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Chapter 18: The multiple routes of photosynthetic electron transfer in *Chlamydomonas reinhardtii*

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Non-print items - Abstract

Like all organisms performing oxygenic photosynthesis, *Chlamydomonas* captures light energy in two photochemical steps to drive linear electron flow from water to NADPH and to produce ATP. However, this process alone is not sufficient to drive CO₂ fixation in the Calvin-Benson-Bassham cycle and to respond to environmental and metabolic constraints, e.g. light availability or metabolic needs in term of ATP and NADPH. A complex network of alternative electron flows, which comprise the Cyclic Electron Flow around PSI or the various water-to-water cycles utilising O₂ as alternative electron acceptor, provide an additional degree of freedom to face this challenge. The present chapter presents the various alternative routes of photosynthetic electron transfer in *Chlamydomonas*, describes how they coordinate to optimize photosynthesis and gives a retrospective on the early physiology work on those alternative electron flows across model photosynthetic organisms.

Non-print items – Keywords: *Chlamydomonas*, Alternative electron flows, photosynthesis, Mehler, flavodiiron proteins, PTOX, Cyclic Electron flow.

Abbreviations:

PETC: Photosynthetic electron transport chain

PSI/PSII: Photosystem I / II

cyt. *b₆f*: cytochrome *b₆f* complex

- 28 LEF: linear electron flow
- 29 PQ/PQH₂: plastoquinone/plastoquinol
- 30 PC: plastocyanin
- 31 FNR: Fd:NADP⁺ reductase
- 32 NADP⁺/NADPH: dinucleotide phosphate
- 33 $\Delta\mu_{H^+}$: electrochemical proton gradient
- 34 ΔpH : proton concentration gradient
- 35 $\Delta\psi$: electric potential
- 36 CBB: Calvin-Benson-Bassham
- 37 NPQ: Non-Photochemical Quenching of chlorophyll fluorescence
- 38 qT: state transition
- 39 qE: energy-dependent quenching
- 40 AEF: alternative electron flows
- 41 CEF: Cyclic Electron Flow
- 42 WWC: Water-to-Water Cycle
- 43 ROS: Reactive Oxygen Species
- 44 LHCI: Light Harvesting Complex II
- 45 PTOX: plastid terminal oxidase
- 46 Fd: ferredoxin
- 47 FQR: Fd-PQ oxidoreductase
- 48 PGR5: *proton gradient regulation 5*
- 49 PGRL1: PGR5-like 1
- 50 NDH: nucleotide dehydrogenase
- 51 WT: wildtype
- 52 FLV: Flavodiiron protein
- 53 AsA: Ascorbate
- 54 MDA: monodehydroascorbate
- 55 PhQ: phylloquinones

56 CCM: carbon concentration mechanisms

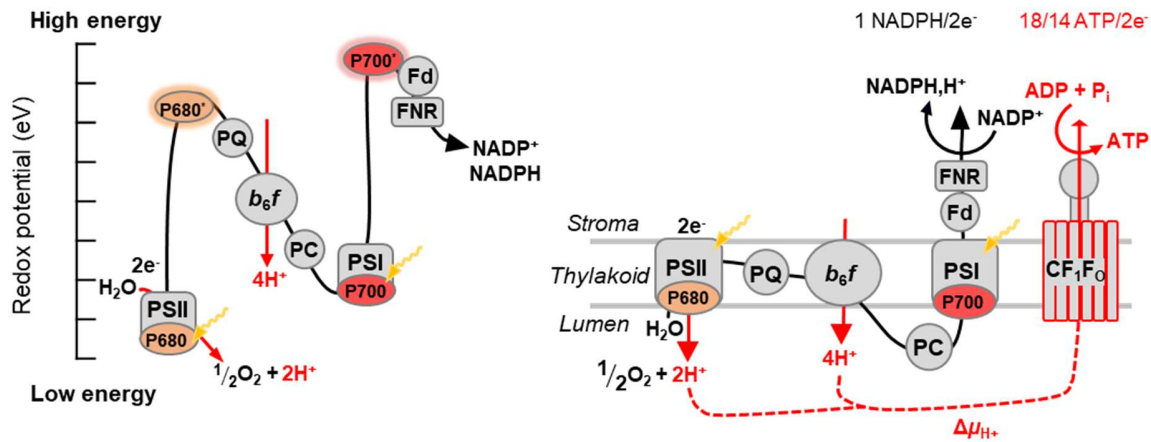
57 GlcDH: glycolate dehydrogenase

58

59 **Introduction**

60 Like all organisms performing oxygenic photosynthesis, *Chlamydomonas* captures light
61 energy in two photochemical steps to drive the photosynthetic electron transport chain (PETC) in
62 the thylakoid membrane. Electron transport involves the action of three major molecular
63 complexes embedded in the thylakoid lipid phase: the photosystems (PS) I and II (Volume 2,
64 Chapter 15) and the cytochrome *b₆f* complex (cyt. *b₆f*, Chapter 16). In the main linear electron
65 flow (LEF) pathway (Fig 1), the primary electron donor, water, is oxidized at the PSII reaction
66 center. Both PS work in series (Hill & Bendall, 1960) transferring electrons along redox cascades.
67 Between photosystems, electrons transit through the cyt. *b₆f* via two mobile carriers, the
68 hydrophobic and membrane soluble plastoquinone (PQ)-pool connecting PSII to cyt. *b₆f* and the
69 water-soluble plastocyanin (PC) shuttle connecting cyt. *b₆f* to PSI in the thylakoid lumen. At the
70 PSI acceptor side, Fd:NADP⁺ reductase (FNR) accepts electrons from Fd to reduce dinucleotide
71 phosphate (NADP⁺) into NADPH. The LEF allows water splitting on one side, production of
72 reducing power on the other side, and the generation of an electrochemical proton gradient ($\Delta\mu_{H^+}$)
73 across the membrane. Proton accumulation in the lumen is coupled to LEF through water splitting
74 at PSII, and through the Q-cycle at the cyt. *b₆f* (Joliot & Joliot, 2006). The proton-motive force
75 $\Delta\mu_{H^+}$ comprises two energetic components, a proton concentration gradient (ΔpH) and an electric
76 potential ($\Delta\psi$) both driving CF₁F₀-ATP synthase catalytic rotation (Mitchell, 1966; Kramer *et al.*,
77 2003) (Volume 2, Chapter 16). The intermediate molecules NADPH and ATP are the two energy

78 sources fueling the Calvin-Benson-Bassham (CBB) cycle (Volume 2, Chapters 7 and 8).



79

80 Figure 1: the photosynthetic Linear Electron Flow (LEF). A. LEF in the Z scheme of
 81 photosynthesis. B. Representation of the LEF in the thylakoid membranes. Abbreviations: PSII,
 82 Photosystem II; PSI, Photosystem I; b_6f , cytochrome b_6f ; CF_1F_0 , CF_1F_0 ATPase; PC, plastocyanin; PQ,
 83 Plastoquinol/Plastoquinone; Fd: ferredoxin; FNR: Ferredoxin/NADP Reductase; $\Delta\mu_{H^+}$, electrochemical
 84 proton gradient.

85 A description of the photosynthetic electron transfer chain restricted to LEF would give an
 86 overly simplistic view of the photochemical phase of photosynthesis. LEF produces a fixed ratio
 87 of ATP and NADPH, and in a context where the light input and the metabolic demand in ATP and
 88 NADPH are constantly changing, photosynthesis gets the best of LEF only by allowing it to work
 89 with some “degrees of freedom”. One of them is the biological regulation of the light utilization
 90 by the two photosystems, through the non-photochemical quenching (NPQ) at the PSII (Volume
 91 2, Chapter 25) or state transition (qT) (Volume 2, Chapter 24) which is a process particularly
 92 important in *Chlamydomonas*. Another main mode of regulation of the photochemical phase of
 93 photosynthesis relates to the flexibility of photosynthetic electron flows. In all organisms
 94 performing oxygenic photosynthesis, LEF components (PSI, PSII, $cyt\ b_6f$) are always involved in

95 a complex network of alternative electron flows (AEFs) which divert electron transport from
96 NADPH production or assimilation of CO₂. The present chapter focuses on those AEFs and is
97 structured as follows; in Section 1, we first explain the input and output constraints on LEF
98 operation (light availability and metabolic needs in term of ATP and NADPH) and how AEFs
99 provide an additional degree of freedom to face this challenge. Then we present the various AEFs
100 in Section 2, from the first experimental evidence to recent works more specific to
101 *Chlamydomonas*. We will especially focus on the two main AEFs modes (schematized in Fig 2
102 and 3), the Cyclic Electron Flow (CEF) around PSI, where electrons at the acceptor side of PSI
103 are reinjected upstream the *cyt. b₆f*, and the various water-to-water cycles (WWC) (or pseudo-
104 cyclic electron fluxes), which utilise O₂ as alternative electron acceptor instead of CO₂ (Curien *et*
105 *al.*, 2016). In Section 3, we discuss how the various AEFs coordinate to optimize photosynthesis
106 in response to changes in environmental conditions. Finally, in relation to the adaptive role of
107 AEFs in green algae, this review ends with a retrospective on the early physiology work on AEFs
108 across model photosynthetic organisms.

109

110 **1. AEFs provide flexibility to the Linear Electron Flow**

111 The operation of LEF, which uses light as a substrate and synthesizes ATP and NADPH as
112 end-products, is constrained at these two extremities. First, when light fluctuates, light absorption
113 must be adjusted to the electron transport capacity; and second, the ATP/NADPH ratio must adjust
114 to the metabolic needs of the moment. All AEFs share some common features: they play a role of
115 valves, offering an outlet for an additional activity of one photosystem or both. By doing so, they
116 also allow the pumping of extra protons into the lumen, thereby driving an extra $\Delta\mu_{H^+}$ and ATP

117 production. In this first section we will describe first how those common features of AEFs help
118 responding to light and metabolic constraints. Only in the Section 2 which describes AEFs one by
119 one, will their differences and specificities be pointed out, e.g., in terms of photon budget for
120 proton pumping and ATP production.

121 Exposure to excess light can lead to over-reduction of PS acceptor-side electron carriers
122 (iron-sulfur centers, Fd and NADPH at PSI; Q_A , Q_B and the PQ pool at PSII), augmenting the
123 chances for excited chlorophyll *a* to transition into a highly unstable triplet state reacting with O_2 .
124 The latter can result in the production of Reactive Oxygen Species (ROS) and photooxidative
125 damage, including photoinhibition of the two PSs (Volume 2, Chapter 25). At PSII, the induction
126 of a series of mechanisms, collectively referred to as NPQ allow to diminish the light pressure on
127 PSII (Volume 2, Chapter 25). In *Chlamydomonas*, the major component of NPQ is the energy-
128 dependent quenching (qE) which dissipates excess light energy as harmless heat, and prevents
129 photoinhibition of both PS (Roach *et al.*, 2020). Another NPQ process particularly important in
130 *Chlamydomonas* is state transition (qT) where a reversible kinase-dependent migration of light
131 harvesting antennae LHCI from one photosystem to the other modulates PSII and PSI light
132 harvesting and rebalances energy fluxes (Volume 2, Chapter 24). The two processes are regulated
133 differently since qE depends on the luminal pH whereas the activity of the kinase involved in the
134 qT is regulated by the redox state of the PQ in the Q_o site of the cyt. *b₆f* (Wollman, 2001; Dumas
135 *et al.*, 2017). When considering the necessary adjustment of the light absorption to the capacity of
136 electron transfer, NPQ manages the downregulation of the former where AEFs allow the
137 upregulation of the later. Therefore, by providing an alternative route for excess electrons, AEFs
138 play the role of redox exhaust valves and protect PSs from photoinhibition.

139 In addition to the response to light changes, the PETC also faces a constraint related to the
140 stoichiometry of NADPH and ATP. The LEF produces ATP from H^+ accumulated in the lumen
141 and NADPH from e^- transfer along the PETC. Because of the H^+/e^- coupling, ATP/NADPH
142 production is fixed in LEF. The water oxidation at the PSII level produces one proton in the lumen
143 per electron transferred. At the level of the cyt. b_6f , 2 protons are pumped per electron transferred
144 along the chain towards PC, thanks to the Q-cycle (Volume 2, Chapter 17). PQH_2 , which acquired
145 two protons from the stroma when reduced at the Q_B site, is oxidized to PQ at the luminal facing
146 Q_o site of cyt. b_6f , where the two transported electrons take bifurcated pathways but both protons
147 are released in the lumen. One electron follows the high potential chain of the Rieske iron-sulphur
148 protein and cyt. f and attains PC. The second electron follows the low potential chain via haem b_L
149 and haem b_H . In Mitchell's original proposal (1975), this electron in the low potential chain was
150 used to reduce PQ to PQH_2 on the stromal side of the membrane via an electron coming from PSII.
151 However, based on works on the respiratory cyt. bc_1 , a modified Q-cycle was proposed where the
152 b haems can act as an electron reservoir and that PQH_2 is solely fully regenerated after two cycles
153 (Zhang *et al.*, 1998; Crofts *et al.*, 2003; Cramer *et al.*, 2011). The modified Q-cycle is largely
154 accepted nowadays, which is constitutively at place and transfers two protons per electron
155 (Sacksteder *et al.* 2000; but see section Cyclic Electron Flow). Altogether, the LEF produces 3 H^+
156 per electron but, from a metabolic perspective, what matters is the relative amount of reducing
157 power and ATP produced by the PETC, often reflected by the ATP/NADPH ratio. Since two
158 electrons are required to reduce $NADP^+$, this leads to a value of 6 protons per NADPH. The
159 question mark lies in the proton requirement per ATP synthesized, which can vary between species
160 depending on the stoichiometry of the subunits forming the membrane intrinsic c -ring of the
161 CF_1F_0 -ATP synthase (Petersen *et al.*, 2012; Turina *et al.*, 2016). For most authors, each proton

162 crossing the CF₁F₀-ATP synthase induces a one incremental step rotation of the *c*-ring on the F₀
163 sector transduced via a central stalk to catalytic conformational changes of the α₃β₃ subunits on
164 the F₁ sector. Although it remains uncertain whether the work accomplished by each translocated
165 proton is homogeneous (Turina *et al.*, 2016), the yield of 3 ATP molecules synthesized/hydrolysed
166 per CF₁F₀ 360° rotation is well established (Adachi *et al.*, 2007). No structural information of the
167 CF₁F₀-ATP synthase allows to give a definitive stoichiometry in *Chlamydomonas*, but the 14 *c*-
168 subunits of the ATP synthase rotor in spinach is usually used as a reference for eukaryotic
169 photosynthetic organisms (Seelert *et al.*, 2000; Hahn *et al.*, 2018). Then 6 protons released in the
170 lumen yield ~1.28 ATP (6*3/14) and the 3 H⁺/e⁻ coupling leads to 1.28 ATP per NADPH. This
171 ratio is below the 3/2 requirement of the CBB cycle (Allen, 2002). Consequently, without
172 additional flexibility, LEF from water to carbon assimilation is condemned to accumulating
173 NADPH until the photosynthetic activity is fully arrested. AEFs permit an additional activity of
174 the photosynthetic complexes involved in proton pumping, PSII and/or the cyt. *b₆f*. From this
175 point of view, AEFs can be seen as degrees of flexibility for the electron transfer, allowing for
176 proton pumping without net production of NADPH. This, in turn, generates extra ATP and respond
177 to the mismatch between the ATP/NADPH produced by the PETC and the ATP/NADPH
178 requirement for carbon assimilation. Many reports aimed at calculating the required activity of
179 AEFs to adjust the ATP/NADPH ratio of the CBB cycle (Allen, 2002, Amthor, 2010, Alric *et al.*,
180 2010) and conclude that AEFs should accumulate one additional proton in the lumen per NADPH
181 produced by the LEF (6 + 1 = 7 protons per NADPH would produce 7*3/14 = 1.5 ATP).

182 However, it would be naive to see AEFs solely as a balance for the shortcomings of the 14 *c*-
183 subunits of the CF₁F₀ ATP synthase. In the stroma, the reducing power in the form of reduced
184 ferredoxin or NADPH not only drives the CBB cycle but also stromal enzymes involved in

185 essential metabolic pathways like nutrients assimilation (Volume 2, Chapter 4) or amino acid
186 biosynthesis (Volume 2, Chapter 6). Moreover, the substrate availability for the PETC (light) and
187 for the CBB cycle (inorganic carbon) can largely and suddenly vary, limiting the general relevance
188 of such a static view. In low CO₂ conditions, carbon concentration mechanisms (CCM) are induced
189 to gather high CO₂ density around Rubisco confined in pyrenoids (reviewed in *Chlamydomonas*
190 in (Wang *et al.*, 2015), see also Volume 2, Chapter 7). Due to the ATP demand of CCMs, the
191 ATP/NADPH ratio for carbon assimilation is further influenced by CO₂ availability. The network
192 of AEFs in organisms performing oxygenic photosynthesis, including *Chlamydomonas*, should be
193 seen as a dynamic flexibility to abiotic conditions and metabolic needs, by fulfilling three major
194 roles: (i) AEFs can dynamically optimize the ATP/NADPH ratio produced by the PETC to the
195 metabolic needs, and thereby avoid the ATP/NADPH stoichiometric cul-de-sac intrinsic to the
196 sole LEF. (ii) They offer electron valves in conditions where light absorption exceeds the capacity
197 of the sole LEF, preventing the over-reduction of the PETC and risks of photoinhibition. (iii)
198 Finally, by generating additional $\Delta\mu\text{H}^+$, AEFs participate to the pH-mediated regulation of the
199 PETC under saturating light conditions.

200 The pH control of the PETC comprises the regulation of NPQ (Volume 2, Chapter 15) and the so-
201 called “photosynthetic control”. In conditions of electron transfer limitation downstream of PSI
202 (e.g., low temperature or low CO₂), PSI can be photoinhibited (Chaux *et al.*, 2015). The
203 “photosynthetic control” (Volume 2, Chapter 17) which occurs when a low luminal pH slows down
204 PQH₂ oxidation at the Q_o site of the cyt. *b₆f* (Bendall, 1982), prevents this harmful situation by
205 moving the limiting step of the PETC limiting upstream of PSI (Sukenik *et al.*, 1987). The redox
206 regulation of the CF₁F_o-ATP synthase, which is not covered in this chapter (but see Volume 2,
207 Chapter 17), also plays a crucial role in the modulation of the ΔpH (Kramer *et al.*, 1990). The γ -

208 subunit of the CF₁F₀-ATP synthase contains a cysteine couple permitting a disulfide formation
209 under light which decreases the $\Delta\mu_{H^+}$ required for CF₁F₀-ATP synthase rotation (Junesch &
210 Gräber, 1987). This mechanism is conserved and restricted to the green lineage, including
211 *Chlamydomonas* (Buchert *et al.*, 2017; Buchert *et al.*, 2021).

212 **2. Diversity of AEFs in Chlamydomonas**

213 With the definition used in this chapter for AEFs, i.e. electron routes involving photosynthetic
214 complexes (PSII, PSI, cyt *b₆f*) without resulting in CO₂ fixation, the diversity of AEFs in
215 *Chlamydomonas* is very large. Some of them are already covered in other chapters: one can
216 consider that the use of photosynthetically reduced ferredoxin or NADPH for nutrient assimilation,
217 e.g., nitrogen or sulfur metabolism (Volume 2, Chapter 4) or for amino acid biosynthesis (Volume
218 2, Chapter 6) enter that category. This is also the case of the coupling between the PETC and the
219 hydrogenase which uses reduced ferredoxins as substrate, in anaerobic conditions (Volume 2,
220 Chapter 9 and 10). In a way, the recombination events in PSs meet the definition strictly speaking
221 but are covered already in the chapter dedicated to photosystems (Volume 2, Chapter 16) and will
222 not be considered here. Finally, the chlororespiration pathway is a minimal respiratory chain in the
223 thylakoid and cannot be considered an AEF but its components are involved in AEFs. This section
224 will especially cover PSI CEF and the various WWCs.

225 **2.1 Chlororespiratory pathway**

226 A minimal respiratory pathway exists in the thylakoids of most organisms performing oxygenic
227 photosynthesis. Bennoun (1982) first reported that PQH₂ could be oxidised in darkness by a plastid
228 terminal oxidase (PTOX). PTOX, together with a NAD(P)H plastoquinone oxidoreductase, forms
229 a chlororespiratory transport chain using electrons from NAD(P)H to reduce O₂ into H₂O (see

230 review on PTOX (Nawrocki *et al.*, 2015)). In plants, PTOX was initially investigated to decipher
231 its role in chloroplast development and carotenoids biosynthesis (Wu *et al.*, 1999), presumably by
232 regenerating (oxidized) PQ in darkness, which acts as an electron acceptor to activate the phytoene
233 desaturase upstream of the carotenoids' synthesis pathway (Carol & Kuntz, 2001; Bennoun, 2002).
234 Two PTOX enzymes are expressed by *Chlamydomonas*, PTOX2 being the main oxidase with a
235 rate ~10 fold faster than PTOX1 (4.5 vs. 0.4 e⁻ PS⁻ s⁻¹) (Houille-Vernes *et al.*, 2011).
236 *Chlamydomonas* phytoene desaturase mutants show similar phenotypes to plants mutants with
237 regards to carotenoids synthesis (McCarthy *et al.*, 2004; Couso *et al.*, 2011). However,
238 demonstrations of PTOX's involvement in this pathway remain inconclusive, notably because
239 *ptox2 Chlamydomonas* mutants (see *Chlamydomonas* AEF mutants strains in Table 1) do not show
240 changes in carotenoids content (Houille-Vernes *et al.*, 2011). This function could be undertaken
241 by PTOX1 (Li *et al.*, 2020) as suggested in the green algae *Haematococcus pluvialis* (Wang *et al.*,
242 2009); however, two observations make the role of PTOX in carotenoid synthesis of green algae
243 unclear. Not only the O₂ uptake by PTOX during the dark segment of *Chlamydomonas*'
244 photoperiod is almost null (Strenkert *et al.*, 2019) but, in contrast to plants, most carotenoids seem
245 to be synthesized under light in both *Chlamydomonas* (Janeiro & Barnett, 1982) and *H. pluvialis*
246 (Wang *et al.*, 2009).

247 In plants, the chlororespiratory pathway also involves a chloroplast nucleotide dehydrogenase
248 (NDH) complex, called NDH-1. NDH-1 is closely related to mitochondrial respiration complex I
249 (Sazanov *et al.*, 1998), contains 11 subunits with multiple transmembrane domains and reduces
250 quinones with electrons from reduced Fd. *Chlamydomonas* and other green algae possess instead
251 the NAD(P)H dehydrogenase 2 (NDA2) (Jans *et al.*, 2008), which exhibit similar function as
252 NDH-1 in cyanobacteria and higher plants. NDA2 also utilizes electrons from NAD(P)H to non-

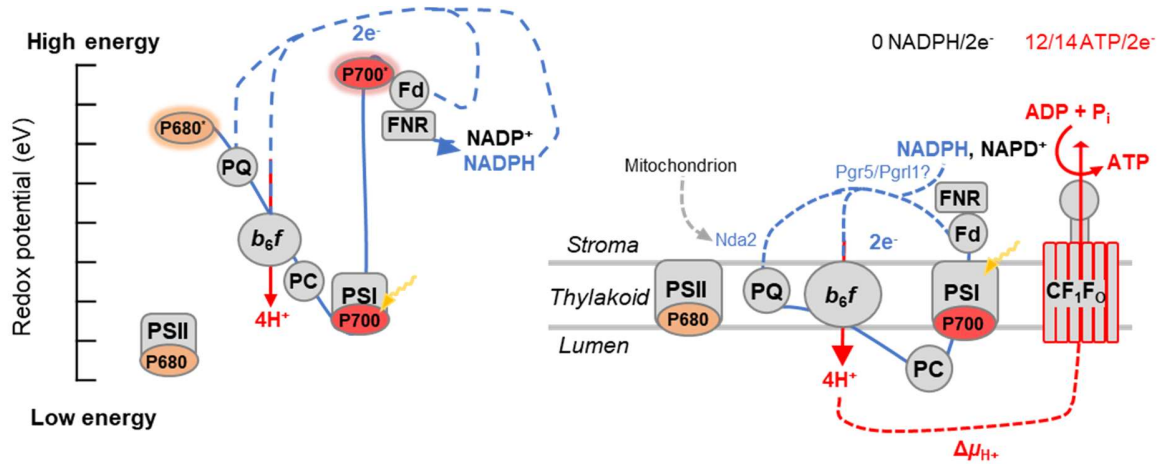
253 photochemically reduce the PQ-pool, thanks to a non-covalently bound flavin mononucleotide co-
254 factor (Jans *et al.*, 2008; Desplats *et al.*, 2009). But it also shows important disparities with NDH-
255 1 (reviewed in (Peltier *et al.*, 2016)): it is a monomeric flavoenzyme membrane-bound on the
256 stromal side of the thylakoid and it uses NAD(P)H as a substrate (Jans *et al.*, 2008). Moreover,
257 NDA2 is non-electrogenic (Melo *et al.*, 2004), opposingly to NDH-1 (Strand *et al.*, 2017).
258 Although *Chlamydomonas*' NDA2 can utilize NADPH, it favors NADH as a substrate (Desplats
259 *et al.*, 2009). Interestingly *Chlamydomonas*' plastid genome encodes for a transhydrogenase which
260 could convert NADPH to NADH in the stroma (Mus *et al.*, 2007).

261 Although chlororespiration was initially proposed to generate an electrochemical proton gradient
262 in *Chlamydomonas* (Bennoun, 2002), this model was later disproven. The electrochemical proton
263 gradient in the dark stems from the hydrolysis by the CF₁F₀-ATPase of ATP from mitochondrial
264 origin or in the absence of ATP hydrolysis by an ATP dependent ionic pump (Bennoun, 1994).
265 Because of the absence of electrogenicity of NDA2 and the position of PTOX on the stromal side
266 of the thylakoid, the chlororespiratory pathway is now considered non-electrogenic in
267 *Chlamydomonas*. Strictly speaking, chlororespiration cannot be considered a photosynthetic AEF
268 because it does not involve photochemical event. However, the two enzymes NDA2 and PTOX
269 are independently involved in CEF and WWC, respectively (see 2.2 and 2.3).

270 **2.2 Cyclic electron flow around PSI**

271 Like in other organisms, *Chlamydomonas* shows a fast ($t_{1/2} \sim 100\text{ms}$) reduction of P₇₀₀₊ at
272 the offset of an illumination, in the presence of DCMU (Maxwell & Biggins, 1976), but this phase
273 is largely slowed-down in the presence of a cyt. *b₆f* inhibitor (Canaani *et al.*, 1989). This was seen
274 as evidence for an electron transfer from the PSI acceptors in the stroma towards P₇₀₀₊ via cyt. *b₆f*.
275 If the existence of a CEF around PSI is well accepted in *Chlamydomonas* (Finazzi *et al.*, 1999,

276 Iwai *et al.*, 2010, Alric *et al.*, 2010) the question of the electron transfer pathways from PSI
 277 acceptors to the cyt. *b₆f*, the identity of the molecular players and the maximal rate of CEF have
 278 given rise to intense debate in the last decades (recently reviewed in (Nawrocki *et al.*, 2019a)).



279

280 Figure 2: the Cyclic Electron Flow (CEF) around Photosystem I. A. CEF in the Z scheme of
 281 photosynthesis. B. Representation of the different routes of the CEF in the thylakoid membranes.
 282 Abbreviations: PSII, Photosystem II; PSI, Photosystem I; *b₆f*, cytochrome *b₆f*; CF₁F₀, CF₁F₀ ATPase; PC,
 283 plastocyanin; PQ, Plastoquinol/Plastoquinone; Fd: ferredoxin; FNR: Ferredoxin/NADP Reductase; Δμ_{H⁺},
 284 electrochemical proton gradient.

285

286 *The possible routes for CEF in Chlamydomonas*

287 Like in plants (Shikanai, 2007), two major CEF routes have been described in
 288 *Chlamydomonas* (Figure 2). The “major one” corresponds to the original pathway postulated by
 289 Arnon and co-workers (Arnon *et al.*, 1954) following the observation of light-dependent ATP
 290 phosphorylation in isolated chloroplasts, mediated by the stromal electron carrier ferredoxin (Fd)
 291 A membrane-bound Fd-PQ oxidoreductase (FQR) was proposed to reinject electrons from the PSI

292 acceptor side to the inter-system ETC (Moss & Bendall, 1984; Bendall & Manasse, 1995). This
293 pathway was serendipitously “rediscovered” almost 50 years later in a screening for *Arabidopsis*
294 qE-defective mutants, lacking a small, stromal-soluble protein named PGR5 (for *proton gradient*
295 *regulation 5*) (see Table 1) (Munekage *et al.*, 2002). Shortly after, the molecular partner of PGR5,
296 PGRL1 (PGR5-like), was discovered, which is an integral thylakoid protein with both termini
297 stroma-exposed and six redox-active cysteine residues (DalCorso *et al.*, 2008). In *Arabidopsis*,
298 Hertle and co-authors (2013) (but see also (Szymańska *et al.*, 2011)) reported *in vitro* FQR activity
299 from PGRL1 (albeit on a non-physiological quinone species) which they attributed to its redox-
300 active cysteine residues presenting a binding site for a Fe-containing cofactor and triggered by
301 PGRL1 heterodimerization with PGR5 (however see (Strand *et al.*, 2016) for critical discussion
302 on this hypothesis). While both PGR5 and PGRL1 have been shown to modulate *Chlamydomonas*
303 CEF regulation (Alric, 2014; Johnson *et al.*, 2014; Jokel *et al.*, 2018; Buchert *et al.*, 2020), their
304 direct involvement in electron recycling from PSI acceptor to the PQ-pool remains debated
305 (Nawrocki *et al.*, 2019a). Although this PGR5/PGRL1 pathway was sensitive to inhibition by
306 antimycin-A (a mitochondrial Complex III inhibitor) in plants, it is not the case in *Chlamydomonas*
307 (Iwai *et al.*, 2010, Antal *et al.*, 2013).

308 The second CEF pathway was first described in *Synechocystis* mutated in the membrane-
309 bound, nucleotide dehydrogenase (NDH) gene (Ogawa, 1991; Mi *et al.*, 1995). In the mutants the
310 PQ-pool remained oxidized after illumination in the presence of PSII inhibitor DCMU, as opposed
311 to the wildtype where PQ re-reduction was attributed to NDH-1 (Mi *et al.*, 1995). In
312 *Chlamydomonas* and other green algae, the secondary CEF pathway involves a different NAD(P)H
313 dehydrogenase, NDA2 (Jans *et al.*, 2008), already described in the chlororespiratory section (see
314 2.1). In CEF, NDA2 utilize electrons from NAD(P)H to non-photochemically reduce the PQ-pool

315 and *nda2* mutants show a shorter post-illumination fluorescence rise than wild-type because
316 NAD(P)H can not be mobilized to reduce PQ (Jans *et al.*, 2008).

317 The light sensitivity of *Arabidopsis* mutants lacking both NDH and PGR5/PGRL1
318 pathways confirmed the essential role of CEF in photosynthesis (Munekage *et al.*, 2004). It also
319 suggested that these two routes, functionally redundant, represented the only possibilities for CEF
320 in plants. However, emerging structural information on cyt. *b₆f* (Stroebel *et al.*, 2003; Malone *et*
321 *al.*, 2019) have stimulated the emergence of a third potential pathway for CEF in *Chlamydomonas*.
322 In this model, the CEF cycle could be completed via the direct reinjection from a stromal electron
323 donor to the cyt. *b₆f* following the classical Q-cycle originally proposed by Mitchell (1975). This
324 model, first proposed by Chain (1982) and reconsidered more recently on the basis of kinetic
325 considerations (Joliot & Johnson, 2011; Nawrocki *et al.*, 2019a; Buchert *et al.*, 2020), does not
326 involve the lateral diffusion of PQ in the thylakoid membrane. It supposes that the reduction of the
327 quinone at the Q_i site is bifurcated, one electron coming from a stromal reductant, the other from
328 the low-potential chain.

329 ***The maximal rate of CEF in Chlamydomonas***

330 To evaluate the physiological importance of the CEF around PSI, the value of the maximal rate of
331 CEF, relatively to the maximal rate of the LEF, has been a long-lasting question. In
332 *Chlamydomonas*, the maximal rate of LEF is usually in the 100-150 electron per second per
333 photosystem (Maxwell and Biggins 1976, Alric, 2010; Nawrocki *et al.*, 2019b). In the presence of
334 DCMU, the rate of P₇₀₀⁺ re-reduction at the offset of a saturating light was used as a direct measure
335 of the rate of CEF and provided typical values of 5-15 electrons per second per PSI in oxic
336 conditions (Maxwell & Biggins, 1976, Alric *et al.*, 2010; Takahashi *et al.*, 2013). Such a rate of
337 CEF would be insufficient to supply the LEF with the additional ATP required for carbon

338 assimilation, alone. However, the rate of CEF in the presence of DCMU is not always a valid
339 estimation of the rate of CEF in physiological conditions. If LEF and CEF are in competition for
340 a common substrate, oxidized PQ or reduced ferredoxin, inhibition of LEF would increase CEF
341 (Fan et al, 2016). In contrast, CEF can be limited by the lack of reduced ferredoxin / NADPH
342 (Alric *et al.*, 2010; Lucker & Kramer, 2013). This latter hypothesis is supported by higher rates of
343 CEF measured in anoxic conditions, where the reducing power generated by glycolysis in the
344 chloroplast maintain reducing pressure on the PETC. In these conditions (DCMU and anoxia),
345 rates as high as 60 electrons per second per PSI were measured (Alric *et al.*, 2010), which were
346 further corroborated during the first seconds following a dark-to-light transition in the absence of
347 DCMU (Nawrocki *et al.*, 2019b).

348 With this value in mind, it becomes possible to evaluate the relevance of the NDA2 and
349 PGR5/PGRL1 pathways for CEF on a kinetic basis. The slow rate of NDA2 under aerobic
350 conditions ($2-4 \text{ e}^- \text{ PSI}^{-1} \text{ s}^{-1}$) (Houille-Vernes *et al.*, 2011) suggested that its role may be restricted to
351 chlororespiration (Nawrocki *et al.*, 2015). However, during N-deprivation inhibiting the CBB and
352 leading to the accumulation of stromal reductants, a doubling of the rate of P_{700}^+ re-reduction,
353 dependent upon NDA2 but not upon PGR5/PGRL1, was reported (Saroussi *et al.*, 2016). This
354 discrepancy could stem from a different redox state of the stromal reductants in the two
355 experiments: the rate of NDA2 would be limited by the availability of NAD(P)H in oxic
356 conditions. In *Chlamydomonas*, PGRL1 mutants were shown to exhibit transiently the same
357 maximal CEF rate as wildtype (Nawrocki *et al.*, 2019b). This was also the case in PGR5 mutants
358 of *Arabidopsis* where the CEF maximal rate was not affected compared to the wild type (Nandha
359 *et al.*, 2007). In both cases, it was suggested that PGR5 and PGRL1 could play a regulatory role
360 in CEF, possibly via the redox poisoning of the chloroplast, instead of playing a direct FQR function.

361 The supposed low rate of NDA2, together with the unchanged maximal rate of CEF in *pgrl1*
362 mutants, were taken as clues for the existence of another CEF pathway involving the reinjection
363 of electrons in the Q_i site of the cyt. *b₆f* and able to take in charge the high rates of CEF measured
364 in *Chlamydomonas*. It is to note, however, that a compensation by NDA2 in *Chlamydomonas pgrl1*
365 mutants can not be fully excluded yet. A NDA2/PGRL1 double mutant in *Chlamydomonas* would
366 help testing the redundancy of NDA2 and PGR5/PGRL1 pathways and/or the hypothesis that none
367 of them represent the major route of CEF.

368 *A classical (Mitchellian) Q-cycle involved in CEF?*

369 Independently from the kinetics analysis discussed above, a regain of interest for a classical Q-
370 cycle mediated CEF model comes from crystallography and structural analysis of the differences
371 between cyt. *b₆f* and cytochrome *bc₁* (see also Volume 2, Chapter 11 and Chapter 17). Notably
372 cyt. *b₆f* possesses three unique prosthetic groups per monomer: one chlorophyll *a*, one β-carotene
373 and one special haem *c_i* (Stroebel *et al.*, 2003) which could be involved in direct electron transfer
374 from reduced ferredoxin to the quinone in the Q_i site (Stroebel *et al.*, 2003; Malone *et al.*, 2019).
375 Haem *c_i* is unique by its lack of coordination of the haem iron (no amino acid axial ligand) and by
376 being covalently bound in the vicinity of the high potential *b_H* at the Q_i site (Stroebel *et al.*, 2003;
377 Alric *et al.*, 2005; Yamashita *et al.*, 2007) yielding strong magnetic dipolar coupling between the
378 two haems (Baymann *et al.*, 2007). Interestingly, FNR is known to interact with cyt. *b₆f* stromal
379 surface (Clark *et al.*, 1984; Zhang *et al.*, 2001; Mosebach *et al.*, 2017) and FNR has been proposed
380 to tether reduced Fd in proximity to the two high potential haems enabling PQ reduction which
381 would assign the FQR function to cyt. *b₆f* (Joliot & Johnson, 2011; Goss & Hanke, 2014;
382 Nawrocki *et al.*, 2019a). New structural insights on cyt. *b₆f* so far seems to support this model
383 (Malone *et al.*, 2019) which resembles the Mitchellian Q cycle model with one electron coming

384 from the stroma. Especially, the propionate of haem c_i can switch conformation upon PQ binding
385 to the Q_i pocket, which could reflect the previously documented decrease in c_i redox potential in
386 dark-adapted algae (reducing conditions) (Alric *et al.*, 2005) and give a mechanistic basis for
387 electron channelling from the FNR:Fd complex to PQ mediated by haem c_i (Malone *et al.*, 2019).
388 Highlighting the homodimer structure of cyt. b_6f , its central cavity and the edge-to-edge distance
389 allowing electron transfer between opposing haems b_L (Lanciano *et al.*, 2013), Nawrocki *et al.*
390 (2019a) proposed that oxidized PQ in the Q_o site of one monomer could be shuttled to the Q_i site
391 of the other monomer. In this model, CEF and LEF would not compete for a common pool of
392 oxidized PQ; instead PSII would reduce the PQ pool freely diffusing in the thylakoid membrane,
393 whereas the CEF would inject an electron in a PQ located in the cyt. b_6f cavity, allowing high
394 CEF even under conditions where the PQ pool is highly reduced by LEF. Interestingly, a natively
395 bound PQ molecule was observed by cryo-electron microscopy between haems c_i and b_H of
396 opposing cyt. b_6f monomers, which could represent a glimpse at this putative trans-monomer
397 shuttle (Malone *et al.*, 2019). By measuring redox kinetics associated to the different haems of cyt.
398 b_6f , Buchert *et al.* (2020) proposed that the switch between the modified Q-cycle associated to
399 LEF and a classical Q-cycle driving CEF requires PGR5, explaining the different reports of CEF
400 phenotypes in *pgr5* mutants (Munekage *et al.*, 2002; Alric, 2014; Johnson *et al.*, 2014; Godaux *et*
401 *al.*, 2015).

402 ***Influence of Supercomplexes and State transitions on CEF***

403 Various early studies (Canaani *et al.*, 1989; Herbert *et al.*, 1990; Finazzi *et al.*, 2002) indicated a
404 relationship between state transitions, which regulates the attachment of LHCII to PSII (state 1) or
405 PSI (state 2) (see Volume 2, Chapter 24), and CEF in *Chlamydomonas*. While PSII sets the redox
406 poise of the chain, only PSI participates to the CEF. Because the formation of State 2 increases

407 PSI antenna size, it expectedly increases PSI turnover and CEF if the later is light-limited. During
408 the formation of state 2, a fraction of the *cyt b₆f* complex also moves from the PSII-enriched
409 appressed regions of the thylakoid membrane to the stroma lamellae where PSI is localized (Vallon
410 *et al.*, 1991). Because the co-localization of PSI and *cyt b₆f* and the increase of PSI antenna size
411 coincide during state transitions, the question of their relative effects on CEF was rather difficult
412 to address.

413 In 2010, Iwai and collaborators isolated a PSI-LHCI-LHCII-*cyt.b₆f*-PGRL1-FNR
414 supercomplex (but lacking PGR5) under state 2. At first, the “Supercomplex model proposed CEF
415 activation upon state 1 to state 2 transition, allowing for **i**) compartmentalization between CEF and
416 LEF limiting their competition for the mobile electron carriers (PQ, PC, Fd) (Joliot & Joliot, 2002;
417 Alric *et al.*, 2010) and, **ii**) tight interactions between Fd-FNR, *cyt b₆f* and the PQ-pool favoring
418 fast electron transfer and high CEF rates *in vivo* (Iwai *et al.*, 2010; Joliot & Joliot, 2002; Alric *et*
419 *al.*, 2010). However, those experiments could not disentangle the effect of state transitions per se,
420 and the one of the anaerobic treatment used for their induction (which also lead to a decrease of
421 the cellular ATP and an increase of the reducing power). When a mutant specifically devoid of
422 state transition were used as a control, the link between state transitions and increased CEF or
423 supercomplex formation was ruled out: increase in CEF and supercomplex formation is therefore
424 induced by redox rather than state transitions (Lucker & Kramer, 2013; Takahashi *et al.*, 2013).
425 Accordingly, whether it involves supercomplexes or not, electron fluxes partitioning between the
426 LEF and the PGR5/PGRL1 CEF pathway seem to obey a competition model regulated by the
427 stromal ATP/NADPH ratio (Alric *et al.*, 2010; Johnson *et al.*, 2014). Based on the absence of the
428 PSI antennae subunits LHCA2 and LHCA9 in supercomplex, Steinbeck and collaborators (2018)
429 recently proposed a mechanistical model for CEF supercomplex assembly driven by the

430 dissociation of these LHC under anoxia. Remarkably, $\Delta lhca2$ knockout mutants exhibited higher
431 CEF rate under aerobic conditions than wildtype (WT) under either aerobic or anaerobic conditions
432 (Steinbeck *et al.*, 2018). In any case, direct electron transfer from FNR:Fd to cyt. b_6f seems
433 possible whether cyt b_6f forms a supercomplex with PSI or not. Furthermore, rates of CEF in
434 supercomplexes remain to be measured experimentally as *in vivo* experiments in yeast showed that
435 bc1-CcOx supercomplex do not display a faster kinetics of cytochrome *c* mediated electron
436 transfer between the two complexes (Trouillard *et al.*, 2011; see however Berndtsson *et al.*, 2020).

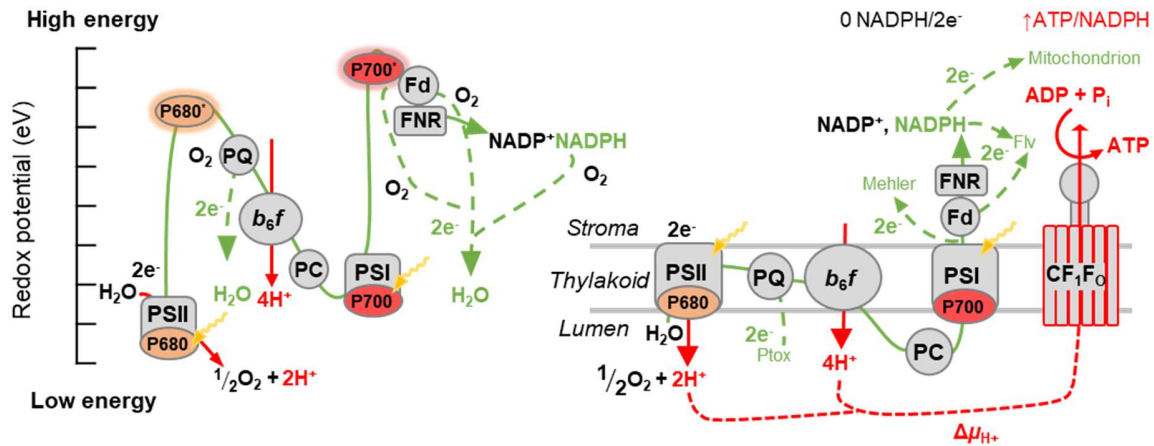
437 ***Proton pumping and regulatory role of CEF***

438 At present we can only speculate on the path of electrons in the CEF pathway, but through the Q-
439 cycle, it undoubtedly participates to the pumping of extra protons into the lumen. In plants, the
440 yield of protons pumped per electron recycled around PSI is different between PGR5/PGRL1 (2
441 H^+/e^-) and NDH-1 (3 or 4 H^+/e^-) pathways, due to the electrogenicity of the NDH-1 complex
442 (Strand *et al.* 2017; Strand *et al.*, 2019). Because NDA2 is non-electrogenic (Melo *et al.*, 2004), the
443 NDA2 CEF pathway in *Chlamydomonas* participates to the $\Delta\mu_{H^+}$ only to the same extent as the
444 PGR5/PGRL1 pathway or the CEF based on the classical Q cycle, i.e. 2 H^+/e^- .

445 **2.3 Water-to-water cycles**

446 Electrons extracted from water at the PSII level can be rerouted from the LEF to various
447 chloroplastic oxidases which utilise O_2 as electron acceptor and produce water (Curien *et al.*,
448 2016). This creates various AEFs linking the photo-oxidation of water into O_2 at one extremity to

449 the reduction of O₂ into water on the other, creating a water-to-water cycles (WWC) (or pseudo-
 450 cyclic electron fluxes).



451 Figure 3: the Water-to-Water Cycles (WWC). A. Water-to-water cycles in the Z scheme of photosynthesis.

452 B. Representation of the different water-to-water cycles in the thylakoid membranes. Abbreviations: PSII,
 453 Photosystem II; PSI, Photosystem I; b₆f, cytochrome b₆f; CF₁F₀, CF₁F₀ ATPase; PC, plastocyanin; PQ,
 454 Plastoquinol/Plastoquinone; Fd: ferredoxin; FNR: Ferredoxin/NADP Reductase; Δμ_{H⁺}, electrochemical
 455 proton gradient.

456 PSII-PTOX pathway

457 By reoxidizing PQ, PTOX can divert electrons from the main transport chain. Therefore, it has
 458 been suggested to have a function of safety-valve relieving excitation pressure on PSII under light
 459 exposure (Cournac *et al.*, 2000; Niyogi, 2000; McDonald *et al.*, 2011). It may indeed fulfill such
 460 function in organisms inhabiting harsh environments and accumulating large PTOX content
 461 (Stepien & Johnson, 2009; Laureau *et al.*, 2013; Ghotbi-Ravandi *et al.*, 2019). Because electrons
 462 are initially extracted from H₂O at PSII in LEF, oxidation of PQH₂ coupled to O₂ photoreduction
 463 by PTOX form a WWC. However, a photoprotective role for PTOX seems contradictory with its
 464 pro-oxidant activity (Heyno *et al.*, 2009; Krieger-Liszkay & Feilke, 2016) although we can not
 465 discount that those ROS may serve signaling purposes (Rea *et al.*, 2018). It is also hard to reconcile

466 with its much slower rate compared to PSII turnover under light in *Chlamydomonas* (Houille-
467 Vernes *et al.*, 2011) and *Arabidopsis* (Joliot & Joliot, 2002). Indeed, comparable electron transport
468 rates measured between *Chlamydomonas* WT and *ptox2* mutants under steady illumination
469 suggests that PTOX main function is not a photoprotective valve (Nawrocki *et al.*, 2019c).
470 Additional observations that WT and *ptox2* mutants have similar growth rates under continuous
471 illumination but that the mutants are severely impaired under intermittent light, prompt the authors
472 to posit PTOX's role is to balance the PQ-pool redox state during transient light fluctuations to
473 avoid hampering PSII driven LEF (Nawrocki *et al.*, 2019c) (see also (Houyoux *et al.*, 2011)).
474 Slower growth of *ptox2* mutants compared to WT under intermittent light further reveals the
475 crucial role of this pathway in the redox modulation of the PQ-pool and PSI acceptors in this
476 condition. Heterotrophic and phototrophic metabolism intersect at the PQ-pool of which the redox
477 state is a major electron transport regulation hub. Therefore interplay between NDA2 and PTOX
478 influence LEF and CEF respective rates (Nawrocki *et al.*, 2019c), state transition (Houille-Vernes
479 *et al.*, 2011) and metabolic exchanges (Wei *et al.*, 2014).

480 ***Flavodiiron proteins***

481 Flavodiiron proteins (FLV) were first identified in cyanobacteria (Helman *et al.*, 2003) but
482 have since been documented in all green lineages groups except angiosperms (Ilik *et al.*, 2017). In
483 red algae, *flv* genes have never been observed. They are also absent from most brown algae
484 genomes (see reviews (Peltier *et al.*, 2010; Alboresi *et al.*, 2019)), even though homologs in the
485 dinoflagellate *Symbiodinium* were reported (Roberty *et al.*, 2014; Shimakawa *et al.*, 2021).
486 *Chlamydomonas* synthesizes both FLVA and FLVB isoforms (homologous to FLV1 and FLV3
487 respectively in cyanobacteria (Peltier *et al.*, 2010)) which are believed to associate in hetero-dimer
488 to perform a WWC by photo-reducing O₂ at PSI acceptor side (Mustila *et al.*, 2016; Chaux *et al.*,

489 2017). So far, only a partial structural resolution of FLV1/3 lacking the C-term domain has been
490 revealed in *Synechocystis* (Borges *et al.*, 2019). Using *in silico* modeling, Alboresi and co-authors
491 (2019) suggested distinct catalytic sites organisation between FLVA and FLVB (in the bryophyte
492 *Physcomitrella patens*), enabling their action as a dimer and a possible conformational change
493 allowing swift regulation answering to external cues like stromal redox-state. The electron donor
494 for FLVs has been matter of debate in recent years. In *Synechocystis*, it was first proposed that
495 FLVs may be able to receive electrons directly from NAD(P)H via a C-terminal flavin
496 oxidoreductase-like module (Vicente *et al.*, 2002). However, FLVs were also reported to possibly
497 interact with Fd in both *Chlamydomonas* (Peden *et al.*, 2013) and *Synechocystis* (Cassier-Chauvat
498 & Chauvat, 2014). Most recently, evidence from comparison between re-oxidation kinetics of
499 NADPH and of the iron sulfur cluster comprising Fd, F_X and F_AF_B (the terminal PSI acceptors)
500 between WT and *flv1/3* *Synechocystis* mutants, strongly suggested that reduced Fd-F_AF_B and not
501 NADPH is the redox partner of FLVs (Sétif *et al.*, 2020). Interestingly, the P₇₀₀ re-oxidation signal
502 of *Chlamydomonas* WT, *flv* and CEF mutants (Jokel *et al.*, 2018) have similar kinetics as
503 *Synechocystis* homologous strains (Sétif *et al.*, 2020), which possibly indicate both organisms'
504 FLVs receive electron via reduced Fd-F_AF_B as previously proposed by Jokel and co-authors
505 (2018).

506 FLVs act as a safety valve to alleviate PSI acceptor limitation and pertaining photodamage,
507 hence accurate regulations is essential to avoid futile competition for reducing power with the CBB
508 (Alboresi *et al.*, 2019). Interestingly, FLVs are an extremely efficient immediate electron sink
509 upon sudden light intensity shifts (e.g. while CBB's enzymes are activating), but their activity
510 under steady state illumination is barely detectable (Chaux *et al.*, 2017).

511 ***The Mehler reaction***

512 The Mehler reaction was postulated following the observation that isolated pea thylakoids can
513 photo-reduce O₂ to peroxide (H₂O₂) (Mehler, 1951). Later seminal investigations by Asada and
514 co-workers led to the identification of O₂^{•-} as the initial transient product generated by charge
515 transfers from an internal PSI transporter on its acceptor side to O₂ (Asada & Kiso, 1973;
516 Takahashi & Asada, 1988). The superoxide O₂^{•-} anion is instantly disproportionated to H₂O₂ and
517 O₂ by the thylakoid bound superoxide dismutase and both products are released in the stroma
518 (Ogawa *et al.*, 1995). Although less toxic and a more efficient cellular messenger than O₂^{•-} (Rea *et*
519 *al.*, 2018), H₂O₂ remains harmful in excessive concentrations and it is scavenged in the stroma via
520 an ascorbate peroxidase using two ascorbate (AsA) molecules as electron acceptors and yielding
521 two water (thus making the Mehler reaction a WWC) and monodehydroascorbate (MDA)
522 molecules as products (Asada, 1999). Afterward, a MDA-reductase use NADPH to recycle MDA
523 back to AsA and play a role in *Chlamydomonas*' photooxidative stress tolerance (Yeh *et al.*, 2019).
524 Alternatively, MDA can spontaneously disproportionate to AsA and dehydroascorbate, which is
525 converted to a supplemental AsA via the glutathione cycle also consuming NADPH (Lin *et al.*,
526 2018).

527 The PSI pigment-protein complex encompasses two symmetrical bifurcated electron
528 chains spanning from P₇₀₀ and converging to F_X, the phylloquinones (PhQ) A and B, located on
529 PSI heterodimer PsaA and PsaB, respectively (Volume 2, Chapter 15). Due to differences in
530 protein interactions, the electron transfer to F_X is slower from PhQ_A than from PhQ_B, with lifetimes
531 of ~300 and ~15 ns respectively, making PhQ_A^{•-} much more susceptible to yield electrons to
532 exogenous O₂ and generate ROS (Cherepanov *et al.*, 2017). However, a residue mutation delaying
533 even further PhQ_A^{•-} decay does not affect the quantum yield of PSI as electron overflow is
534 redistributed to the PhQ_B chain (Santabarbara *et al.*, 2015). Recently, Kozuleva and co-authors

535 (2021) proposed a novel mechanistic model for the Mehler reaction after measuring the light-
536 dependent second-order rate of O₂ photoreduction in various *Chlamydomonas* PSI complex
537 isolates showing mutations in different electron carriers (see other crucial works which led to the
538 following model proposal (Kozuleva & Ivanov, 2010; Kozuleva *et al.*, 2014; Santabarbara *et al.*,
539 2015)). In this new model, F_AF_B participates to some extent to O₂ photoreduction but its rate
540 saturates under moderate irradiance intensities and the major O₂ photoreduction sites is located at
541 PhQ_A- (Kozuleva *et al.*, 2021). The alternative classical view is that the sole electron donor is
542 reduced Fd and that O₂ photoreduction is favored by limited NADP⁺ availability (Furbank &
543 Badger, 1983). While the Mehler reaction can partake to the $\Delta\mu_{H^+}$, quantifying its contribution *in*
544 *vivo* is challenging due to its transient products and interactions with other AEFs and electron flux
545 regulation mechanisms (see conflicting views on its significance in plants (Heber, 2002; Ort &
546 Baker, 2002)). For example, in *Chlamydomonas* exposed to high light intensity, it was,
547 counterintuitively, reported that the Mehler action is most active when CO₂ concentration is
548 elevated and LEF optimally functioning. When CO₂ is low, qE induction and state transition are
549 sufficient to limit excitation pressure and H₂O₂ evolution (Roach *et al.*, 2015). Based on
550 experimental data and the thermodynamics parameters of electron transfers within PSI redox
551 chains, Cherepanov and co-authors (2017) developed a model predicting more than 0.3% of total
552 electron flux could be diverted to the Mehler reaction, although it is not clear how that electron
553 flux could be affected in the presence of FLV in *Chlamydomonas* (Chaux *et al.*, 2017). Likewise,
554 it is likely that some, if not most, of the light-dependent O₂ uptake attributed to the Mehler reaction
555 in previous works on *Chlamydomonas* (Peltier & Thibault, 1985, Forti & Caldiroli, 2005, Franck
556 & Houyoux, 2008) was in fact due to the action of the then unknown FLVs (sometime called
557 Mehler-like reaction, as FLVs do not generate H₂O₂) (see section 3.1). Simultaneous quantification

558 of O₂ uptake and H₂O₂ evolution in FLVs mutants will be necessary to determine substantial of an
559 electron sink the Mehler reaction can be in *Chlamydomonas*.

560 ***Other WWCs***

561 Other O₂ photoreduction processes can occur in the photosynthetic process, which are described
562 in more detail in other chapters of this volume and will be only briefly described here. One of them
563 is photorespiration (see Volume 2, Chapter 7 and 8). When O₂ rather than CO₂ enters Rubisco's
564 catalytic site, it can trigger the oxidation of ribulose 1,5 biphosphate and generate 3-
565 phosphoglycerate (3PGA) and 2-phophoglycolate (2PG). The subsequent suite of enzymatic
566 reactions recycling these products (also called the C₂ cycle in reference to these two carbon
567 intermediates) is described in Volume 2, Chapters 7 and 8. A crucial trickle-down effect of 2PG
568 recycling to 3PGA, is that along the enzymatic reactions cycle, terminal acceptors like NADP+,
569 NAD+, ADP and oxidized Fd are restored, fostering non-CO₂-assimilatory electron transport,
570 which makes photorespiration a key response to harsh conditions in plants (chill, high light, CO₂
571 limitation) by limiting the otherwise associated overreduction of the PETC (reviewed in (Voss *et*
572 *al.*, 2013)). Rubisco's oxygenase activity is unavoidable but its output tends to be limited in
573 microalgae due to carbon concentration mechanisms (CCM) which consume ATP to gather high
574 CO₂ density around Rubisco confined in pyrenoids (reviewed in *Chlamydomonas* in (Wang *et al.*,
575 2015)). The photorespiration pathway is conserved across photosynthetic phyla with two major
576 divergences (i) reactions compartmenting in different organelles as peroxisomes and pyrenoids are
577 not presents in all taxa, *Chlamydomonas* possesses pyrenoids but no peroxisomes and, (ii) the
578 nature of the enzyme which oxidizes glycolate to glyoxylate. It is currently accepted that
579 *Chlamydomonas* (and all Chlorophytes) replaced the Glycolate oxydase of plants by a glycolate
580 dehydrogenase (GlcDH) similar to cyanobacteria (which possess both Glycolate oxydase and

581 GlcDH) (Esser *et al.*, 2014). *Chlamydomonas* 'GlcDH harbors three spanning regions likely bound
582 to the mitochondrion membrane and potentially feeds electrons to the ubiquinone pool of the
583 respiratory transport chain (Beezley *et al.*, 1976; Nakamura *et al.*, 2005; Aboelmy & Peterhansel,
584 2014). Cross-talk between photorespiration and mitochondrial activity was hypothesized to
585 explain the simultaneously up-regulated transcription of their related genes under high light, which
586 could reflect enzyme synthesis for glyoxylate conversion to malate in the mitochondria (Davis *et al.*
587 *et al.*, 2013). A study by Nakamura and co-workers (2005) strongly supported a photorespiratory
588 function to be dependent on GlcDH by characterizing a high CO₂ requiring phenotype in a
589 *Chlamydomonas* mutant with a disrupted *GlcDH* gene, very similar to typical photorespiration
590 defects in higher plants. Moreover, *GlcDH* mutants showed exacerbated glycolate excretion in the
591 medium (Nakamura *et al.*, 2005). To a lesser extent, increase in glycolate exudation was reported
592 in *Chlamydomonas* WT exposed to high light, low CO₂, in which the photorespiration pathway
593 was inhibited (Moroney *et al.*, 1986; Nakamura *et al.*, 2005) and in immobilized cells (for which
594 slowly diffusing O₂ concentration is high due to photosynthetic activity) (Garbayo *et al.*, 2005).
595 However, increased extracellular glycolate accumulation is often short-lived (Moroney *et al.*,
596 1986; Garbayo *et al.*, 2005; Günther *et al.*, 2012). This is possibly due to overcompensation by
597 enhanced CCM to limit photorespiratory carbon loss, as exemplified by steady up-regulation of
598 CCM genes compared to transient increase for photorespiration genes upon transition to low CO₂
599 concentrations (Tirumani *et al.*, 2019). In hope of developing sustain methane bioproduction from
600 glycolate, Wilhelm and co-workers (Günther *et al.*, 2012; Taubert *et al.*, 2019) demonstrated that
601 acclimating *Chlamydomonas* to low O₂/CO₂ conditions before a shift to scarce CO₂ availability
602 with addition of the CCM and GlcDH inhibitor 6-ethoxy-2-benzothiazolesulfonamide can yield
603 elevated glycolate production sustained for up to 21 d.

604 Another kind of WWC consists in a cooperation between photosynthesis and respiration,
605 whereby the rerouting of the reducing power generated by the PETC towards the mitochondrial
606 electron transfer chain eventually fuels the cytochrome oxidase (complex IV) and Alternative
607 Oxidase. Such WWCs, described in *Chlamydomonas* and in plants (Lemaire *et al.*, 1988; Krömer
608 & Heldt, 1991) involves the malate/oxaloacetate valve as well as other metabolic shuttles, which
609 enable the transport of reducing power from the chloroplast to the mitochondrion via the cytosol
610 (Scheibe *et al.*, 2005). Reversely, the extra ATP generated thereby in the mitochondrion can be
611 imported back in the chloroplast through mitochondrial ATP/ADP translocators and potentially
612 DHAP/3-PGA shuttle (Hoefnagel *et al.*, 1988). The study *Chlamydomonas* mutants affected in
613 mitochondrial respiration point to an important role of those energetic exchanges between
614 organelles (Cardol *et al.*, 2009). Such a cooperation can restore photoautotrophic growth in a
615 *Chlamydomonas* strain lacking the chloroplastic CF₁F₀-ATPase, by rerouting excess reducing
616 power from the chloroplast to the mitochondrion and by importing mitochondrial ATP for CO₂
617 fixation (Lemaire *et al.*, 1988).

618 **3- An integrated and historical view of the AEFs**

619 We now identify the importance of alternative electron transfer pathways in their common
620 functions: poisoning the redox state of the electron transfer chain, playing the role of exhaust valves,
621 or increasing the proton-motive force and ATP production. AEFs actions are integrated within a
622 cohesive response to limit photosynthetic electron transport bottlenecks. In the last two decades,
623 the extensive use of mutants has revealed that while interplays and redundancies are inherent to
624 the AEFs network, it makes-up for bioenergetic resilience rather than a weakness, giving plasticity
625 to photosynthesis to operate under changing environmental conditions and metabolic demands.

626 Some redundancy between AEFs is indeed observed, especially in the recent years between
627 CEF around PSI and WWCs mediated by FLVs. Artificial introduction of *Flv* genes in *Arabidopsis*
628 (Yamamoto *et al.*, 2016) or rice (Wada *et al.*, 2018) can partially increase growth in *pgr5* mutants.
629 In *P. patens* double mutants exhibit exacerbated defects under fluctuating light compared to single
630 *pgr11* or *FlvA* mutants (Storti *et al.*, 2019). The redundancy of those two AEFs seems to be at place
631 in *Chlamydomonas* too, where the *pgr11* mutants compensate deficient CEF by up-regulating FLVs
632 synthesis (Dang *et al.*, 2014). The light-dependent O₂ uptake was increased in this mutant,
633 reflecting a higher activity of FLVs together with an energetic cooperation with mitochondria
634 (Dang *et al.*, 2014). Recently, it was shown that the rate of carbon fixation in *Chlamydomonas*
635 decreases under low inorganic carbon in the double mutant of PGRL1 and FLVs compared to the
636 wild type, but not in the respective single mutants (Burlacot *et al.*, 2021). This indicates that the
637 supplementary ATP demand for CO₂ concentrating mechanisms is met by the synergistic action
638 of FLVs and PGRL1-mediated CEF (Burlacot *et al.*, 2021). Moreover, it is likely that accelerated
639 CEF historically reported for *Chlamydomonas* under anoxia are not only the result of a more
640 reduced photosynthetic electron chain (Alric *et al.*, 2010) but also caused by the decrease of
641 electron leaks towards FLVs (Nawrocki *et al.*, 2019b).

642 This raises the question of the relative importance of the different AEFs: what are the rates of the
643 different pathways under steady-state photosynthesis? How do they change with the environmental
644 conditions (CO₂, temperature) or metabolic status of the cell? Because of this redundancy,
645 comparing mutants of the different AEFs will not be sufficient to answer such questions;
646 methodological advances in measuring and distinguishing the different electron pathways in
647 photosynthesis are needed to address these questions. During the pioneering era of photosynthesis
648 research, scientists were aiming at measuring precisely the maximum quantum yield of the

649 photosynthetic process. At that time, in order to estimate what the photochemical reactions were
650 at the molecular level, it was crucial to decide on precise values, to quantify the minimum number
651 of photons required for the production of an O₂ molecule (or the assimilation of a CO₂ molecule).
652 If we take the Emerson and Lewis value of 0.09 for the quantum yield (Emerson & Lewis, 1943),
653 it means that ~11 photons are needed (quantum requirement) to produce one molecule of O₂ or to
654 fix one molecule of CO₂. We now know that 8 electrons transferred linearly through PSI and PSII
655 are required for one O₂, that the quantum yield of PSI is close to 1 and that of PSII is about 0.8, so
656 there would remain about 1-2 reducing equivalents rerouted to “alternative pathways”. Now that
657 we know the molecular players of photosynthesis, and that we have mutants of AEFs, it might be
658 worth revisiting these studies; the maximum quantum yield of photosynthesis is expected to
659 depend on the relative participation of the alternative pathways compared to the linear electron
660 transfer, and on the energy-requirement of the CO₂-concentrating mechanism.

661 Another fundamental question relates to the kinetics of activation/deactivation of the different
662 AEFs in transitory conditions. While both the PGR5/PGRL1 and FLVs help limit PSI
663 photodamage during growth under rapidly fluctuating lights, FLVs have been shown to be
664 particularly crucial because of their more rapid induction compared to CEF (Jokel et al. 2018).
665 Comparison between *pgr5*, *pgrl1* and *Flv Chlamydomonas* mutants showed that FLVs are essential
666 for survival under fluctuating light while *pgr5/pgrl1* growth was only slowed-down (Jokel *et al.*,
667 2018). It was therefore posited that FLVs act as a frontline defense in the first few seconds
668 following light shifts which also promote rapid ΔpH and NPQ development (Chaux *et al.*, 2017),
669 while CEF takes longer to reach sustained high functioning rates under excess light (Jokel *et al.*,
670 2018; Storti *et al.*, 2019). The best example of the sequential coordination of the different AEFs is
671 probably the dark-to-light transition in anaerobic *Chlamydomonas* cells, which has been

672 extensively studied for biohydrogen production. In these conditions, the initial photosynthetic
673 activity is entirely associated to an electron transfer from water oxidation at the PSII level toward
674 the hydrogenase, downhill of PSI, and is fully arrested in hydrogenase mutants (Godaux et al,
675 2015; Burlacot et al, 2021). This electron flow from PSII to the hydrogenase does not last more
676 than one or two minutes in the wild type and is then replaced by other AEFs that play the role of
677 relay between hydrogenase activity and CO₂ fixation. Interestingly, Godaux and collaborators,
678 who measured PSI and PSII activity at the onset of light but did not consider WWCs, concluded
679 that CEF was the relay (Godaux et al, 2015). Later, Burlacot and collaborators performed a similar
680 experiment including FLV mutants and light-induced O₂ uptake measurements (but no CEF
681 measurements) and concluded that FLVs were the major relay (Burlacot et al, 2019). Concomitant
682 measurements of CEF, H₂ production, CO₂ fixation and FLV mediated O₂ uptake at the dark-to-
683 light transitions would be useful to reconcile those reports, which however suggest that, again, a
684 synergic action of CEF and FLVs allow the transition from hydrogen production to carbon fixation.

685 How does *Chlamydomonas* relate to the great diversity of organisms performing oxygenic
686 photosynthesis, in terms of alternative photosynthetic electron routes? It is difficult to judge in
687 which species or for which kind of stress condition a particular pathway plays a more important
688 role: why should a regulatory pathway, identified as important for drought resistance in plants, be
689 conserved in oceanic algae that do not experience drought stress? Perhaps here we should
690 recognize the “chance” in the scientific approach: some AEFs have been identified and extensively
691 studied in a specific organism for practical or historical reasons. For example, the genes of the
692 chloroplast NADPH:dehydrogenase complex involved in chlororespiration were identified in
693 tobacco by homology with mitochondrial complex I (Matsubayashi *et al.*, 1987) after the whole
694 chloroplast genome sequencing in tobacco (Shinozaki *et al.*, 1986), not because of the study of

695 chlororespiration in tobacco. Similarly, CEF around PSI was not detected as a proton-motive force
696 dependent on PSI excitation, but as an ATP production in spinach thylakoid membranes (broken
697 chloroplasts) reconstituted with Fd (Tagawa *et al.*, 1963). In algae like *Chlamydomonas* (or
698 *Chlorella*), the detection of AEFs involving O₂ as a terminal electron acceptor instead of CO₂ was
699 favored because (i) from an experimental point of view, while it is difficult to assess the flow along
700 a cyclic pathway where the reaction intermediates do not change concentration over time, it is
701 relatively easy to measure the accumulation of an end-product of photosynthesis, like the net O₂
702 evolution induced by a continuous illumination, (ii) they are aquatic species and the detection of
703 dissolved O₂ is easy and inexpensive, and (iii) there is no, or little photorespiration (high-CO₂
704 conditions or active CCM). *Chlamydomonas* is adapted to the measurements of dissolved O₂, an
705 accurate and sensitive technique using a polarographic method (Clark electrode) independent of
706 the mass transfer of O₂ between the liquid and the gas phase. These O₂ exchange measurements
707 are done more cheaply and more easily in a liquid suspension of unicellular algae than on plant
708 leaves where the gas flow through a measuring chamber must be carefully controlled, and the
709 detection of CO₂ is often monitored using an infrared gas analyzer. In addition to the observation
710 of the red drop (Emerson & Lewis, 1943) and enhancement effect (Brody & Emerson, 1959),
711 which suggested the existence of two different photochemical centers, other observations, often
712 based on the transient gush and gulps of O₂, showed the existence of pools of carriers in the
713 electron transport chain (Joliot 1965). O₂ exchange was not only used to detect O₂ evolution but
714 was also a pathfinder for O₂ photoreduction reactions. Perhaps the most illustrative example of the
715 sensitivity of oxygen exchange measurements in liquid suspensions was the observation of the
716 “Kok effect” in the green alga *Chlorella*, a break in the slope of light-response curve of the net O₂
717 exchange near the light compensation point (Kok 1949), suggesting an inhibition of respiration

718 under weak illumination, a first insight into the interaction between photosynthesis and respiration.
719 In O₂ exchange measurements, membrane inlet mass spectrometry (Hoch *et al.*, 1963) allowed for
720 significant progress in identifying alternative pathways using isotopic discrimination of different
721 O₂ species. The PSII-dependent oxygen evolution from water (E_O) is monitored at a mass-to-
722 charge ratio (m/e = 32, unlabeled ¹⁶O₂) while the oxygen uptake rate (U_O), corresponding to
723 mitochondrial respiration, photorespiration, chlororespiration, Mehler reaction, are measured at
724 m/e = 36 from labeled ¹⁸O₂ added to the sample before the measurement. These experiments, more
725 specific to respiration, confirmed the light-induced changes in O₂ exchange observed earlier (Kok,
726 1949). In the case of *Scenedesmus*, O₂ photoreduction can compete with CO₂ reduction to the point
727 it replaces it (Radmer & Kok, 1976), a similar phenomenon was also later observed in
728 *Chlamydomonas* and hypothesized to contribute to the energy requirement of the CO₂-
729 concentrating mechanism (Sültemeyer *et al.*, 1993). We now know that such large O₂
730 photoreduction is dependent on FLVs proteins (Chaux *et al.*, 2017) and is mostly restricted to
731 terrestrial plants (gymnosperms), green algae (Chlorophyceae and Prasinophyceae), mosses and
732 cyanobacteria (Peltier *et al.*, 2010). Chlororespiration was also evidenced very early on using non-
733 labelled oxygen (Diner & Mauzerall, 1973), and later confirmed using membrane inlet mass
734 spectrometry (Peltier *et al.*, 1987, Vermeglio *et al.*, 1990, Cournac *et al.*, 2000).

735 Because of this part of “chance” in the studies of AEFs in different model species, a comparative
736 approach may be appropriate to understand the physiological role of alternative pathways in the
737 photosynthetic diversity. It also suggests that comparisons between models or species should not
738 be restricted to concepts and experimental results, but also take into account the materials and
739 methods used in the work.

740 **Table 1: Molecular actors of the Alternative Electron Flows.** Gene name, CreNumber, protein
741 name and plastid localisation, mutants name, known abiotic triggers for up-regulation of gene
742 transcription in *Chlamydomonas* and important literature concerning the corresponding protein.
743 One asterisks beside literature reference indicate the first observation of the pathway, two asterisks
744 indicate the identification of the protein involved in the pathway and indicate ground-breaking
745 results in *Chlamydomonas*. CEF PSI; cyclic electron transfer around photosystem I: WWC; water-
746 water-cycle: HL; high light. The Mehler reaction, malate shuttle and photorespiration are excluded
747 from WWC as they rely on a large suite of enzymes interacting with complete cell metabolism.

	Gene	CreNumber	Protein	Protein localization	Mutants	Transcription up-regulation	Literature
CEF PSI	<i>pgr5</i>	Cre05.g242400	PGR5	Stroma	<i>Crpgr5</i> , <i>hpm91</i>	-Fe	1*, 2**, 3, 4
	<i>pgrl1</i>	Cre07.g340200	PGRL1	Thylakoid	<i>pgrl1</i>	-Fe	1*, 5**, 6, 7
	<i>nda2</i>	Cre19.g750547	NDA2	Thylakoid	Nda2-RNAi	-N, -S	8*, 9**, 10
WWC	<i>flvA</i>	Cre12.g531900	FLVA	Stroma	<i>flvB</i>	-CO ₂ , -S, HL	4, 11*, 12**, 13
	<i>flvB</i>	Cre16.g691800	FLVB	Stroma	<i>flvB</i>	-CO ₂ , -S, HL	4, 11*, 12**, 13
	<i>PTOX1</i>	Cre07.g350750	PTOX1	Thylakoid	<i>ptox1i</i>		14*, 15**, 16
	<i>PTOX2</i>	Cre03.g172500	PTOX2	Thylakoid	<i>ptox2</i> , <i>ptox2i</i>	-N	14*, 15**, 16, 17

748
749 **Literature:** 1: Arnon et al., 1954, J. Am. Chem. Soc.; 2: Munekage et al., 2002, Cell; 3: Johnson et al.,
750 2014, Plant Physiol.; Am. Soc. Plant. Biol. 4: Jokel et al., 2018, Plant J.; 5: Dal'Corso et al., 2008, Cell; 6 :
751 Petroustos et al., 2009 J. Biol. Chem.; 7 : Nawrocki et al., 2019b, BBA-Bioenergetics; 8 : Ogawa et al.,
752 1991 Proc. Natl. Acad. Sci.; 9: Jans et al., 2009 Proc. Natl. Acad. Sci.; 10: Desplats et al., 2009 J. Biol.
753 Chem.; 11: Radmer and Kok 1976 Plant Physiol.; 12: Gerotto et al., 2016 Proc. Natl. Acad. Sci.; 13: Chaux
754 et al., 2017 Plant Physiol.; 14: Bennoun 1982 Proc. Natl. Acad. Sci.; 15: Wu et al., 1999 Plant Cell; 16:
755 Houilles-Vernes et al., 2011 Proc. Natl. Acad. Sci.; 17: Nawrocki et al., 2019 Plant Physiol.

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