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Nonphotochemical Chlorophyll Fluorescence Quenching: Mechanism and Effectiveness in Protecting Plants from Photodamage.

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“The final publication is available at http://www.plantphysiol.org/content/170/4/1903.short”

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Topical review

Non-photochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protection against photodamage

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One-sentence summary: A review of the current state of the knowledge of the mechanism and protective effectiveness of non-photochemical chlorophyll fluorescence quenching is presented.

Footnotes: The author acknowledges the Royal Society Wolfson Research Merit Award, The Leverhulme Trust grant RPG-2012-478 and a grant from Biotechnology and Biological Sciences Research Council BB/L019027/1.

34 **Abstract**

35 The mechanism of non-photochemical chlorophyll fluorescence quenching, NPQ, and its role in
36 protecting plants against photoinhibition is reviewed. An introduction to the phenomenon, a brief
37 history of the major milestones, definitions, and a discussion of quantitative measurements of
38 NPQ have been presented. The up-to-date knowledge and unknown aspects in the NPQ scenario
39 that includes proton gradient (ΔpH) – *trigger*, the photosystem II (PSII) light harvesting antenna
40 (LHCII) – *site*; changes in the antenna induced by ΔpH – *change* leading to creation of the
41 *quencher* have been discussed. It is concluded that the minimum requirement for NPQ *in vivo*
42 consists of ΔpH, LHCII complexes and the PsbS protein. The most important unknown in the
43 NPQ scenario is highlighted to be the mechanism of PsbS action upon the LHCII antenna. A novel
44 emerging technology for the assessment of the photoprotective 'power' of NPQ has been reviewed
45 and its insightful outcomes are explained using several examples.

46

47 *"Real knowledge is to know the extent of one's ignorance."*

48 ***Confucius***

49 Non-photochemical chlorophyll fluorescence quenching (NPQ) refers to a process of
50 increased absorbed light energy dissipation into heat that takes place in the photosynthetic
51 membrane of plants, algae and cyanobacteria (Demmig-Adams et al., 2014). Early photosynthetic
52 organisms facing the problem of shady environments evolved the light harvesting antenna that
53 collect the dilute energy of light for the photosynthetic reaction centres (Clayton, 1980;
54 Blankenship, 2002). However, high light exposure in this case causes rapid saturation of the
55 photosynthetic reaction centres and their eventual closure, leading to a reduction in the fraction of
56 energy utilized in photosynthesis and the subsequent build-up of harmful excess excitation energy
57 in the photosynthetic membrane (Björkman and Demmig-Adams, 1995). This energy can damage
58 the most delicate part of the photosynthetic apparatus, the photosystem II (PSII) reaction centre
59 (RCII) that drives water splitting and oxygen evolution (Powles, 1984; Barber, 1995; Ohad et al.,
60 1984). A RCII repair mechanism does exists but the process occurs on the time scale of hours
61 (Barber and Andersson, 1992; Aro et al., 1993; Nixon et al., 2010; Nath et al., 2013). In addition,
62 excess light can potentially be harmful to the antenna pigments (Fleming et al., 2012). This can
63 lead to a sustained decline in photosynthetic efficiency and in extremes to the death of the
64 photosynthetic cell, tissue or organism.

65 Evolution supplied a range of solutions to the problem of high light exposure that vary in
66 efficiency, level of action and promptness of response (Gall et al., 2011; Niyogi and Truong,
67 2013; Ruban, 2014; Demmig-Adams et al., 2014; Goss and Lepetit, 2015). There are adaptations
68 to control light absorption capacity as well as adaptations that deal with the light energy that has
69 already been captured (Chow et al., 1988; Koller, 1990; Ruban, 2009; Cazzaniga et al., 2013; Xu
70 et al., 2015). At the molecular level there is both long-term (acclimation) and short-term
71 (regulatory mechanisms) control of the input of light energy into RCs. The first type is
72 predominantly developmental in nature, and is the result of light-dependent regulation of complex
73 gene expression, occurring on transcriptional, translational and post-translational levels (Anderson
74 et al., 1988). However, since the response time of acclimation is long, it limits photoprotective
75 efficiency while at the same time consuming energy and resources. On its own it is insufficient
76 since profound damage to the RCII can occur within minutes of excess light exposure (Tyystjarvi
77 and Aro, 1996).

78 NPQ is a molecular adaptation that represents the fastest response of the photosynthetic
79 membrane to the excess light (Demmig-Adams et al., 2014). The NPQ process directly or
80 indirectly relates to the processes of light harvesting by the photosynthetic antenna complexes,

81 their structure, captured energy transfer to reaction centers, electron transport, proton translocation
82 across the membrane, ATPase activity and carbon assimilation (Walker, 1987; Ruban, 2013;
83 Demmig-Adams et al., 2014). At various times NPQ research progressed through new
84 developments in the fields of defining and quantifying this protective process (Papageorgiu and
85 Govindjee, 1968; Murata and Shugahara, 1969; Schreiber, 1986; Oxborough and Horton, 1988;
86 Weis and Berry, 1987), the structure of the photosynthetic antenna complexes (Nield and Barber,
87 2006; Liu et al., 2004) and their organisation in the membrane (Dekker and Boekema, 2005;
88 Ruban and Johnson, 2015), dynamics of the antenna complexes (Garab et al., 1988; Ruban et al.,
89 1994; Miloslavina et al., 2008; Krüger et al., 2012, Liguori et al., 2015) pigment compositions
90 (Rees et al., 1989; Demmig-Adams, 1990) and dynamics in the membrane (Demmig-Adams and
91 Adams III, 1992; Matsubara et al., 2001; Jahns et al., 2009), excitation energy transfer and
92 dissipation (van Amerongen et al., 2000; Polivka and Sundstrom, 2004; Renger and Holzwarth,
93 2008; Cheng and Fleming, 2009; Scholes et al., 2011). It was a long and often convoluted path
94 towards the complete understanding of the molecular mechanism. Indeed, it took some time to
95 define and separate NPQ, to learn how to measure and quantify it, to obtain molecular insights
96 into antenna structure, to learn its dynamic nature and understand its role in protection. Recent
97 years witnessed a great emergence of review articles on various aspects of NPQ. A recent
98 collection of which have been published in the 40th volume of the series Advances in
99 Photosynthesis and Respiration 2014 (Demmig-Adams et al., 2014). Hence, the aim of this review
100 is to provide a complementary information highlighting the most recent known and unknown
101 aspects of the most investigated *mechanism* of NPQ that takes place in plants. This article also
102 discusses emerging work on quantitative approaches to assessing the *effectiveness* of NPQ in
103 protection against photoinhibition.

104 **DEFINITION OF NPQ**

105 NPQ was introduced as a reflection of the processes that arise in the photosynthetic
106 membrane that are not photochemical in origin. Indeed, the activity of the RCII causes a
107 significant decrease, or quenching, of chlorophyll fluorescence, since it consumes light energy that
108 otherwise could be released through fluorescence, interconversion or intersystem crossing
109 (Duysens and Sweers, 1963; Govindjee and Papageorgiu, 1971; Myers, 1974). However, it was
110 also discovered that fluorescence can be quenched in conditions when all RCII are closed, hence
111 not consuming any absorbed light energy (Papageorgiu and Govindjee, 1968; Murata and
112 Shugahara, 1969; Wright and Crofts, 1970). This was achieved first by using the PSII acceptor site
113 inhibitor DCMU added to chloroplasts constantly illuminated by actinic light. The inhibitor
114 caused the closure of RCII's within the first second of illumination, quickly reversing the

115 photochemically quenched fluorescence while the remaining part of the quenched fluorescence
116 reversed on a much slower time scale (Papageorgiu and Govindjee, 1968). This slowly relaxing
117 quenching was called 'non-photochemical quenching', or energy-dependent quenching qE
118 (Wright and Crofts, 1970). The term qE still remains popular and is considered to be the major
119 part of NPQ (Figure 1A).

120 In the 1980's the introduction of the pulse amplitude modulated (PAM) fluorescence
121 technique opened up a powerful opportunity for the detailed study of NPQ (Shereiber, 1986;
122 Oxborough and Horton, 1988). Figure 1A depicts a typical PAM induction measurement assessing
123 the state of PSII in the dark, the F_o fluorescence level, when all RCIIs are open and the F_m level,
124 when all of them are closed by the high intensity pulse (normally of 0.5-1.0 s duration). From this
125 simple start one can calculate the quantum efficiency of PSII as $\Phi_{PSII} = (F_m-F_o)/F_m$. In fact this is
126 actually the relative amount of fluorescence that was photochemically quenched due to the activity
127 of the reaction centres. It is interesting to note that the fluorescence does not immediately return to
128 the initial F_o level which is due to the fact that the acceptor site of the PSII stays reduced for some
129 time. This can be accelerated by the use of far red light that preferentially excites photosystem I
130 (PSI), causing faster oxidation of the Cyt*b*/*f* complex and the pool of mobile electron carriers,
131 plastoquinones (PQ), that removes electrons from PSII (Hill and Bendall, 1960; Blankenship,
132 2002). Then the actinic light illumination was applied for about 5 min. During this time saturating
133 light pulses are used every minute to determine the level of F_m. It can be clearly seen that this
134 level is being progressively quenched and stabilises at the end of the illumination period. The
135 quenched F_m is termed F_m'. Hence the level of NPQ can be calculated as $(F_m-F_m')/F_m'$. Another
136 parameter called qN is used to calculate non-photochemical quenching: $qN = (F_m-F_m')/F_m$. This
137 effectively gives a percentage of quenching in a similar manner to Φ_{PSII}. The NPQ calculation
138 reflects the ratio of the rate constant of NPQ to the sum of the rest of the constants reflecting all
139 other dissipation pathways in the membrane, such as fluorescence, internal and interconversion
140 (Krasuse and Weis, 1991). qE is defined in the context of this analysis as the rapidly-reversing
141 component of qN or NPQ (Figure 1A). Normally this component is considered to recover within 5
142 minutes of switching off the actinic light. It is worth noting that the trigger of qE, ΔpH, usually
143 collapses within 10-20 s (Ruban, 2013). Hence, it was proposed in the early days of NPQ research
144 that the process involved some conformational changes within the photosynthetic membrane that
145 respond to ΔpH. As shown on the figure, qE appears to be the major component of NPQ. The rest
146 used to be termed qI or the irreversible NPQ component related to photoinhibition/damage to RCII
147 (Krause and Weis, 1991). Later, it was discovered that the formation of zeaxanthin is closely
148 related to the NPQ mechanism (Demmig-Adams et al., 1989; Demmig-Adams, 1990; Demmig-
149 Adams and Adams III, 1992; for review see Demmig-Adams et al., 2014) and as such a part of qI

150 is often termed qZ to reflect the long-term quenching effect that correlated with the presence of
151 this pigment (Nilkens, 2010). In addition, other sustained components of NPQ have been reported
152 that were triggered by low temperature acclimation (Verhoeven, 2013), prolonged illumination in
153 the presence of zeaxanthin (Ruban and Horton, 1995), slow proton equilibration between different
154 membrane compartments (Ruban and Horton, 1995; Joliot and Finazzi, 2010) or simply by
155 formation of large levels of NPQ in some types of photosynthetic material (Ruban et al., 1993;
156 Ruban et al., 2004; Ware et al., 2015). Hence qI appeared to be a very complex component of
157 NPQ that remained difficult to interpret and the temporal criterion for quantification of qE is
158 rather ambiguous. Hence, we will use here the term protective NPQ (or just NPQ) instead of qE,
159 meaning that the former includes all moderately or slowly reversible components that are not
160 related to photoinhibition (see for details in PROTECTIVE EFFECTIVENESS OF NPQ).
161

162 **MECHANISM OF NPQ**

163 NPQ resides in the antenna (Bassi and Caffarri, 2000; Fleming et al., 2012; Ruban et al.,
164 2012; Wilk et al., 2013) (*site*) that undergoes a *change* triggered by ΔpH (*trigger*) (Horton et al.,
165 1996; Strand and Kramer, 2014). As a result of this change the *quencher* pigment(s) start
166 receiving and dissipating the energy harvested by the LHCII antenna into heat. Hence ΔpH
167 provides a feed-back control over light harvesting efficiency in the photosynthetic membrane
168 (Ruban et al., 2012; Strand and Kramer, 2014).

169 ***Trigger*: protons**

170 NPQ is triggered by ΔpH either directly by protonation of antenna components or
171 indirectly by the xanthophyll cycle(s) activity (Ruban et al., 2012). It also makes sense to refer to
172 the proton gradient as the *trigger* since in some organisms like diatom algae where large levels of
173 NPQ can be induced and sustained in the dark or upon addition of uncouplers in the absence of
174 ΔpH (Ruban et al., 2004; Lepetit et al., 2012). It was also established that acidification of the
175 incubation buffer can induce fluorescence quenching that possessed features similar to NPQ (Rees
176 et al., 1992). This finding provided a justification of the use of acidification technique in studies of
177 fluorescence quenching in isolated antenna complexes (Ruban et al., 1994; Bassi and Caffarri,
178 2000). Importantly, since ΔpH build-up is generated as a result of electron transport, a variety of
179 pathways contribute to its amplitude and the reader is referred to the most recent comprehensive
180 review (Strand and Kramer, 2014). In addition, ATPase by consuming protons exerts a
181 modulatory effect upon ΔpH. Also, a recent report showed that not only ATPase but a specialised
182 proton/potassium antiporter can influence the rate of NPQ relaxation at low light by accelerating
183 the collapse of ΔpH (Armbruster et al., 2014). In fact, the *trigger* is kept under control too (Figure

184 1B, regulatory points 1&2). It appears that cyclic electron transport around PSI is the major
185 contributor to the component of ΔpH that triggers the larger part of NPQ (Munekage et al., 2004).
186 Recent work by Sato and co-workers (2015) discovered that the cyclic electron transport-
187 generated ΔpH contributes 60-80% to NPQ formation. Therefore, the ratio between PSII and PSI
188 defined, for example, in the course of acclimation is likely to affect the *trigger* and therefore the
189 amplitude of NPQ (Brestic et al., 2015). Remarkably, chloroplasts from plants grown on
190 lincomycin, and have therefore lost almost all of PSII and 80% of PSI, were found to form levels
191 of ΔpH close to those from the control plants as well as to form very large levels of NPQ (Belgio
192 et al., 2012; Belgio et al., 2015). The modulation of ΔpH by artificial proton shuttles such as
193 diaminodurene (DAD) has recently been successfully used to provide vital mechanistic clues
194 about the sensitivity of responses of antenna components to lumen acidification during the
195 induction of NPQ (see below in *Site*: LHCII antenna and PsbS). Lumen protons target three key
196 components involved in NPQ: violaxanthin de-epoxidase (Figure 1B, target point 3) (Jahns et al.,
197 2009), the PsbS protein (Figure 1B, target point 4) (Li et al., 2004) and the LHCII antenna (Figure
198 1B, target point 5) (Ruban et al., 1994; Walters et al., 1994; Ruban et al., 1996; Liu et al., 2008;
199 Belgio et al., 2013). The pK of the lumen-exposed side of the thylakoid membrane is as low as 4.1
200 (Åkerlund et al., 1979). The estimates of the *in vivo* lumen acidification as a result of ΔpH
201 formation give pH 5.5 (Noctor et al., 1991; Kramer et al., 1999). The pK for NPQ in chloroplasts
202 devoid of zeaxanthin is 4.7 and pK of the quenching in the isolated major LHCII complex without
203 zeaxanthin is about 4.5 (Wentworth et al., 2001) but is 1-2 units of pH higher in the presence of
204 zeaxanthin or in monomeric LHCII, CP26 (Ruban and Horton, 1999; Wentworth et al., 2001). The
205 pK for PsbS according to the study by Dominici and co-workers (2002) should be in the region of
206 6.0-6.5. A similar pK for the violaxanthin de-epoxidation was reported by Jahns and co-workers
207 (2009). Hence, it appears that the most lumen pH sensitive components of the thylakoid
208 membrane are PsbS, violaxanthin de-epoxidaze, monomeric antenna complexes and LHCII that
209 bind zeaxanthin produced by de-epoxidase (Ruban at al., 2012). Therefore, for the LHCII antenna
210 to respond to lumen pH (Figure 1B, target point 5) and become quenched it is important to achieve
211 activation of de-epoxidase (target point 3) in order to produce zeaxanthin and activation of the
212 PsbS protein (target point 4). Both LHCII and PsbS contain a number of lumen exposed residues
213 that can receive protons. Two of them have been identified for monomeric LHCII and two for
214 PsbS using DCCD labelling and site-directed mutagenesis (Walters et al., 1996; Li et al., 2004).
215 However, tritium labelling of LHCII *in vivo* suggested that each monomer can sequester up to 17
216 protons (Zolotareva et al., 1999). It may well be possible that since monomeric antenna receive
217 protons at lower levels of ΔpH they are the primary sites for the quenching that eventually spreads
218 into the bulk of LHCII trimers. The idea that the minor antenna are the site for NPQ is currently

219 being the most supported by the work of groups of Fleming and Bassi (Ahn et al., 2008; Avenson
220 et al., 2009).

221 There was never an easy way to measure the proton gradient. The use of 9-aminoacridine
222 was a most common way to assess it in thylakoids or chloroplasts (Ruban, 2013). However, it
223 appears not to be an easy task to do this on leaves and the only method was the indirect
224 measurement using the light-induced absorption change at 518 nm that is believed to reflect the
225 electrochromic shift of carotenoids (Kramer et al., 1999). However, this method was recently
226 subjected to a critical reassessment that claimed that the observed steady-state component of the
227 518 nm absorption change that was used as a measure of the proton gradient (Kramer et al., 1999)
228 was due to the interference with the NPQ-associated absorption at 535 nm (for more detailed
229 discussion see Johnson and Ruban, 2013). This work has also cast doubt that the electric field
230 gradient $\Delta\psi$ makes a noticeable contribution to the proton motive force in photosynthesis. The 535
231 nm change is tightly related to NPQ and, since the latter is triggered by ΔpH, measurements of
232 absorption at 518 nm would reflect to a certain extent the amplitude of NPQ and therefore,
233 indirectly, ΔpH. Therefore development of accurate, direct and non-destructive ways to measure
234 ΔpH *in vivo* would be a crucial step towards monitoring the dynamics of this important parameter
235 in a course of light and metabolic alterations in order to find the causes of altered NPQ levels.

236 ***Site*: LHCII antenna and PsbS**

237 Some 25 years ago modelling of the relationship between NPQ and the PSII yield
238 prompted a point towards the involvement of the PSII antenna in NPQ (Genty et al., 1989).
239 Indeed, the NPQ quencher was found to decrease not only F_m but F_o fluorescence (see Figure 1A)
240 (Horton and Ruban, 1993). The quencher persisted at 77K and preferentially quenched major
241 LHCII complex bands at 680 and 700 nm (Ruban et al., 1991). Early fluorescence lifetime
242 analysis was consistent with quenching taking place in the PSII antenna (Genty et al., 1992). Later
243 this type of spectroscopy revealed similarities between decay-associated spectral changes upon the
244 transition into the quenching state in both isolated LHCII complexes and intact chloroplasts
245 (Johnson and Ruban, 2009). Plants lacking a majority of LHCII antenna complexes displayed
246 strongly reduced NPQ (Jahns and Krause, 1994; Havaux et al., 2007). The remaining quenching in
247 the chlorina mutants or intermittent light grown plants was attributed to the presence of some
248 minor LHCII antenna complexes (Jahns and Krause, 1994; Havaux et al., 2007) as was previously
249 proposed (Andrews et al., 1995). NPQ was also found to be modulated by cross-linkers, tertiary
250 amines, antimycin A, DCCD and magnesium in the same way as the quenching in isolated LHCII
251 antenna complexes (Ruban et al., 1994; Ruban et al., 1996; Ruban et al., 1992; Johnson and
252 Ruban, 2009). The latter was induced at the detergent concentration below *cmc* and led to the

253 aggregation of the complex. Hence, the hypothesis of the *in vivo* aggregation of the LHCII
254 antenna as a mechanism underlying NPQ has been put forward (Horton et al., 1991) (for
255 discussion see *Change*: LHCII aggregation and other). Moreover, discovery that the xanthophyll
256 cycle carotenoids were localised exclusively in LHCII antenna complexes (Thayer and Thornber,
257 1992; Bassi et al., 1993) and later that NPQ was entirely dependent upon the xanthophylls
258 zeaxanthin and lutein (Pogson et al., 1998; Niyogi et al., 2001) caused little doubt that the NPQ
259 site was the LHCII antenna (for more details read Ruban et al., 2012).

260 The evolving knowledge of PSII antenna composition, structure and organisation in the
261 photosynthetic membrane revealed its structural and functional heterogeneity (Boekema et al.,
262 1995; Jansson, 1994; Dekker and Boekema, 2005; Caffarri et al., 2009; Kouřil et al., 2011; Kouřil
263 et al., 2013). The current structure proposes that the LHCII antenna is built of three monomeric
264 LHCII antenna complexes, CP24, CP26 and CP29, collectively called the minor LHCII antenna
265 and several trimeric LHCII known as the major LHCII antenna. The minor LHCII antenna build
266 the structural and apparently functional (Dall'Osto et al., 2014) bridge between the major trimeric
267 LHCII complexes and the core antenna in the PSII supercomplex dimer (Figure 2). Three types of
268 LHCII trimers are distinguished based on their binding strength to the PSII supercomplex: S, M
269 and L, strongly, medium and loosely bound, respectively. Only the localisation of S and M trimers
270 have been identified. It is supposed that loosely bound trimers are relatively free to diffuse in the
271 membrane, therefore it is difficult to predict their localisation. There can be 2 to 4 and sometimes
272 more loosely bound trimeric LHCII complexes per one PSII monomer (Melis and Anderson,
273 1983; Kouřil et al., 2012; Wientjes et al., 2013). Work on DCCD binding, *in vitro* quenching and
274 carotenoid binding work on the monomeric LHCII complexes CP26 and CP29 showed that they
275 are both capable acceptors of protons as well as able to attain large levels of quenching and are
276 enriched in xanthophyll cycle carotenoids (Walters et al., 1994; Walters et al., 1996; Ruban et al.,
277 1996; Ruban et al., 1997; Bassi and Caffarri, 2000). It allowed researchers to put forward a
278 proposal that the site of NPQ is localized in the monomeric LHCII complexes (Bassi and Caffarri,
279 2000; Ahn et al., 2008; Avenson et al., 2009). This opinion was weakened by the fact that
280 antisense and knockout mutants of *Arabidopsis* lacking one or even two of the three monomeric
281 LHCII (CP24/29 double mutant) possessed significant levels of NPQ (Andersson et al., 2001; de
282 Bianchi et al., 2008). In addition, the efficiency of violaxanthin de-epoxidation located in the L2
283 site (Pan et al., 2011) was found to be very low in the minor antenna complexes, particularly in
284 CP29, due to a strong binding into the site (Duffy and Ruban, 2012) implying that they cannot
285 bind any significant amounts of the postulated quencher zeaxanthin in this site. However, it may
286 well be that the quenching in the monomeric LHCII antenna complexes proceeds by the same
287 mechanism (Mozzo et al., 2008) as that suggested for the major trimeric LHCII (Ruban et al.,

288 2007). Now, further clarification of the role of monomeric LHCII complexes in NPQ is expected
289 to come from a study of the already reported triple minor antenna knock-out mutant (NOM)
290 (Dall'Osto et al., 2014).

291 Another component that was discovered to play a crucial role in enabling the rapidly-
292 reversible component of NPQ, qE, is the PsbS protein (Li et al., 2000). Structural work on the
293 localisation of this protein in the photosynthetic membrane suggested that it is not a part of the
294 PSII supercomplex (Nield et al., 2000). Biochemical work convincingly showed that PsbS does
295 not specifically bind pigments (Bonente et al., 2008). Recently the atomic structure of PsbS has
296 been solved (Fan et al., 2015). The structure of the protein is a dimer that is more stable at low pH.
297 Acidification was suggested to cause a conformational change associated with alteration in
298 lumenal intermolecular interactions. Hence, it appears that PsbS acts rather like a *switch* that is
299 triggered by ΔpH and not a quenching site. Therefore, this switch has to be localised closer to the
300 LHCII antenna in order to prompt it into the NPQ state or make it sensitive to protonation (Ruban
301 et al., 2012). It seems to be appropriate to use the term "sensitive" here since it was shown that qE
302 can actually form without PsbS provided ΔpH is high enough (Johnson and Ruban, 2011). Hence,
303 the model in Figure 1B draws a straight line from the *trigger* to *site* (LHCII antenna) (action point
304 5) bypassing PsbS and zeaxanthin and putting them rather as components of modulation. These
305 components are actually important for physiological adjustment of NPQ (see in *Change*: LHCII
306 aggregation and other). Since PsbS was not found in the PSII supercomplex it has got to be
307 localised somewhere in the domains of the LHCII antenna (Figure 2). The recent report that
308 biochemically probed the site of PsbS binding in PSII in the moss *Physcomitrella patens* proposed
309 that in the dark the protein binds to several Lhcb proteins with preferential binding to the
310 periphery of the LHCII M trimer of the PSII supercomplex (Gerotto et al., 2015). Hence this work
311 has pointed out that the likely NPQ site is trimeric rather than monomeric LHCII complexes.
312 However, it would be interesting to apply this approach to the higher plant PSII in both dark-
313 adapted and NPQ states. Interestingly, plants that grew on lincomycin (mentioned above) and
314 possessed very few RCII retaining trimeric and some reduced amounts of monomeric LHCII
315 complexes, also contained PsbS protein (see above) (Belgio et al., 2012; Belgio et al., 2015). NPQ
316 in these plants was modulated by PsbS (Ware et al., 2015) suggesting that the site of NPQ is
317 LHCII antenna and PsbS together. However, this work did not prove that the monomeric LHCII
318 was not involved, but it produced a simpler model system for NPQ studies. It looks like only ΔpH,
319 the LHCII antenna and PsbS are required for NPQ *in vivo*. It is likely that PsbS is needed to make
320 the LHCII antenna more rapidly responsive to natural levels of ΔpH. The structural arrangement
321 of the LHCII antenna and PsbS around PSII does not seem to matter for the quenching to be
322 observed, provided they are in the membrane. However, the core complex may play a role in

323 tuning NPQ kinetically by initiating the reassembly of the antenna around it in the dark (Dong et
324 al., 2015; Ware et al., 2015). The notion that the RCII core complex is not essential for quenching
325 is consistent with a recent work on reconstitution of PsbS and the major LHCII complex into
326 liposomes (Wilk et al., 2013). Interestingly the liposomal system did not contain any minor
327 antenna complexes suggesting that LHCII trimers are sufficient partners for PsbS interaction and
328 formation of the *quencher*.
329

330 ***Change*: LHCII rearrangements/aggregation and formation of the NPQ *quencher***

331 The requirement for the change in the LHCII antenna triggered by ΔpH was first proposed
332 by the work of Horton's group (Horton et al., 1991). This was the hypothesis that stated that the
333 proton gradient triggered LHCII antenna aggregation that was required to establish the NPQ state.
334 Indeed, isolated major LHCII complex was shown to aggregate at low detergent concentration that
335 was greatly enhanced by acidification of the incubation buffer and this process was followed by a
336 fluorescence quenching that was strong enough to explain any levels of NPQ observed in nature
337 (Ruban et al., 1994). Another attractive physiological implication of this hypothesis was that
338 LHCII antenna aggregation was modulated by xanthophyll cycle carotenoids the fact that
339 explained NPQ with and without zeaxanthin as well as the concept of 'plant illumination memory'
340 and the effect of *hysteresis* (Horton et al., 1996; Ruban et al., 2012). Xanthophyll cycle
341 carotenoids have been discovered to be localised in peripheral binding site V1 of the major LHCII
342 complex (Ruban et al., 1999; Liu et al., 2004) and it is not excluded that they are also bound
343 peripherally to the minor antenna complexes (Ruban et al., 1999; Xu et al., 2015). This peripheral
344 localisation and ability to regulate LHCII antenna aggregation has been explained by different
345 hydrophobicity/polarity of violaxanthin and zeaxanthin (Ruban and Johnson, 2010; Ruban et al.,
346 2012). Presence of zeaxanthin was suggested to slow down reversibility of NPQ and promote the
347 sustained component qZ due to the tuning of LHCII antenna into aggregation that is slowly-
348 reversible (Noctor et al., 1991; Ruban and Horton, 1999). In addition, violaxanthin de-epoxidation
349 was reported to alter LHCII antenna aggregation state *in vivo* as well as energy transfer pathways
350 within LHCII antenna bringing minor LHCII antenna complexes such as CP29 to a closer contact
351 with LHCII trimers (Ilioaia et al., 2013).

352 Although the LHCII antenna aggregation hypothesis for NPQ prompted much of research
353 around LHCII complexes and many attempts to link it to NPQ using indirect biochemical and
354 spectroscopic methods (for the recent review see Ruban et al., 2012) it lacked crucial direct proof
355 of *in vivo* aggregation or rearrangements of LHCII antenna triggered by ΔpH and explanation of
356 the role of PsbS protein in the proposed rearrangements (Ruban et al., 2012). To address these
357 important points recently several groups have undertaken a number of approaches (Miloslavina et

358 al., 2008; Holzwarth et al., 2009; Betterle et al., 2009; Johnson et al., 2011; Ware et al., 2015).
359 Although indirect, however, novel spectroscopic *in vivo* evidence emerged suggesting that upon
360 formation of NPQ a part of the major LHCII complexes undergo separation from the PSII
361 supercomplex and aggregation (Miloslavina et al., 2008; Holzwarth et al., 2009). Further, a
362 biochemical and structural evidence has been obtained suggesting that in NPQ PsbS controlled the
363 dissociation of a part of the PSII–LHCII supercomplex containing LHCII, CP24 and CP29 and
364 that the average distances between PSII core complexes became shorter (Betterle et al., 2009).
365 Later, freeze-fracture electron microscopy studies revealed similar alterations in PSII distances
366 and most importantly clustering of LHCII antenna particles on the protoplasmic fracture face of
367 the stacked thylakoid membrane (PFs) (Johnson et al., 2011; Ruban et al., 2012). This clustering
368 was found to be promoted by the presence of zeaxanthin and PsbS protein (Johnson et al., 2011;
369 Goral, 2012). Further, overexpression of PsbS caused massive LHCII antenna aggregation, even in
370 the absence of RCII complexes (Ware et al., 2015). It was also shown that the antenna
371 composition has a strong effect upon NPQ and the dynamics of the related rearrangements
372 triggered by ΔpH (Goral et al., 2012). Therefore, these advances provided a first direct
373 experimental confirmation of the LHCII antenna aggregation hypothesis of NPQ. Moreover the
374 data showed the common nature of qE and zeaxanthin-dependent qZ NPQ components as
375 manifestations of the same LHCII aggregation phenomenon. Crucially the observed structural
376 alterations induced by illumination occurred on a timescale consistent with the formation and
377 relaxation of qE (Johnson et al., 2011).

378 Despite all of this progress many details of the *change* that leads to the establishment of
379 the quenched state are not agreed upon or not known at all. Although there is no denial that the
380 LHCII antenna undergoes reorganisation into the NPQ state, recent data suggest that it does not
381 uncouple energetically from RCII (Johnson and Ruban, 2009; Belgio et al., 2014) as was
382 previously proposed (Holzwarth et al., 2009) and in total agreement with the earlier established
383 and experimentally confirmed relationship between the yield of PSII and NPQ (Genty et al.,
384 1989). Moreover it was shown that NPQ protects closed, not open, RCII which makes this
385 protective strategy *economic*, not allowing much competition between NPQ and RCII traps for
386 energy when light intensity is low or moderate (Belgio et al., 2014). Figure 3A depicts a model of
387 the fragment of the grana membrane that shows arrangement of PSII core and LHCII complexes.
388 The arrangement of cores and C2S2M2 supercomplexes (orientation and distances) that contained
389 core dimer, all monomeric LHCII, S and M trimers have been taken from Kouřil et al. (2011). The
390 L trimers were added randomly (positions and orientations) to match the LHCII trimer/RCII ratio
391 of 5. The localisation of PsbS is considered unknown, however the paper of Gerotto et al. (2015)
392 hinted it can be anywhere in the LHCII antenna with a slight preference for the M trimer (Figure

393 2) although this still needs to be demonstrated for higher plants. In the NPQ state clustering of
394 PSII and LHCII complexes has been displayed schematically adapting the work by Johnson et al.
395 (2011) (Figure 3B). Note that the major assumption here is that the structure of the C2S2
396 supercomplex is preserved. However, this is not certain (Dong et al., 2015) and has to be verified
397 along with the localisation of PsbS. It was found that this protein changes its conformation (Fan et
398 al., 2015) that can alter, for example, its affinity of binding within the LHCII antenna that could
399 trigger the observed rearrangement. But what is the mechanism of this PsbS effect, its interaction
400 with the LHCII antenna and its specificity? Is the interaction promoted by altered hydrophobicity
401 or potentiated by promotion of N-terminal interactions? If the scheme on the Figure 1B is correct
402 why does PsbS make the LHCII antenna more sensitive to lumen pH? Is it because it somehow
403 enhances hydrophobicity of the environment of proton-receiving aminoacids that can certainly
404 make their pK higher? (Mehler et al., 2002; Thurlkill et al. 2006). Also, while both PsbS and
405 zeaxanthin promote rapid formation of NPQ (Li et al., 2000; Demmig-Adams et al., 1989), why
406 has the former an acceleratory and the latter an inhibitory effect on its recovery as well as opposite
407 effects on chlorophyll excited state relaxation dynamics (Sylak-Glassman et al., 2014)?

408 Another aspect of the change is LHCII antenna clustering a primary cause of the
409 quenching or is it simply a thermodynamic consequence of the inner conformational change
410 within each trimer or monomer that actually creates the *quencher*? First evidence that isolated
411 LHCII complexes can be quenched without significant aggregation has been obtained by using
412 high hydrostatic pressure or polymerising it into the polyacrylamide gel and gradual removal of
413 detergent (van Oort et al., 2007; Ilioia et al., 2008). The features of this quenching were similar to
414 those of the aggregated low-pH-quenched LHCII. It began to emerge that the LHCII
415 monomer/trimer undergoes some kind of conformational change into the quenching state that
416 involved specific changes in some of the xanthophyll (neoxanthin and lutein) and chlorophyll
417 pigments as was previously observed on LHCII aggregates (Robert et al., 2004; Ilioaia et al.,
418 2011). There exists, however, only the structure of the quenched conformation of trimeric LHCII
419 (Lui et al. 2004; Pascal et al., 2005). Recently a few attempts have been made to understand the
420 scale and possible specificity of the conformational transition into the quenched state. Exciton
421 annihilation experiments along with the high hydrostatic pressure work revealed very small
422 volume alteration of the quenched trimeric LHCII (van Oort et al., 2007; Rutkauskas et al., 2012).
423 NMR studies and accompanying theoretical analysis revealed subtle alterations in some
424 chlorophyll *a* pigments and their interactions with neoxanthin and lutein 1 and 2 (Pandit at al.,
425 2013: Duffy et al., 2014). These observations were consistent with the discovered role of the
426 lumenal loop of trimeric LHCII that is localised close to neoxanthin domain in modulation of
427 quenching *in vitro* (Belgio et al., 2013). This notion was recently confirmed by the first molecular

428 dynamics study that revealed significant flexibility of trimeric LHCII mostly in neoxanthin and
429 lutein 1 (terminal emitter) domains (Liguori et al., 2015).

430 In parallel to the structural work on the LHCII antenna, novel single molecule fluorescence
431 spectroscopy of all types of LHCII, trimeric and monomeric, has been intensely applied in recent
432 years (Krüger et al., 2012; 2013; 2014). The rapidly fluctuating levels of the LHCII fluorescence,
433 known as fluorescence intermittency or *blinking*, has been found to be modulated by the
434 xanthophyll cycle composition as well as low pH treatments and therefore closely related to NPQ.
435 The blinking was found to reflect local conformational fluctuations within the complex thermally
436 accessing distinct conformational states that have strong quenching (lutein 1 and 2 domains) or
437 red-shifted fluorescence properties (around 700 nm) (Krüger et al., 2014).

438 All above mentioned studies on the intrinsic dynamics of the LHCII complexes were
439 absolutely essential in the search of the possible NPQ quencher(s). The quencher is simply 'born'
440 out of the change in conformation triggered by protonation. Currently there are several theories
441 proposing the identity and the physical mechanism of the quenching process. Since this falls out of
442 the scope of this review the reader is referred to the most recent account of the state of the
443 knowledge on the physics of NPQ quencher (Duffy and Ruban, 2015). In brief, pigments
444 zeaxanthin, lutein and chlorophyll *a* have been proposed as possible NPQ quenchers. Zeaxanthin
445 as a quencher was suggested some time ago (Frank et al., 1996; for review see Demmig-Adams,
446 1990) and recently received strong insightful support from the group of Fleming, Niyogi and Bassi
447 who proposed the quencher localization within the minor LHCII antenna complex CP29 (Holt et
448 al. 2005, Ahn et al., 2008). Lutein bound to the major and minor LHCII as a quencher has also
449 been proposed by several groups (Ruban et al., 2007; Avenson, 2009). Whilst there exist only one
450 theory about the zeaxanthin action as a quenching – a radical cation formation with chlorophyll
451 (Holt et al., 2005), there are several theories explaining how lutein (and other xanthophylls) can
452 quench the excess energy that include coherent and incoherent energy transfer pathways from
453 chlorophyll to xanthophyll (Duffy and Ruban, 2015). Whilst there is some evidence of how
454 zeaxanthin is being activated as a quencher (Holt et al., 2005; Ahn et al., 2008) there is a pool of
455 reports attempting to explain the changes in protein and lutein making this pigment a quencher as
456 well as modelling work assessing the effectiveness of this quencher in taking excess excitation
457 energy from chlorophyll *a* (Ilioaia et al., 2013; Duffy et al., 2013a; 2013b; 2014; Chmeliov et al.,
458 2015). Formation of quenching chlorophyll-chlorophyll dimers has also been recently advocated
459 (Müller et al., 2010). It is worth to note that this multiplicity of the identity and physics of the
460 NPQ quencher(s) may well reflect the complex nature of the process involving formation of a
461 variety pigment-pigment interactions. Therefore the existence of multiple types of quenchers that

462 include xanthopohylls as well as chlorophylls was recently contemplated (Holzwarth et al., 2009;
463 Liguori et al., 2015).

464 **PROTECTIVE EFFECTIVENESS OF NPQ**

465 The attention to the details of the mechanism of NPQ has been and remains enormous. In
466 contrast, not much is actually known how quantitatively efficient NPQ is in protecting the
467 photosynthetic membrane against photodamage and how to separate its protective component. In
468 addition, there are reports that claim that NPQ plays little or no role in photoprotection of PSII
469 against photodamage (Santabarbara et al., 2001). However, the majority of *in vivo* studies reported
470 observations that clearly established a crucial role of NPQ protection against photoinhibition that
471 led to early senescence and reduction in plant growth and fitness (Niyogi et al., 1998; Verhoeven
472 et al., 2001; Külheim et al., 2002; Niyogi and Truong, 2013). However, a quantitative aspect of
473 protective effectiveness of NPQ and the determination of the critical light intensity plants can
474 tolerate without showing signs of photoinhibition required the development of new approaches.
475 As it was mentioned at the beginning of this review, qE is a rather inaccurate parameter since
476 there are less readily reversible but also protective parts of NPQ different from the qI that reflects
477 photoinhibition. Existing and commonly used measures for photoinhibition include the dark-
478 adapted F_v/F_m ratio or the yield of PSII, O_2 evolution or D1 protein degradation. Whilst these have
479 been effective for assessing the threshold for the damage they have drawbacks for physiological
480 analyses especially where lab-based biochemical analysis is required (D1 turnover). In addition
481 these methods require disruption of the light treatment, either by destructive sampling or
482 imposition of a sustained dark period. The length of the dark period used for F_v/F_m measurements
483 itself can be ambiguous. Recently we developed a novel principle of NPQ analysis that enables a
484 better understanding and quantification of the effectiveness of the protective action of NPQ. In
485 this approach the extent of photochemical quenching (qP) measured in the dark was used to
486 monitor the state of active PSII reaction centres, enabling detection of the early signs of
487 photoinhibition (Ruban and Murchie, 2012; Ruban and Belgio, 2014). It is important to notice that
488 both NPQ/qE and photodamage to RCIIs diminish the quantum yield of PSII. This can be
489 illustrated by the following formula derived by Ruban and Murchie (2012):

490 $$\Phi_{PSII} = qP \times (F_v/F_m) / [1 + (1 - F_v/F_m) \times NPQ], \quad (1)$$

491 where qP is the photochemical quenching. F_v/F_m is the yield of PSII before illumination. qP is
492 defined as $(F_m'-F_o'_{act.})/(F_m'-F_o'_{calc.})$, where $F_o'_{act.}$ is a measured dark fluorescence level and $F_o'_{calc.}$
493 is a dark fluorescence level calculated using Fm' (Oxborough and Baker, 1988). When formula (1)
494 was applied to leaves that had been exposed to gradually increasing light intensity, like in light
495 saturation curves but for longer periods of illumination with short periods of darkness in order to

496 assess qP levels (Figure 4A), it perfectly matched the experimental data (Figure 4B) up to a
497 certain high actinic light intensity, above which the experimentally determined yield started to
498 decrease more steeply with NPQ than the theoretical value Figure 4B). This discrepancy in the
499 measured and calculated yield came from the fact that qP started to show values lower than 1
500 (Figure 4B). This is because the measured values of F_o started to become higher than the values of
501 F_o predicted using F_m' amplitude (Oxborough and Baker, 1988) (Figure 4A). This discrepancy
502 comes from the fact that when RCII become closed due to photoinhibition, they stay closed in the
503 dark, hence they cannot photochemically quench fluorescence causing an increase in F_o' in a
504 similar way to the increase in F_o' that would be caused by the addition of DCMU or illumination
505 making this level effectively F_s. Therefore, at this conditions F_o' becomes less appreciably
506 quenched in relation to F_m' that manifests in the observed deviation of the experimental from
507 predicted F_o' levels and hence brings qP level down from 1. This qP was called qP_d to indicate
508 that it was always measured in the dark in the routine of the gradually increasing actinic light
509 intensity (Ruban and Murchie, 2012; Ruban and Belgio, 2014). Critical work has been undertaken
510 to ensure that the novel method is free from artefacts of PSI contribution to the novel PAM
511 fluorescence measurements (Giovagnetti et al., 2015) and that the fluorescence parameter qPd is
512 in good correlation with the electron transport rates measured by oxygen evolution techniques
513 (Giovagnetti and Ruban, 2015).

514 Application of the described approach enabled the obtaining of a number of important
515 parameters without the need to use the dark relaxation step: a) amplitude of all protective
516 components of NPQ, pNPQ; b) the maximum tolerated light intensity at which all RCIIs remain
517 functional; c) the minimum pNPQ sufficient to protect against the unit of light intensity; d) the
518 amount of potentially wasteful pNPQ: e) the light tolerance curves for a particular type of plant
519 (Ruban and Belgio, 2014; Ware et al., 2014). As a result of this development the highest light
520 intensity tolerated by 50% of various tested plants has been obtained (Figure 4C). One important
521 conclusion of this work is that regardless of the type of mutation, the light tolerance was solely
522 determined by the amplitude of pNPQ (Ruban and Belgio, 2014; Ware et al., 2014). Hence, pNPQ
523 of about 1 in *Arabidopsis* was capable of protecting plants exposed to about 400 μmol $m^{-2}s^{-1}$ PAR.
524 This was an almost linear relationship, meaning that in order to tolerate 1600 μmol $m^{-2}s^{-1}$ PAR of
525 light intensity, almost the highest attainable on the planet (total light intensity of ~3200 μmol $m^{-2}s^{-1}$
526), plants have to develop pNPQ of about 4, which is probably the top of reported values for this
527 species. As was expected, plants acclimated to low light showed lower light tolerance (Ware et al.,
528 2015). Formation of larger antenna caused higher excitation pressure hence changing the
529 steepness in the relationship between NPQ and tolerated light intensity. Also different plant
530 species differ in their sensitivity to light and therefore the requirement for pNPQ may vary

531 significantly (Ruban, 2015). In addition, in low light acclimated plants part of the large LHCII
532 antenna was uncoupled from RCII. Interestingly, this uncoupling was associated with increased
533 levels of F_o quenching. However, this additional quenching did not contribute to light tolerance
534 implying that if uncoupled LHCII indeed participated in NPQ process, like was suggested before
535 (Holzwarth et al., 2009) it would contribute little to protection – a fact rendering the existence of
536 two uncoupled sites for NPQ totally unnecessary. In addition, an interesting trend in light
537 tolerance has been observed during ontogenetic development (Carvalho et al., 2015). Seedlings of
538 1 week old were almost 20 times less tolerant to light than established 8 week old plants. This
539 indicates that the most significant high light damage occurs in young plants or developing leaves.
540 Therefore, the major focus of plant physiologists, ecologists and breeders has to be directed
541 towards monitoring and improving light tolerance specifically at early stages of plant
542 development.

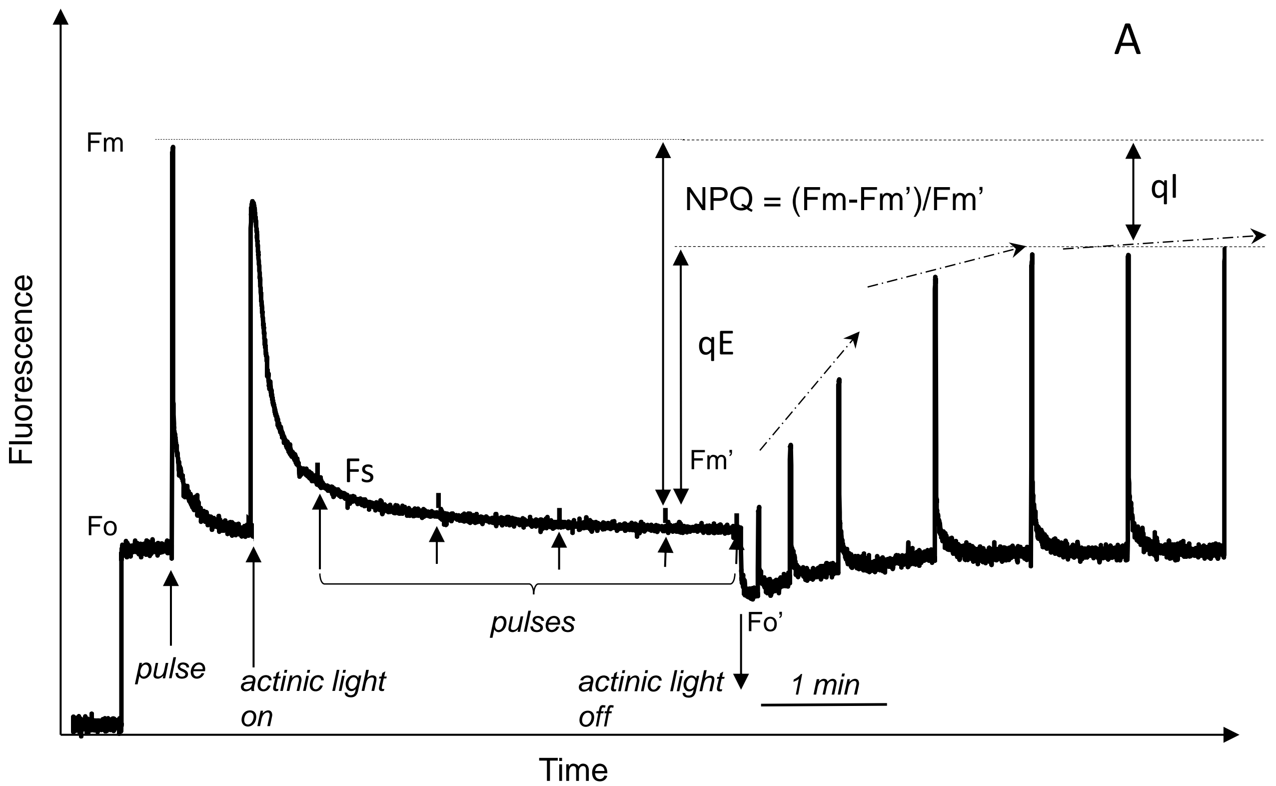
543 The novel method of NPQ assessment should be very useful in order to evaluate the real
544 effectiveness of NPQ in protection for example in cyanobacteria, diatoms and other classes of
545 photosynthetic organisms. It has got to be realised that the fact of the existence of NPQ is
546 apparently not enough. Modern times require understanding of its value in doing the protective job
547 by analysing in parallel NPQ amplitude and efficiency of photochemistry.
548
549 **Acknowledgments**
550 The author would like to acknowledge contributions of his lab members to the various aspects
551 discussed in this review: Erica Belgio, Fabricio Eulálio Leite Carvalho, Vasco Giovagnetti, Petra
552 Ungerer and Maxwell Ware. The author is also grateful to Christopher Duffy for the critical
553 reading of the manuscript.
554
555 **Figure legends**
556
557 **Figure 1. A.** Typical PAM fluorescence measurement of Arabidopsis leaf showing induction and
558 relaxation of NPQ. Fm and F_o maximum and minimum fluorescence levels in the dark before
559 actinic light illumination (1000 μmol $m^{-2}s^{-1}$). Fs is a steady state fluorescence level. F_m’ is
560 maximum fluorescence during actinic light illumination. Pulses of light (10000 μmol $m^{-2}s^{-1}$) are
561 applied to close all RCII and estimate F_m and F_m’. qE and qI are quickly- and slowly-reversible
562 components of NPQ. **B**. The course of NPQ development, *scenario*, showing key factors
563 triggering and regulating the process (for more details see the text). The formula for the minimum
564 component requirement for NPQ is shown under the diagram.

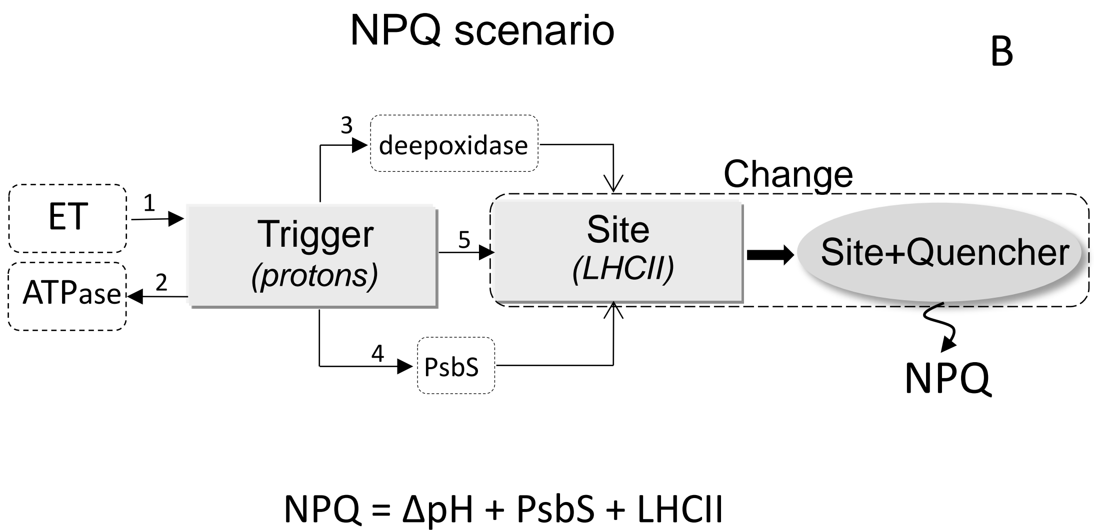
565 **Figure 2.** The structure of PSII antenna components. S, M and L are the major LHCII strongly,
566 medium and loosely bound to the RCII core trimers. CP24, 26 and 29 are the minor monomeric
567 antenna complexes. PSII core dimer is shown in red. PsbS dimer is shown with the dashed line
568 pointing to the putative preferential interaction cite in the dark.

569 **Figure 3.** The schematic representation of the putative PSII arrangements in the grana membrane
570 in the dark (A) and NPQ (B) states. A. 18 PSII C2S2M2 complexes (outlined by yellow lines)
571 with peripheral LHCII trimers (L trimers) (after Kouřil et al., 2011). Total LHCII trimer to RCII
572 monomer ratio is approx. 5. B. 18 PSII core dimers rearranged/clustered intro the NPQ state
573 (following Johnson et al., 2011). C2S2 structure is shown (outlined with the dashed red line, see
574 the inset) preserved in the 3 supercomplexes shown in the tip left corner. A mix of unquenched
575 (black contour) and quenched (red contour) S, M and L trimers and monomers of the minor
576 antenna (not specified here) is shown. The localisation and interactions of PsbS protein are
577 unknown.

578 **Figure 4.** **A.** A fragment of the gradually increasing illumination procedure in PAM measurement
579 on *Arabidopsis* leaf. The formula on the top shows how qPd was calculated. $F_o'_{act.}$ and $F_o'_{calc.}$ are
580 the measured and calculated (Oxborough and Baker, 1997) dark fluorescence levels. P1, 2, 3 are
581 saturating pulses. AL and FR are actinic and far red light, respectively. 625 and 820 are intensities
582 of actinic light in µmol $m^{-2}s^{-1}$. **B**. The relationships between the PSII yield, qPd and NPQ in the
583 dark in the course of the gradually increasing actinic light intensity procedure (Ruban and Belgio,
584 2014). The formula shows the relationship between PSII yield, qP and NPQ. **C**. Light intensity (in
585 µmol $m^{-2}s^{-1}$) tolerated by 50% of tested various types of *Arabidopsi*s mutant plants: –Zea (npq1); -
586 PsbS (npq4); +PsbS (wt) and ++PsbS (PsbS overexpressor, L17).

Figure 1





NPQ = ΔpH + PsbS + LHCII

Figure 1. A. Typical PAM fluorescence measurement of Arabidopsis leaf showing induction and relaxation of NPQ. Fm and F_o maximum and minimum fluorescence levels in the dark before actinic light illumination (1000 μmol $m^{-2}s^{-1}$). Fs is a steady state fluorescence level. F_m' is maximum fluorescence during actinic light illumination. Pulses of light (10000 μmol $m^{-2}s^{-1}$) are applied to close all RCII and estimate F_m and F_m'. qE and qI are quickly- and slowly-reversible components of NPQ. **B**. The course of NPQ development, *scenario*, showing key factors triggering and regulating the process (for more details see the text). The formula for the minimum component requirement for NPQ is shown under the diagram.

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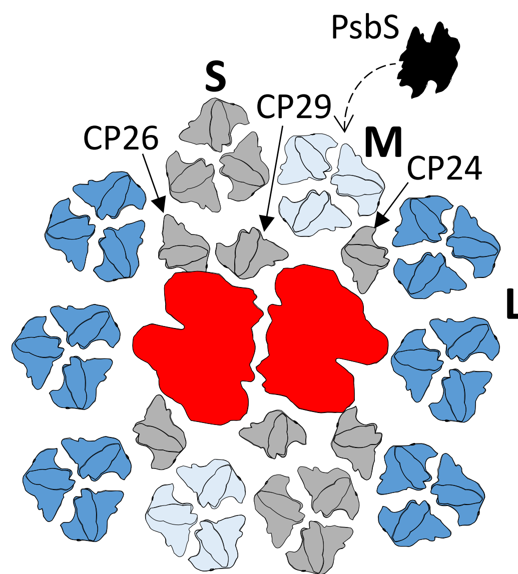

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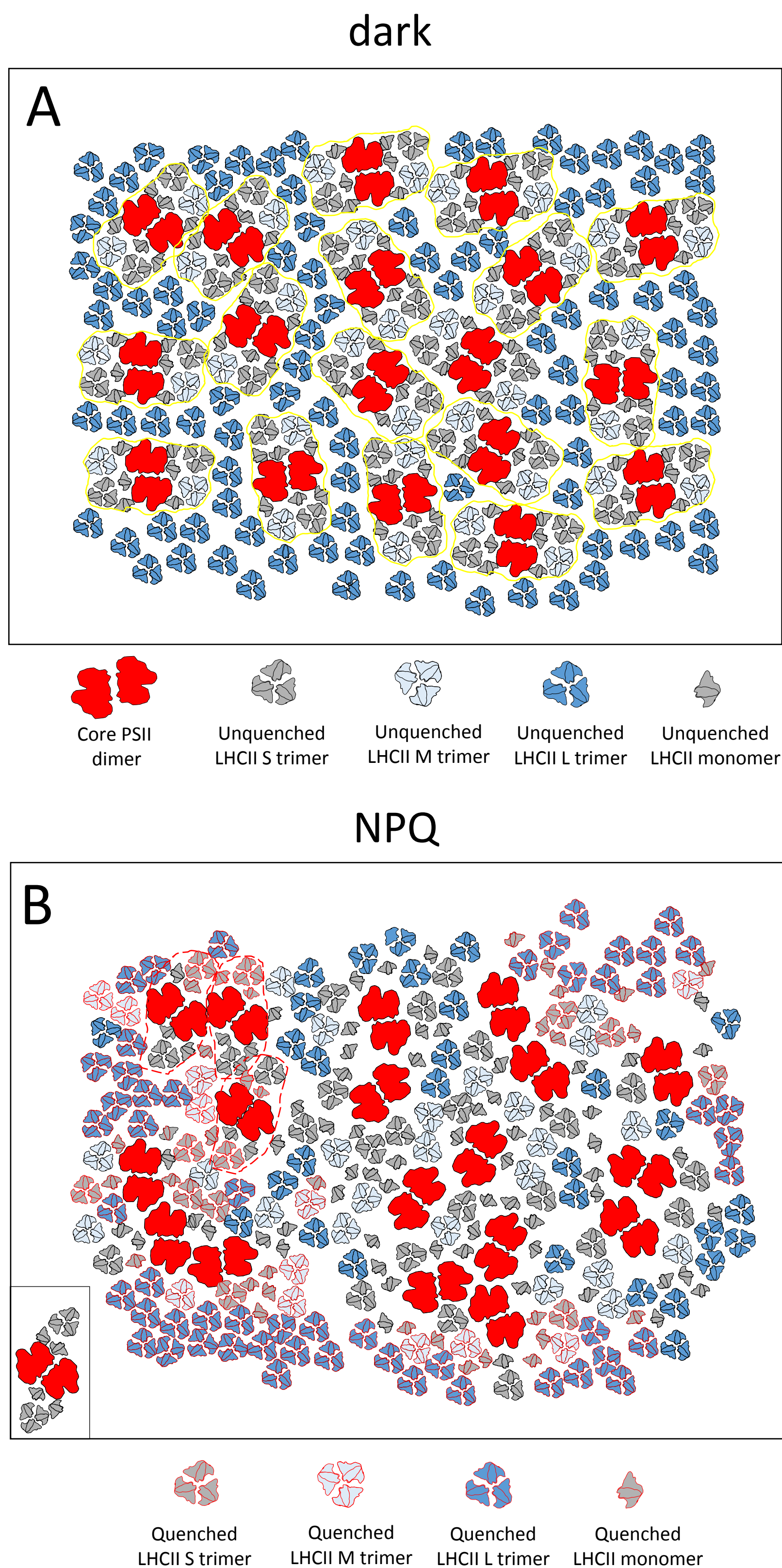

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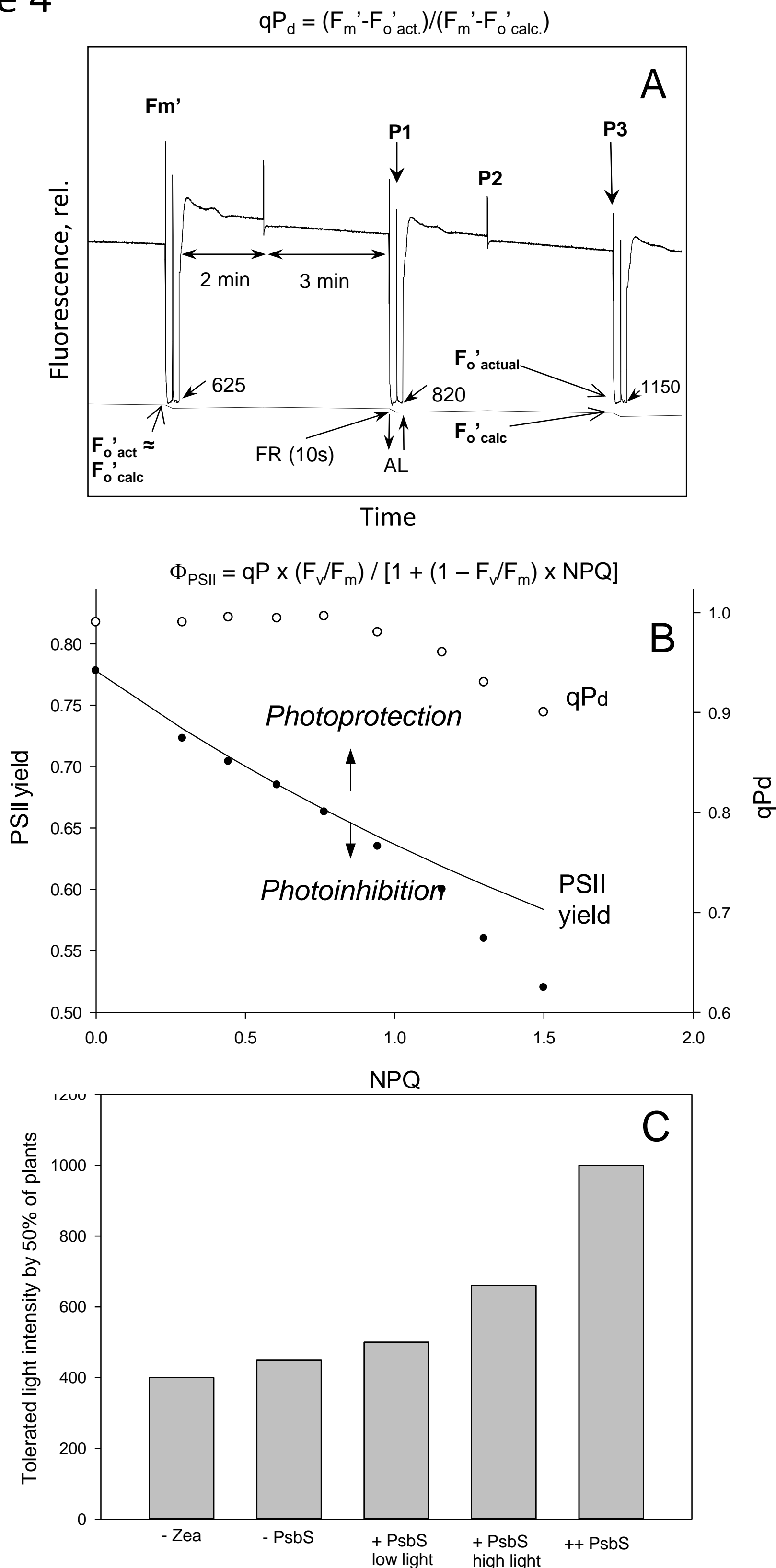
Figure 4



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