed, when an over-reduction of the acceptor
157 side of PSII and/or PSI occurs, the photochemical yield decreases and the yields of other
158 relaxation pathways increase in a complementary way. The probability of charge recombination
159 between the oxidized special chlorophyll *a* pair of PSII (P680⁺) and reduced phaeophytin in
160 PSII, forming the triplet state of chlorophyll *a* (³Chl), increases when electrons cannot be moved
161 fast enough (Krieger-Liszkay 2005; Vass 2011). There is also the possibility of direct
162 population of ³Chl in the PSII antennae by electron spin flip (Santabarbara et al. 2001;
163 Triantaphylidès and Havaux 2009). When ³Chl interacts with O₂, singlet oxygen (¹O₂) is
164 produced, a very toxic molecule which can degrade lipids, pigments or proteins, like the D1
165 protein (Krieger-Liszkay 2005; Halliwell 2006; Nixon et al. 2010; Triantaphylidès and Havaux
166 2009; Vass 2011). PSI acceptor side limitation (and possibly PSII acceptor side limitation as
167 well (Pospíšil 2009)) also favors reduction of O₂ into superoxide anion radicals and hydrogen
168 peroxide (H₂O₂). In the presence of free transition metals such as iron, copper or manganese,
169 H₂O₂ can be converted via the Fenton reaction into the very reactive hydroxyl radical, which
170 e.g. eventually destroys the iron-sulfur centers involved in the electron transfer (Halliwell 2006;
171 Pospíšil 2009; Dietz et al. 2016; Sonoike 2011). The process is almost irreversible because there
172 is no known repair mechanism for PSI (Sonoike 2011). Collectively, ¹O₂, superoxide, H₂O₂ and
173 the hydroxyl radical are called reactive oxygen species (ROS).

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

181 the carbon fixation and other metabolic pathways fueled by the light phase of photosynthesis
182 (Allen 2002). The ratio of ATP to NADPH produced by the LEF is lower than that required for
183 C fixation in the Calvin-Benson-Bassham cycle (CBB cycle). Based on the stoichiometry of 14
184 c subunits per ATP synthase from spinach (Hahn et al. 2018), 14 protons are needed to produce
185 3 ATP, which are, together with 2 NADPH+H⁺, required to reduce one molecule of carbon
186 dioxide in the CBB cycle. With the constitutive Q cycle taking place at the cyt b₆f (Mitchell
187 1975; Sacksteder et al. 2000), a total of 12 H⁺ are translocated to the lumen for the movement
188 of 4 electrons needed to reduce 2 NADP molecules in LEF. Therefore, the ATP-to-NADPH
189 ratio produced by the LEF is 1.28. However, the ATP-to-NADPH requirement for the CBB
190 cycle is 1.5 and can increase due to carbon concentrating mechanisms (CCM), resulting in an
191 ATP shortfall (Eberhard et al. 2008; Peltier et al. 2010; Curien et al. 2016). Here again, the
192 flexibility of the ATP/NADPH stoichiometry produced by the photosynthetic machinery is
193 modulated by the pmf, which is increased by alternative electrons flows (AEFs) fueling the
194 ATP synthase (see “2.2 Alternative electron flows provide photoprotection and flexibility in
195 response to metabolic demand”). In plants and green algae, the flexibility of photosynthesis is
196 therefore largely dependent on the pmf, which plays the dual role of driving ATP and regulating
197 photoprotection mechanisms through its osmotic component, the ΔpH (Kramer et al. 2003).
198 Whether the pmf is a master regulator of the photosynthetic electron transfer in diatoms like in
199 plants is still an open question. In diatoms, the ATP/NADPH produced by the LEF could be
200 different depending on the efficiency of the Q cycle and on the (yet unknown) stoichiometry of
201 c subunits per ATP synthase (Fig. 1). The occurrence of a Q cycle in diatoms seems to be at
202 play based on electrochromic shift (ECS) measurements, i.e. changes in absorption of
203 photosynthetic pigments due to Δψ (Witt 1979; Bailleul et al. 2010a). Like in plants, the
204 increase of ECS concomitant with the cyt b₆f turnover indicates the move of two positive
205 charges (protons) for one electron transferred to cytochrome c₆ (Bailleul et al. 2015). Also, the
206 high ATP demand of the CCM in diatoms (Hopkinson et al. 2011) strongly suggests that
207 mechanisms increasing the pmf are needed (see next section). Clearly, the rapid and reversible,
208 energy dependent regulation of the light harvesting system of PSII (=qE, a major
209 photoprotection mechanism) is regulated by the ΔpH in diatoms (see “3.4 The molecular
210 regulation and characteristics of qE”). So far, there is no clear evidence for a ‘photosynthetic
211 control’ in diatoms but the observation that P700, the special pair of PSI, is oxidized after a
212 pulse of high light could reflect such a control (Shimakawa and Miyake 2018).

213

214

215 ***1.2 Alternative electron flows provide photoprotection and flexibility in response to metabolic***
216 ***demand***

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

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

240

241 ***1.3 Cyclic electron flow around PSI***

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

249 plants, rates of the cyclic electron flow (CEF) rate can reach up to ~ 100 electrons s^{-1} PSI⁻¹ (Joliot
250 and Johnson 2011), but which of the three proposed mechanisms dominates is still a matter of
251 debate. The NDH is not found in diatoms (nor in other microalgae with the notable exception
252 of prasinophytes, Oudot-Le Secq et al. 2007). PGRL1 and PGR5 are present in diatoms
253 (Grouneva et al. 2011; Grouneva et al. 2016) and recent reports suggest an involvement of
254 PGRL1 in CEF of *Phaeodactylum tricornutum* (Zhou et al. 2020). The existence of CEF,
255 measured as a PSI activity in conditions of PSII inhibition, was demonstrated in diatoms using
256 both P700 reduction and ECS (Maxwell and Biggins 1976; Bailleul et al. 2015) (Fig. 1). The
257 measured rates, however, correspond to 5 to 10 electrons s^{-1} PSI⁻¹ in most diatom species
258 (Maxwell and Biggins 1976; Bailleul et al. 2015), even though higher rates were measured in
259 polar diatoms (~ 25 electrons s^{-1} PSI⁻¹, Goldman et al. 2015) or in iron stress conditions (up to
260 55 electrons s^{-1} PSI⁻¹, Thamtrakoln et al. 2013). This suggests that if CEF may not play such
261 a constitutive and ubiquitous role as in plants, it can become a key player of the photosynthetic
262 regulation in some species and conditions.

263

264 **1.4 Water-to-water cycles**

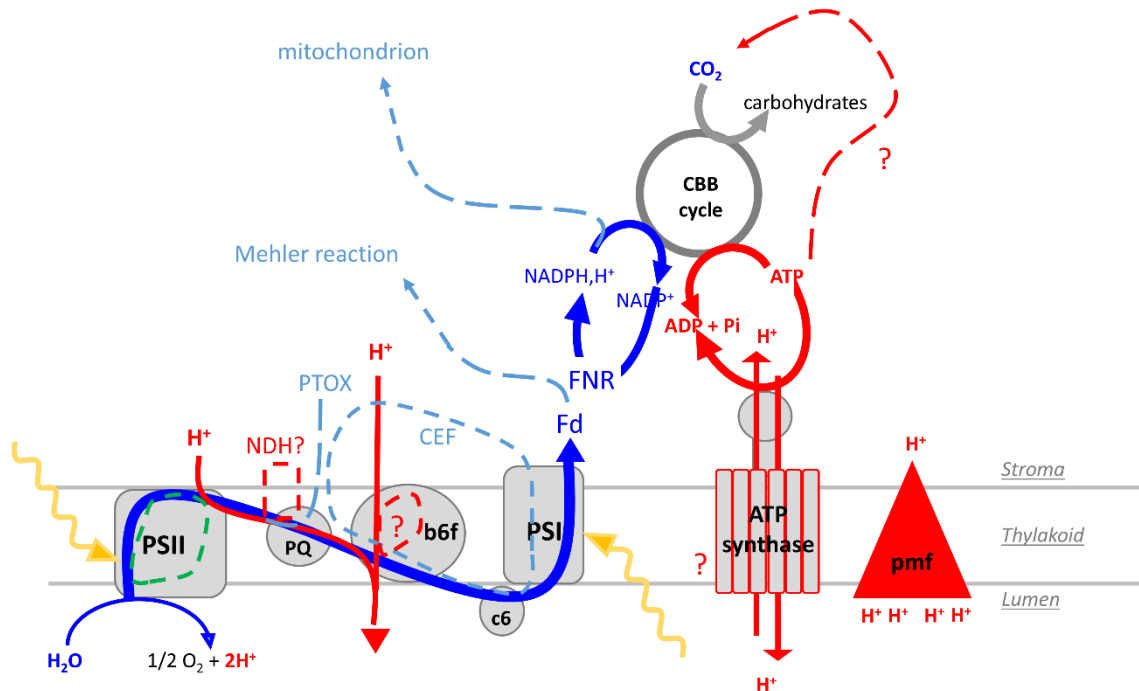
265 The occurrence of WWCs in diatoms were first tested by comparing oxygen and fluorescence
266 measurements derived photosynthetic electron transport rates (ETR). While there is a strong
267 correlation between O₂ production and ETR under low light conditions, discrepancies were
268 measured under higher light intensities (Wagner et al. 2006). Later, direct measurements of
269 photosynthesis-driven oxygen consumption, even in conditions minimizing the
270 photorespiration, confirmed the presence of the WWC (Eisenstadt et al. 2010).

271 The Mehler reaction reroutes electrons from Fd to reduce O₂ into superoxide (Fig. 1) (Mehler
272 1951; Asada 2000). Superoxide is then reduced by the superoxide dismutase (SOD) into H₂O₂,
273 which is further scavenged by the ascorbate peroxidase to form water and oxidized ascorbate
274 (Asada 2000). Such WWC has been hypothesized to contribute to the generation of extra ATP
275 and to protect PSI from over-reduction of its electron acceptors (Ort and Baker 2002). The
276 Mehler reaction has been identified in plants (Asada 2000), green algae (Chen et al. 1996), and
277 cyanobacteria (Asada et al. 1975). In the dinoflagellate genus *Symbiodinium*, the Mehler
278 reaction was proposed as the main alternative electron flow (Roberty et al. 2014). Oxygen
279 photoreduction measured in the diatoms *Nitzschia epithemioides* and *Thalassiosira pseudonana*
280 was ascribed to the Mehler reaction (Waring et al. 2010) but its rate *in vivo* is difficult to
281 estimate because of sources of confusion with other WWCs. Based on the nature of the metal
282 cofactor, Fe-containing SODs and CuZn-containing SODs have been described (Wolfe-Simon

283 et al. 2005). In diatoms, a MnSOD has been found in the plastid of *T. pseudonana* whereas this
284 enzyme is usually present in mitochondria of other species (Wolfe-Simon et al. 2006). This
285 peculiarity could contribute to the ecological success of diatoms in low iron regions of the
286 ocean. Flv proteins play an important role in photoprotection and ATP/NADPH adjustment in
287 cyanobacteria, green algae, mosses and some plants excluding angiosperms (Yamamoto et al.
288 2016) but genes encoding Flv are not found in the genomes of diatoms (Zhang et al. 2009).
289 The electrons downhill PSI can be rerouted to the mitochondria, a transfer of reducing power
290 enabled by malate shuttles with low rates though (Scheibe et al. 2005). Also other observations
291 suggest strong energetic exchanges between organelles in the green lineage (Cardol et al. 2009;
292 Cardol et al. 2010). The reducing power is then converted into ATP through the oxidative
293 phosphorylation pathway, which can occur either via the classical mitochondrial electron flow
294 or via complex I coupled to AOX. The AOX pathway behaves as a valve and dissipates reducing
295 power from the chloroplast under stress conditions in the green lineage (Yoshida et al. 2011;
296 Kaye et al. 2019) but probably also in diatoms (Murik et al. 2019), e.g. under iron stress (Allen
297 et al. 2008). In addition, regardless of the light conditions, there is a strong constitutive coupling
298 between diatom plastids and mitochondria, involving about 10% of photosynthetically
299 generated electrons, which is coupled to the plastidic import of the extra ATP generated in the
300 mitochondrion (Bailleul et al. 2015). Exchanges of ATP between organelles also occur in the
301 green lineage, which is responsible for a pmf across the thylakoids in the dark, resulting from
302 the hydrolysis of ATP of mitochondrial origin (Tanada 1951; Paul and Volcani 1976; Finazzi
303 and Rappaport 1998; Peers and Price 2006; Takizawa et al. 2007). However, the peculiarity of
304 diatom's photosynthesis is the constitutive nature of this energetic interaction. It is unknown
305 how this connection contends with the four membranes surrounding the plastid. One possibility
306 involves an interplay between the CBB cycle and the mitochondrial glycolysis, an unusual
307 metabolic configuration in stramenopiles (Liaud et al. 2000; Smith et al. 2016; Río Bártulos et
308 al. 2018).

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

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



322

323 **Figure 1**

324 Schematic representation of the photosynthetic electron transfer chains. The linear electron flow
 325 is represented as a bold blue arrow. Proton movements are represented by red arrows. The CBB
 326 cycle is represented in grey. The unknowns are represented by blue dashed lines (for alternative
 327 electron flows), a green dashed line (PSII cyclic electron flow), a red dashed line and red
 328 question marks (Q cycle in the cyt b₆f, ATP demand for CCM and number of c subunits). PSI
 329 cyclic electron flow could be mediated via PGRL1/PGR5 or via another yet unknown
 330 plastoquinone reducing pathway.
 331

332

333 **1.5 Chlororespiration, redox state of the plastoquinone pool, and pmf in the dark**

334 Chlororespiration is a respiratory-like electron transport taking place in thylakoids and resulting
 335 in the oxidation of stromal reductants (Fd, NADPH). It can occur in the dark and involves two
 336 enzymes: NADPH dehydrogenase (type I NDH in plants, type II NDH in green algae, Jans et
 337 al. 2008) which transfers electrons from NADPH or Fd towards the (oxidized) PQs, and the
 338 thylakoid-bound plastid terminal oxidase (PTOX) which reduces O₂ into water thanks to
 339 (reduced) plastoquinols (Bennoun 1982) (Fig. 1). Because it combines PQ reducing (NDH) and

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

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

363

364

365

366 **2. Photosystem II photoinactivation and repair**

367 PSII is susceptible to photoinactivation through multiple, non-exclusive paths (reviews Oguchi
368 et al. 2011; Vass 2012; Zavafer et al. 2015; Campbell and Serôdio 2020). A direct path likely
369 acts through a low-probability absorbance of a photon by the manganese cluster of the Oxygen
370 Evolving Complex, leading to loss of capacity for photooxidation of water and then to
371 photochemical destruction of PSII by subsequent photon excitations (Tyystjarvi et al. 2005).
372 This path is provoked primarily by UV and blue photons and shows limited sensitivity to the
373 instantaneous physiological state of the cell (Havurinne and Tyystjarvi 2017; Murphy et al.
374 2017). This direct path occurs across excitation levels at nearly constant probability per photon.
375 Alternately, photons captured by the PSII antennae can provoke formation of ^3Chl within the
376 antennae or reaction center, which can in turn generate destructive $^1\text{O}_2$. This path is thus
377 influenced by the antennae absorbance spectra and cross section and hence likely by qE (see
378 “3.4 The molecular regulation and characteristics of qE”). There is, as yet, no direct evidence
379 that induction of qE actually lowers susceptibility to photoinactivation in diatoms, although
380 such an effect is usually assumed based on investigations on qE in plants (Li et al. 2002). The
381 antenna-dependent photoinactivation path also depends directly upon the degree of PSII
382 closure, which in turn reflects the balance between incoming excitation and the downstream
383 flow of electrons away from PSII, often characterized by the lifetime (τ) for PSII re-opening
384 as measured by Fast Repetition and Relaxation Fluorescence (FRRF) (Kolber et al. 1998).
385 Thirdly, charge recombination within PSII may lead to generation of ^3Chl , and then subsequent
386 $^1\text{O}_2$ generation and damage to PSII. This photoinactivation path may dominate under low light
387 when delivery of sequential excitations to PSII are widely spaced, increasing the probability of
388 recombination within PSII (Ohad et al. 2011; Keren et al. 1997).

389 Diatoms show low primary susceptibilities to PSII photoinactivation when compared to other
390 phytoplankton lineages, and within diatoms large centric diatoms show lower susceptibilities
391 than do smaller centrics, probably related to optical attenuation by the package effect in larger
392 cells (Key et al. 2010; Wu et al. 2011; Wu et al. 2012; Wu et al. 2015; Campbell and Serôdio
393 2020). We speculate that the relatively low sensitivity of diatoms to photoinactivation may
394 relate to the photonic crystal nature of the diatom siliceous frustule (Goessling et al. 2018)
395 which modulates the internal light field of diatom cells. We also note that beyond the rather
396 unusual model species *P. tricornutum* (Havurinne and Tyystjarvi 2017) there are fewer
397 mechanistic studies of photoinactivation of PSII from pennate (Petrou et al. 2010; Petrou et al.
398 2012) than from centric diatoms. It is reasonable to expect different optics in the pennates and

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

401

402 ***2.1 Kinetic overlap of photoinactivation and downregulation of PSII***

403 Loss of [PSII]_{active} through either photoinactivation path leads to lowered variable fluorescence
404 from PSII and thus can overlap both phenomenologically and kinetically with reversible
405 downregulation of [PSII]_{active} through induction of qE (Grouneva et al. 2008; Kuzminov and
406 Gorbunov 2016; Buck et al. 2019). From an ecophysiological point of view the suppression of
407 productivity through sustained loss or downregulation of [PSII]_{active}, through whatever
408 mechanism, may be more important than the direct metabolic burden of PSII repair (Raven
409 2011). Prolonged suppression of PSII activity extending after the end of high light exposure
410 imposes an opportunity cost of loss of potential productivity, but keeps the cell in a state pre-
411 acclimated for a return to higher light, as for example through mixing. Evolution may favor this
412 conservative strategy of prolonged down-regulation over more rapid relaxation of down-
413 regulation to maximize short-term productivity at the risk of oxidative damage to the cell. The
414 kinetic overlap of PSII photoinactivation and repair (also summarized under the term qI,
415 photoinhibitory quenching) with the induction and relaxation of qE can be particularly
416 problematic for mechanistic characterization of the photophysiology of diatoms, where large
417 amplitude inductions of qE-like processes (see “3.3 Non-Photochemical fluorescence
418 *Quenching (NPQ)*”) can persist in darkness, requiring low light for timely relaxation (Goss et
419 al. 2006), thereby becoming difficult to distinguish from the overlapping influence of PSII
420 repair under low light or even in darkness (Li et al. 2016).

421

422 ***2.2 PSII repair***

423 Photoinactivation of PSII is countered by a PSII repair cycle (Nixon et al. 2010; Komenda et
424 al. 2012; Nishiyama et al. 2014) that proteolytically removes photoinactivated subunit(s), in
425 concert with subunit replacement through translation mediated by chloroplastic ribosomes. It is
426 critical to note that although photoinactivation of PSII may precede recovery through repair,
427 the two processes show distinct kinetics and light responses. PSII photoinactivation rate shows
428 a nearly linear dependence upon instantaneous excitation levels ((Oguchi et al. 2011; Vass
429 2012; Campbell and Serôdio 2020). In contrast, PSII repair in diatoms reaches saturation under
430 fairly low light (Wu et al. 2012). Under some conditions diatoms can therefore accumulate
431 considerable pools of [PSII]_{inactive} (Wu et al. 2011; Wu et al. 2012; Campbell et al. 2013; Lavaud
432 et al. 2016) representing intermediate stages in the PSII repair cycle (Grouneva et al. 2011).

433 This temporal offset between photoinactivation and repair can result in a tradeoff between
434 strategies. A 'just-in-time' repair strategy requires cellular investment in sufficient
435 instantaneous PSII repair capacity to counter PSII photoinactivation immediately, with
436 sufficient metabolic capacity allocated to run key proteases and chloroplastic ribosome activity.
437 In contrast, a 'warehouse' strategy involves protein investment into larger pools of [PSII]_{inactive}
438 waiting around for eventual repair. In *T. pseudonana*, the burden of maintaining PSII repair is
439 low under low light, as slow rates of photoinactivation mean that PSII must only be replaced
440 on generational time scales (Li et al. 2015). The low light cells thus follow a 'just-in-time'
441 strategy. As growth light increases, the burden of PSII repair grows, until under light above the
442 growth optima maintenance of PSII repair comes to dominate chloroplastic nitrogen
443 metabolism, thereby restricting capacity for growth and forcing the cells towards a 'warehouse'
444 strategy where [PSII]_{inactive} waits for repair. Behrenfeld et al. (1998) noted that phytoplankton
445 can tolerate a degree of photoinhibitory burn down of the standing pool of [PSII]_{active} without
446 suffering an immediate loss of net photosynthesis, showing that the remaining pool of
447 [PSII]_{active} can accelerate their photochemical turnover to compensate for loss of [PSII]_{active}.
448 This implies a 'warehouse' strategy with an offset between photoinactivation and later repair.
449 Lavaud et al. (2016) found that in *P. tricornutum* a large capacity for NPQ accompanied a 'just-
450 in-time' strategy of repairing [PSII]_{inactive} rapidly. In contrast, *Skeletonema costatum*
451 compensated for limited capacity to induce sustained NPQ with a 'warehouse' strategy by
452 maintaining a large pool of [PSII]_{inactive} awaiting repair. We thus find a compensatory balance
453 between capacity to downregulate PSII through NPQ with capacity to accumulate large pools
454 of [PSII]_{inactive} or excess [PSII]_{active}.
455 Interestingly, in diatoms the PsbA (D1) & PsbD (D2) subunits both turnover at similar rates
456 (Wu et al. 2011; Wu et al. 2012; Campbell et al. 2013; Li et al. 2016), contrary to text book
457 descriptions which focus on PsbA turnover. We have not pursued the implications as to whether
458 PsbA or PsbD are both subject to direct photoinactivation in parallel, or whether turnover of
459 PsbD simply closely tracks primary photoinactivation of PsbA.
460 The FtsH protease complex is a membrane associated structure usually comprised of six FtsH
461 isoform subunits, implicated as the primary protease mediating removal of PsbA from thylakoid
462 membranes (Nixon et al. 2010; Komenda et al. 2012), along with roles in turnover of other
463 complexes (Malnoë et al. 2014). Diatom capacity for PsbA turnover is predictable from the
464 FtsH:PsbA ratio which in turn varies depending upon the predicted light dynamics of the
465 original source habitats of strains (Campbell et al. 2013). The 'just-in-time' strategy requires a
466 higher FtsH:PsbA ratio than the 'warehouse' strategy. Furthermore, PSII repair continues in the

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

475 Although large centric diatoms show lower susceptibility to photoinactivation than their smaller
476 cousins, they can also show 'luxury' turnover of PSII subunits beyond the rates predicted by
477 the photoinactivation (Li et al. 2016). This surprising finding suggests that turnover of subunits
478 can use both [PSII]_{active} and [PSII]_{inactive} as substrates, with a repair system only imperfectly
479 discriminating in favor of [PSII]_{inactive}. The three layer organization of diatom thylakoids may
480 alter or restrict the interaction of the FtsH protease complex with PSII, possibly lowering
481 capacity to discriminate in favor of [PSII]_{inactive} (Komenda et al. 2007), and thereby implying a
482 continuous repair process where the lifetime of a PsbA (or PsbD) is determined by lateral
483 delivery to FtsH rather than by the rate of instantaneous photoinactivation. Recently it was
484 shown that photodamaged PSII reaction centers are physically separated from intact PSII
485 complexes and form repair center clusters (Levitan et al. 2019). A particular steric puzzle is
486 how any PSII housed in the central of the three thylakoid layers can interact with ribosomes
487 and membrane associated FtsH complexes, but these repair centers may be located rather at the
488 outer layers or the thylakoid margins. As a final idiosyncrasy Grouneva et al. (2011) found only
489 a single, plastid encoded FtsH protein isoform in diatom thylakoids (Maxwell, Grouneva, Aro
490 & Campbell; unpublished). In contrast, in other eukaryotic photoautotrophs multiple FtsH
491 protein isoforms are encoded by genes in the nucleus and imported into the chloroplast to form
492 a hetero-hexameric FtsH structure. Thus, either diatoms carry an unusual hexamer of a single
493 isoform of FtsH; or additional divergent subunits have not as yet been annotated as contributing
494 to the chloroplastic FtsH complex of diatoms; or PSII repair in diatoms involves alternate paths.
495

496 **3. Photoprotection in diatoms**

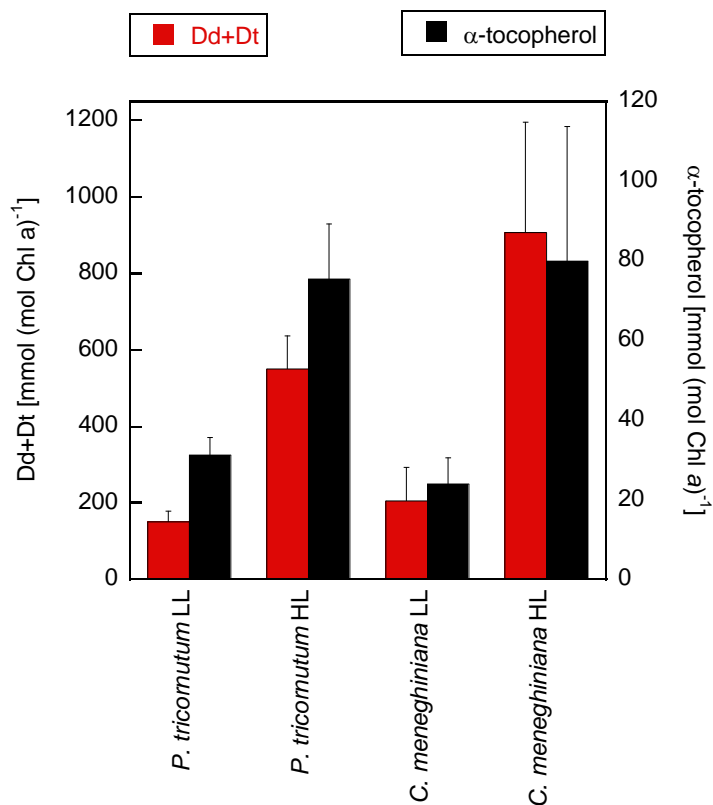
497 When the amount of light absorbed by the light harvesting system exceeds the capacity of the
498 photosynthetic electron transport chain to transfer electrons from the sites of photochemistry to
499 electron acceptors, which also depends on energy consuming pathways such as e.g. the CBB
500 cycle,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

511

512 **3.1 Detoxification of reactive oxygen species**

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

530 Tocopherols are potent antioxidants (Demmig-Adams and Adams 2002; Havaux et al. 2005).
 531 Diatoms possess a full plastid targeted tocopherol biosynthesis pathway based on KEGG
 532 predictions, which is different from other heterokonts/stramenopiles (Nonoyama et al. 2019).
 533 Indeed, tocopherol biosynthesis proteins are present in diatom plastid fractions (Schober et al.
 534 2019) and pronounced amounts of tocopherol are found in diatom thylakoid membranes, which
 535 increase, similarly to the XC pool, upon acclimation to prolonged high light (Fig. 2). As the
 536 antioxidative potential of tocopherols even increases in the presence of carotenoids (Böhm et
 537 al. 1997), tocopherols together with the high amounts of membrane dissolved carotenoids
 538 provide diatom thylakoids with a strong antioxidative capacity.



539

540 **Figure 2**

541 Amount of XC pigments (sum of Dd and Dt) and α-tocopherol, normalized on chlorophyll *a*,
 542 in thylakoids of *P. tricornutum* and *Cyclotella meneghiniana*. Diatoms were grown under low
 543 light (LL, 40 μmol photons m⁻² s⁻¹) or high light (HL, 180 μmol photons m⁻² s⁻¹) for several
 544 generations before thylakoid isolation and pigment quantification was performed as described
 545 in Lepetit et al. (2010). α-tocopherol separation and quantification was performed by Kerstin
 546 Flieger (University of Leipzig, Germany) using a reversed phase column in an HPLC with a
 547 coupled fluorescence detector.
 548

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

552 2001; Rijstenbil 2003; Roncarati et al. 2008; Waring et al. 2010). Other antioxidants such as
553 ascorbic acid, glutathione and phenolic compounds including flavonoids complement the
554 antioxidative capacity of diatoms, but huge species-specific differences in their concentrations
555 are apparent (Foo et al. 2017; Smerilli et al. 2017; Smerilli et al. 2019).

556

557 **3.2 Prevention of reactive oxygen species formation**

558 Besides detoxifying ROS and ROS generated products, carotenoids also protect photosynthetic
559 organisms including diatoms before ROS can actually be created. They are involved in NPQ
560 discussed in chapter 3.3, but carotenoids are also very effective quenchers of ³Chl if orientated
561 closely enough and thereby preempting the formation of ¹O₂ (Triantaphylidès and Havaux
562 2009). Other strategies to avoid the formation of ROS include photorespiration as well as
563 various AEFs (see “1.2 Alternative electron flows provide photoprotection and flexibility in
564 response to metabolic demand”). Interestingly, reversible plastid movement in response to light
565 intensity has been observed in the diatom *Pleurosira laevis*, thus increasing the absorption cross
566 section under low light conditions to maximize light harvesting, but decreasing it under high
567 light conditions due to plastid crowding in the cell center and resulting self-shading (Furukawa
568 et al. 1998). Whether such a phenomenon can contribute to photoprotection in other diatoms
569 remains questionable, as in the diatom *Coscinodiscus granii* plastid movement is also induced
570 after prolonged high light exposure, which is not reversible and is correlated with cell death
571 though (Goessling et al. 2016).

572

573 **3.3 Non-Photochemical fluorescence Quenching (NPQ)**

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

585 There are three classical, primarily kinetically defined NPQ components: qE (energy dependent
586 quenching), qI (photoinhibitory quenching), and qT (quenching based on state transitions). qE
587 comprises photoprotection mechanisms which are rapidly induced upon a generation of a $\Delta\phi$
588 (usually upon exposure to excess light conditions) over time scale of seconds to minutes. qE is
589 also rapidly relaxed upon return to non-saturating light conditions. qI describes processes
590 characterized by a much slower recovery under low light or dark conditions than qE related
591 processes. By virtue of this kinetic definition, qI encompasses drops in fluorescence yield
592 induced by damaged or inactivated PSII reaction centers (see “2.1 Kinetic overlap of
593 photoinactivation and downregulation of PSII”), but also processes induced by a sustained
594 thermal dissipation independent of PSII damage, e.g. in evergreen plants during winter.
595 Therefore, for plants the term qZ was introduced to distinguish some of these slowly recovering
596 processes by their underlying mechanism. qZ describes thermal dissipation processes, which
597 are formed within minutes and exclusively rely on the de-epoxidation of violaxanthin via
598 antheraxanthin to zeaxanthin, independent of the qE providing protein PsbS (Nilkens et al.
599 2010). Its relaxation also follows strictly the epoxidation of zeaxanthin via antheraxanthin to
600 violaxanthin. In diatoms, recent works start to disentangle the various qI components by
601 introducing the sustained NPQ (NPQs) parameter, which describes within qI those slowly
602 recovering NPQ processes that are independent of PSII damage and repair (Wu et al. 2012;
603 Lacour et al. 2018).

604 Despite some debates, qT is well understood in the green lineage. qT includes a reversible
605 movement of LHCII antennae between PSII and PSI, where these LHCII antennae modulate
606 the PSII and PSI absorption cross section (Nawrocki et al. 2016; Pan et al. 2018). Also, state
607 transitions are often paralleled by a change in thylakoid macrostructure, with fewer thylakoid
608 stacked regions when LHCII detaches from PSII and shuttles towards PSI (Chuartzman et al.
609 2008; Nagy et al. 2014). The trigger for state transitions is the redox state of the PQ pool, which
610 is sensed via a thylakoidal kinase, STN7 in plants, STT7 in *Chlamydomonas* (Depege et al.
611 2003; Bellafiore et al. 2005). A reduced PQ pool activates STN7/STT7, which then
612 phosphorylates LHCII and thus induces its detachment from PSII. Diatoms do not display
613 stacked and non-stacked thylakoidal regions under normal growth conditions, which
614 historically has been used to argue against a possible existence of state transitions. Moreover,
615 in the diatom *P. tricornutum* previous experiments indicated the absence of state transitions
616 (Owens 1986). In this study, a protocol adapted from plants was applied which uses green light
617 as ‘PSII light’ and far-red light as ‘PSI light’. We meanwhile know that there is no strict and
618 stable discrimination of far-red absorption in PSII in *P. tricornutum*, as also PSII can absorb in

619 the far-red due to the presence of Lhcf15 (Herbstová et al. 2015; Herbstová et al. 2017) (see
620 “*Photosynthetic light reactions in diatoms. I. The lipids and light-harvesting complexes of the*
621 *thylakoid membrane*”). Interestingly, in *P. tricornutum* there is a putative kinase with strong
622 homology to STT7/STN7, whose function is as yet unclear. Moreover, time resolved
623 fluorescence analyses revealed a spectral component developing under NPQ conditions, which
624 the authors speculated to result from a transfer of some PSII antennae to PSI (Miloslavina et al.
625 2009). Given the fact that not all aspects of diatom NPQ assigned to qE are fully clarified yet
626 (see next chapter) and that most studies on diatom NPQ characteristics have been performed on
627 only a handful of species while there are ~ 100,000 diatom species to explore (Mann and
628 Vanormelingen 2013), the absence of state transitions in diatoms should not be taken for
629 granted yet.

630

631 **3.4 The molecular regulation and characteristics of qE**

632 In recent years, major understandings of the molecular regulation of qE in diatoms have been
633 acquired. In addition, there are numerous reports on the ecophysiological distribution and
634 importance of qE in diatoms (see “4. Variable adjustment of diatom light-response in different
635 ecosystems”). qE strongly depends on the presence of the xanthophyll pigment Dt (Arsalane et
636 al. 1994; Olaizola et al. 1994; Lavaud et al. 2002b; Goss et al. 2006; Park et al. 2010; Lavaud
637 and Lepetit 2013; Roháček et al. 2014; Blommaert et al. 2017; Lacour et al. 2020). This pigment
638 is produced from Dd via action of a de-epoxidase in the presence of a ΔpH across the thylakoid
639 membrane (Hager and Stransky 1970). Usually, this happens in excess light when the
640 photosynthetic light reactions are limited by what the CBB cycle can metabolize (oxidation of
641 NADPH, hydrolysis of ATP). However, the de-epoxidation also occurs to some extent in dark
642 conditions, likely due to a backwards reaction of the thylakoidal ATP synthase pumping protons
643 into the lumen (Bailleul et al. 2015) or possibly some kind of ‘chlororespiration’ (Jakob et al.
644 1999) (see also “1.5 Chlororespiration, redox state of the plastoquinone pool, and pmf in the
645 dark”).

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

653 peculiar feature (Goss et al. 2006), but also another mode of redox control has been postulated
654 recently (Blommaert et al. 2021). The XC of diatoms shows further differences compared to
655 the green lineage: The epoxidation reaction of diatoms is much faster (Goss et al. 2006), but
656 gets downregulated under high light, possibly reflecting its regulation by the stromal pH
657 (Mewes and Richter 2002; Goss et al. 2006) or redox regulation (Blommaert et al. 2021). The
658 de-epoxidase is activated at a much lower ΔpH than in the greens (Jakob et al. 2001), especially
659 when high concentrations of the co-substrate ascorbate are available (Grouneva et al. 2006).
660 Also, the de-epoxidase of diatoms has a considerable higher affinity for ascorbate (Grouneva
661 et al. 2006). Finally, in contrast to the ‘greens’, the abolishment of the ΔpH does not directly
662 remove qE. As long as a Dt is present, it still provides qE (Goss et al. 2006). Hence, the amount
663 of short-term high light induced de-epoxidation of Dd to Dt is usually linearly correlated to the
664 establishment of qE in diatoms, while the epoxidation of Dt back to Dd is linearly correlated to
665 the relaxation of qE (Lavaud et al. 2002a; Goss et al. 2006; Lavaud and Lepetit 2013;
666 Blommaert et al. 2017). In this aspect, the diatom qE rather resembles the qZ mechanism
667 described for plants (see “3.3 Non-Photochemical fluorescence Quenching”), except that
668 diatom qE/qZ operates on a faster timescale. Therefore, the tuning of the XC in diatoms can be
669 best explained in the framework of its utmost importance for induction of qE (Wilhelm et al.
670 2006): As changes in the pH of the lumen/stroma only indirectly trigger qE via
671 activation/deactivation of the XC enzymes, the enzymatic reactions must proceed very rapidly.
672 In line with this, the kinetic properties of both de-epoxidase and epoxidase reaction can be
673 altered in *P. tricornutum* depending on the long term acclimation to different light intensities
674 (Kuczynska et al. 2020). We must emphasize that in the diatoms *C. meneghiniana* and *Navicula*
675 sp. there is a component of qE that is independent of the XC, but rather relies on the
676 establishment of the ΔpH alone (Grouneva et al. 2008; Derks and Bruce 2018). So far,
677 mechanistically little is known about this NPQ component, but for *C. meneghiniana*, Grouneva
678 et al. (2008) demonstrated that it requires the initial presence of certain amounts of Dt.
679 In addition to Dt, thylakoid membrane proteins called Lhcx have a key role for qE in diatoms.
680 These proteins belong to the Lhc superfamily and usually are encoded by multiple slightly
681 different copies in the diatom genome (see “Photosynthetic light reactions in diatoms. I. The
682 lipids and light-harvesting complexes of the thylakoid membrane”). When individual Lhcx
683 proteins are lowered or increased by reverse genetics, the capacity for qE is simultaneously
684 either lowered or increased (Bailleul et al. 2010b; Ghazaryan et al. 2016; Taddei et al. 2016;
685 Lepetit et al. 2017; Buck et al. 2019). Moreover, in various diatom species and communities,
686 Lhcx proteins increase in response to light stress conditions (Bailleul et al. 2010b; Park et al.

687 2010; Zhu and Green 2010; Lepetit et al. 2013; Laviale et al. 2015; Blommaert et al. 2017;
688 Lepetit et al. 2017; Taddei et al. 2018). Other stressors such as iron, copper, phosphorus, or
689 nitrogen limitation increase the amount of some Lhc x , too, also followed by an increase of qE
690 capacity (Zhu et al. 2010; Taddei et al. 2016; Helliwell et al. 2020). Three (Lhc x 1,2,3) of the
691 four Lhc x proteins present in *P. tricornutum* can confer qE independently of each other, while
692 also synergistically adding additional qE capacity (Buck et al. 2019). By using multiple
693 functionally complementary *Lhc x* genes whose expression is dependent on different
694 environmental triggers, diatoms tune their qE capacity depending on the environmental
695 constraints. Interestingly, the Lhc x 4 protein in *P. tricornutum* cannot induce qE by itself (Buck
696 et al. 2019), although it might do so on top of Lhc x 1 mediated NPQ (Taddei et al. 2016). Lhc x 4
697 is also regulated differently, being strongly upregulated under constant darkness (Nymark et al.
698 2009; Taddei et al. 2016).

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

712 How the fluorescence in the detached antennae complexes is actually quenched is still a matter
713 of debate. *Lhc x* genes (also termed LhcSR/Li818) are spread throughout the eukaryotic
714 photosynthetic kingdom, being present in most taxa which rely on light harvesting proteins as
715 main antennae, with the major exception of land plants (Dittami et al. 2010; Blommaert et al.
716 2020). So far, an involvement of Lhc x /LhcSR proteins in qE, besides in diatoms, has been
717 demonstrated in the green alga *C. reinhardtii* (Peers et al. 2009), the eustigmatophyte
718 *Nannochloropsis oceanica* (Park et al. 2019), and the moss *Physcomitrella patens* (Alboresi et
719 al. 2010). Insights from these different organisms may be extrapolated to get clues about the
720 nature of diatom quenching. Based on ultrafast transient absorption and fluorescence

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

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

734 ii) These ultrafast spectroscopy experiments are experimentally challenging, with difficulties
735 to find the ‘right’ experimental laser power and exposure time to avoid artefacts due to
736 bleaching and annihilation processes or due to generation of qI phenomena (see Van Oort et al.
737 2018; Buck et al. 2019).

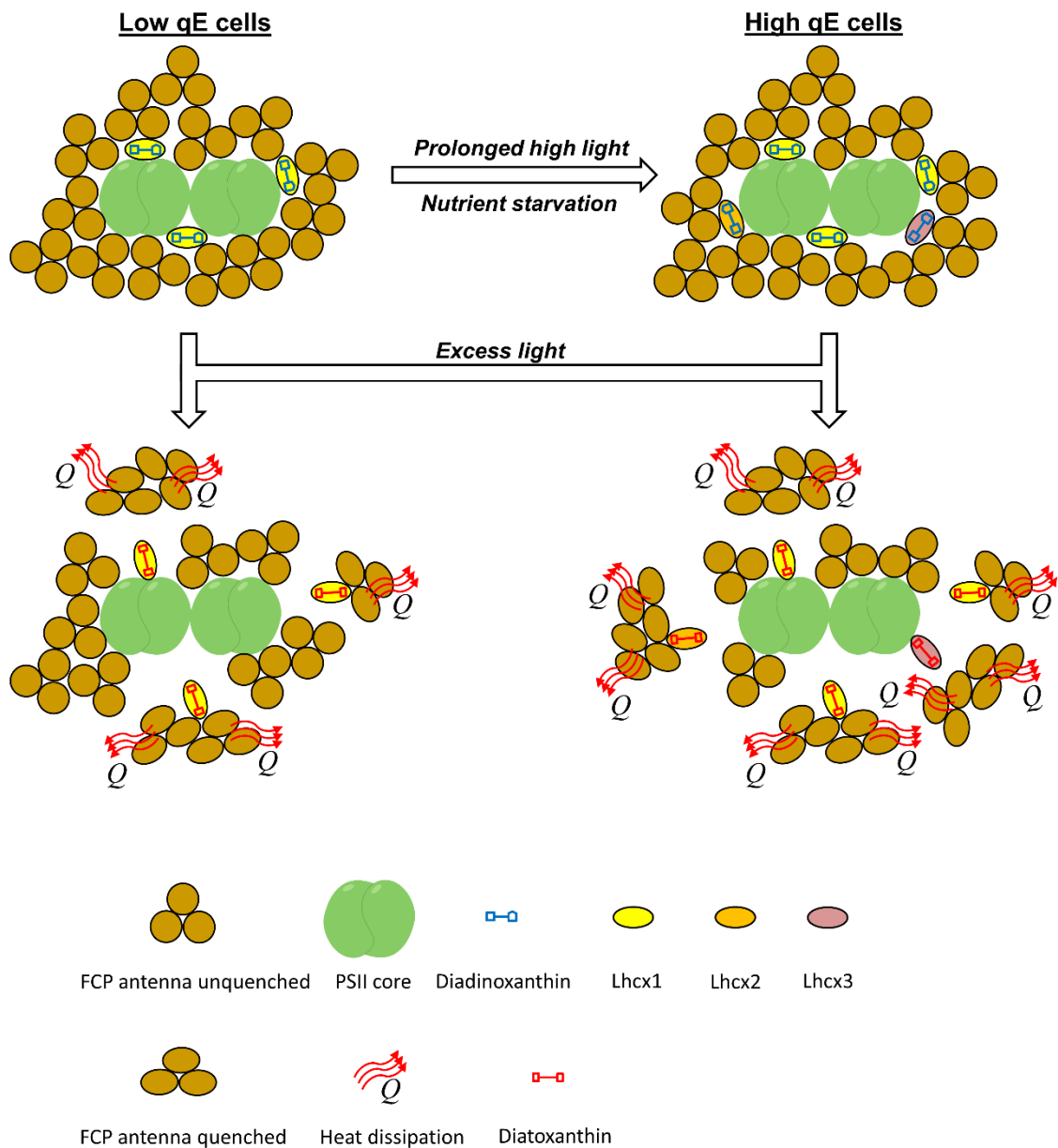
738 Because of these technical challenges, Van Oort et al. (2018) argued that many conclusions
739 based on ultrafast spectroscopic experiment are actually experimental artifacts. As even in the
740 green line the nature of the quenching pigments is unclear, in diatoms there is currently no solid
741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

742 However, several reports indicate the presence of two major qE sites in diatoms. One site is
743 assigned directly dependent on Dt and resides at the PSII core, while the other one is rather
744 induced by Δ pH and located in detached antennae complexes (Miloslavina et al. 2009;
745 Chukhutsina et al. 2014; Giovagnetti and Ruban 2017; Taddei et al. 2018). Such an
746 interpretation is, however, difficult to reconcile with the prime dependency of diatom qE on Dt,
747 with the Δ pH rather having an indirect effect on qE by regulating the XC. We assume that these
748 results may, at least partially, be cofounded by the problems described above and may instead
749 rather represent a mixture of qE and qI processes (Kuzminov and Gorbunov 2016; Buck et al.
750 2019). Also, there may exist diatom species specific differences, with *Cyclotella* possessing a
751 more complex qE behavior than *P. tricornutum* (Grouneva et al. 2008) which could explain the
752 observation of even a third qE site in *Cyclotella* (Chukhutsina et al. 2014). For *P. tricornutum*
753 there is strong evidence that the major qE mechanism is dependent on the presence of Lhcx

754 proteins and the conversion of Dd into Dt, which detaches the peripheral antennae and thus
755 establishes the major site of qE (Fig. 3) (Kuzminov and Gorbunov 2016; Buck et al. 2019).
756 It remains to be elucidated whether LhcX proteins form actual part of these detached quenching
757 complexes or whether, in concert with Dt, they only induce the uncoupling of peripheral
758 antennae and their transformation into the dissipative state. Different biochemical studies do
759 not provide a conclusive picture about localization of LhcX proteins yet: LhcX have been found
760 in preparations of the peripheral antennae (Beer et al. 2006; Lepetit et al. 2010; Taddei et al.
761 2018), PSI (Grouneva et al. 2011; Taddei et al. 2018) but also in PSII (Taddei et al. 2018, Kansy
762 et al. 2020). It is clear that LhcSR/LhcX proteins can bind pigments including substantial
763 amounts of carotenoids (Bonente et al. 2011), strikingly different to PsbS, the protein mediating
764 qE in plants. Hence, in diatoms LhcX proteins may bind XC pigments, which would be the most
765 parsimonious explanation for the intimate connection of the XC and LhcX in conferring qE.
766 Unfortunately, recent x-ray structures of diatom antennae do not include LhcX proteins (Nagao
767 et al. 2019; Pi et al. 2019) and no *in vitro* LhcX protein reconstitution including pigments is
768 available yet. However, it was recently shown that some specific part of the LhcX proteins is
769 essential for providing qE (Buck et al. 2021). By modeling this modified LhcX sequence on the
770 structure of Lhcf4, it became clear that especially one prominent tryptophan in this region may
771 most likely coordinate the binding of a Dd/Dt molecule in the second membrane spanning helix,
772 which therefore would provide an explanation for the intimate link of LhcX and Dt in conferring
773 qE (Buck et al. 2021).

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

785



786

787

788 **Figure 3**

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

795

796

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

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

812 The quenching efficiency of Dt has been considered as a solid index of the adaptation of a strain
813 to a given habitat with a specific light climate (Lacour et al. 2020). Diatoms adapt their fast
814 light-response to the light climate of their habitat, in terms of average light dose and light
815 fluctuations, through the molecular control of NPQ by Dt and Lhcx synthesis. Some authors
816 even proposed a classification of Dd-containing microalgae in three distinct ecological groups
817 based on their XC properties vs. irradiance and light fluctuations (Dimier et al. 2007; Dimier et
818 al. 2009). The quenching efficiency and other NPQ features are indeed influenced by ecological
819 niche adaptation with no apparent phylogenetic connection, the most obvious example being
820 benthic forms that inhabit estuarine intertidal flats (Barnett et al. 2015; Blommaert et al. 2017;
821 Blommaert et al. 2018). In turn, NPQ is regarded as a functional trait likely participating in the
822 cost-benefit photoadaptive strategy, the geographical distribution and seasonal dynamics of a
823 species (Irwin and Finkel 2017). NPQ characteristics have been indeed related to i) latitude
824 (Bailleul et al. 2010b; Laviale et al. 2015), ii) different marine (Strzepek and Harrison 2004;
825 Lavaud 2007) and freshwater (Shi et al. 2016) ecosystems, iii) different habitats of the same
826 ecosystem, i.e. seasonal habitat succession in polar systems (Petrou et al. 2011; Croteau et al.
827 2020) or different intertidal sediment types (Barnett et al. 2015; Blommaert et al. 2017), and iv)
828 seasonal dynamics of phytoplankton in a given ecosystem or habitat (Dimier et al. 2007;
829 Polimene et al. 2014). In the following, we will focus on three ecosystems where diatoms are
830 found abundantly: the water column, the coastal intertidal flats and the polar regions.

831 **4.1 Diatoms of the phytoplankton**

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

847 The ecophysiological connection between NPQ and XC features and the *in situ* light climate
848 was investigated by comparing strains from different habitats (Lavaud 2007; Lacour et al.
849 2020). In general, species adapted to higher average light doses or stronger light fluctuations
850 (estuaries and coasts) showed higher Dt quenching efficiencies than counterparts adapted to
851 more stable light environments (semi-enclosed bays and open ocean). Contrastingly, the latter
852 rely more on regulatory processes better suited to cope with more gradual light changes such
853 as a fast turnover of the D1 protein to balance photodamage (Wu et al. 2012; Lavaud et al.
854 2016) (see also “2.2 PSII repair”). Diatoms that can have both a planktonic and a benthic life
855 (tychoplankton) perform diverse responses, with some representatives showing NPQ features
856 similar to coastal centric diatoms (Perkins et al. 2018; Lacour et al. 2020), while those that
857 inhabit intertidal flats resemble open ocean species (Barnett et al. 2015; Lacour et al. 2020).

858

859 **4.2 Diatoms of the microphytobenthos**

860 Benthic diatoms that inhabit the sediment of intertidal flats experience an extremely complex
861 light environment depending on a multifaceted combination of tidal and diurnal cycles that
862 control the alternation between sharp very low light/darkness periods (during immersion and at
863 night) and open-field like light fluctuations during daytime emersions. They also have to deal
864 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

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

902

903 ***4.3 Polar diatoms***

904 Diatoms also thrive in polar ecosystems, characterized by very different light climates related
905 to specific, often seasonal, habitats: in sea-ice, underneath the ice, at the marginal ice zone, and
906 in summer free-ice open waters. Furthermore, high latitude habitats are characterized by
907 extreme changes in photoperiods over the year, from complete darkness to 24 h light per day.
908 The combined effects of light with temperature, nutrient availability, and ocean acidification
909 on the regulation of photosynthesis in polar diatoms have been recently extensively considered
910 (Petrou et al. 2016; Trimborn et al. 2017; Hoppe et al. 2018; Lewis et al. 2019; Strzepek et al.
911 2019; Yan et al. 2019). In general, polar diatoms show photoadaptive features of very low light
912 and temperature acclimation, for instance: i) specific features of Rubisco activity (Valegård et
913 al. 2018) including a high cellular Rubisco content (Young et al. 2015; Gerecht et al. 2019) to
914 compensate for the slow enzymatic rate, ii) very active AEF processes (Alderkamp et al. 2012;
915 Goldman et al. 2015; Schuback et al. 2015; Trimborn et al. 2019), iii) the ability to repair
916 damaged PSII even below 0°C (Petrou et al. 2010), and iv) a strong antioxidant activity
917 (mycosporine-like amino acids and ROS scavengers (Hernando et al. 2002; Janknegt et al.
918 2008; Ha et al. 2016)).

919 The pattern of NPQ-related light-response and Dd+Dt pool size is similar to the one of
920 temperate plankton diatoms. It correlates with diurnal and seasonal light dynamics
921 (Schallenberg et al. 2019; Schuback and Tortell 2019), depth (Kashino et al. 2002; Hashihama
922 et al. 2010; Alderkamp et al. 2013) and horizontal light climate heterogeneity, i.e. Dd+Dt pool
923 size is larger in free-ice open waters and at the marginal ice zone than in waters covered with
924 ice. It also depends on the depth of snow covering the floe (Aikawa et al. 2009; Alou-Font et
925 al. 2013; Galindo et al. 2017). Also noteworthy is the high number of FCP and Lhcx proteins
926 (11 isoforms) found in the bipolar strain *Fragilariopsis cylindrus* (Mock et al. 2017). Such as
927 in temperate counterparts, most Lhcx isoforms are downregulated in darkness (Kennedy et al.
928 2019) and some are upregulated under high light exposure (Park et al. 2010; Kvernvik et al.
929 2020).

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

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

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

952

953 **Outlook**

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

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

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