



## Fluctuating light takes crop photosynthesis on a rollercoaster ride

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1 **Short title:** Update review on dynamic photosynthesis in crops

2

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8 **Title:**

9 Update on Crop Photosynthesis in Fluctuating Light Intensities

10 **Fluctuating light takes crop photosynthesis on a rollercoaster ride**

11

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18

19 **Summary:** Crops are regularly exposed to frequent irradiance fluctuations, which  
20 decrease their integrated CO<sub>2</sub> assimilation and affect their phenotype

21

22 **Author contributions:** E.K., A.M. and J.H. co-wrote the article. E.K. and A.M.  
23 performed sunfleck measurements. A.M. performed data analysis of sunflecks and  
24 cloudflecks

25

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32 The environment of the natural world in which plants live, have evolved, and within  
33 which photosynthesis operates, is one characterised by change. The time scales over  
34 which change occurs can range from seconds (or less) all the way to the geological  
35 scale. All of these changes are relevant for understanding plants and the vegetation  
36 they create. In this update review we will focus on how photosynthesis responds to  
37 fluctuations in irradiance with time constants up to the range of tens of minutes.  
38 Photosynthesis is a highly regulated process, in which photochemistry as well as the  
39 electron and proton transport processes leading to the formation of ATP and reducing  
40 power (reduced ferredoxin and NADPH) need to be coordinated with the activity of  
41 metabolic processes (Foyer and Harbinson, 1994). Light, temperature, the supply of the  
42 predominant substrate for photosynthetic metabolism ( $\text{CO}_2$ ), and the demand for the  
43 products of photosynthetic metabolism are all factors that are involved in short-term  
44 alterations of steady-state photosynthetic activity. The coordinated regulation of  
45 metabolism with the formation of the metabolic driving forces of ATP and reducing  
46 power is subject to various constraints that limit the freedom of response of the system.  
47 Of these constraints, the most prominent are the need to limit the rate of formation of  
48 active oxygen species by limiting the lifetime of excited states of chlorophyll a and the  
49 potential of the driving forces for electron transport (Foyer and Harbinson, 1994; Foyer  
50 et al., 2012; Rutherford et al., 2012; Murchie and Harbinson, 2014; Liu and Last, 2017);  
51 limiting the decrease of lumen pH to avoid damaging the oxygen evolving complex of  
52 PSII (Krieger and Weis, 1993), and adjusting stomatal conductance ( $g_s$ ) to optimise  
53 photosynthetic water-use efficiency (Lawson and Blatt, 2014).

54 The processes that regulate electron and proton transport, enzyme activation and  $\text{CO}_2$   
55 diffusion into the chloroplast under steady-state conditions also react in a dynamic and  
56 highly concerted manner to changes in irradiance, balancing between light use and  
57 photoprotection. This overview of the physiological control underlying dynamic  
58 photosynthesis is specific to the  $\text{C}_3$  photosynthetic pathway. Much less is known about  
59 the dynamic regulation of the  $\text{C}_4$  and CAM pathways, though given their  $\text{C}_3$  heritage we  
60 expect that they share much of the regulation of  $\text{C}_3$  photosynthesis. We note here that  
61 in comparison to  $\text{C}_3$  plants, some  $\text{C}_4$  species, including maize, show a very slow

62 photosynthetic induction after an irradiance increase (Furbank and Walker, 1985; Chen  
63 et al., 2013) and that this phenomenon deserves further attention.

64 If we grant that the regulation of photosynthesis at steady-state is in some way optimal,  
65 and represents an ideal balance between light-use efficiency and photoprotection, and  
66 an ideal balance between CO<sub>2</sub> diffusion into the leaf with the loss of water vapour from  
67 the leaf, then significance to photosynthesis under a fluctuating irradiance is the loss of  
68 optimal regulation. The faster the response to change, the less is the loss of efficiency,  
69 whether that be in terms of water use efficiency (WUE) or light use efficiency.

70 Since its birth one hundred years ago (Osterhout and Haas, 1918), research on the  
71 dynamics of photosynthesis and the limitations it produces in a fluctuating irradiance  
72 has come a long way (Box 1). While it has been apparent for some time that sunflecks  
73 occur in all kinds of canopies (e.g. Pearcy et al., 1990), research on sunfleck  
74 photosynthesis was until recently driven by its importance for forest understory shrubs  
75 and trees. The ecophysiological importance of sunflecks, photosynthetic responses and  
76 plant growth focussed on the importance of these responses for understory plants  
77 growing in shade (Percy et al., 1996; Way and Percy, 2012). Attention has more  
78 recently shifted to crop stands grown in full sunlight and the fact that the slow response  
79 of photosynthesis to sunflecks is a limitation to crop growth in the field (e.g. Lawson et  
80 al., 2012; Carmo-Silva et al., 2015). The importance of improved photosynthesis as a  
81 route to improving crop yields (Ort et al., 2015) has given new impetus into better  
82 understanding the physiology and the genetics of photosynthetic responses to  
83 fluctuating light, and improving upon them (e.g. Kromdijk et al., 2016).

### **BOX 1. Implications of Recent Advances for Research**

Compared to a constant irradiance with the same average value, fluctuating irradiance negatively impacts time-integrated photosynthesis, growth rates, and fitness (Külheim et al., 2002; Poorter et al., 2016; Vialet-Chabrand et al., 2017a). This decrease is partly caused by decreasing photosynthetic quantum yield with increasing irradiance (as high irradiance is part of the fluctuating light regime) and by the dynamic regulation of electron transport, enzyme activation, and CO<sub>2</sub> diffusion (Kaiser et al., 2015). Decreased performance in fluctuating irradiance implies that plants grown under constant environmental conditions tend to have a different morphology and biomass compared to natural conditions (Poorter et al., 2016). Additionally, photosynthetic processes that may not be important in a constant environment (such as commonly used in controlled environment rooms) may acquire a new relevance under more natural, fluctuating conditions, as recently shown for mutants impaired in PSII repair (Liu and Last, 2017). Indeed, fluctuating irradiance has revealed many phenotypes of Arabidopsis that are not detectable under constant conditions (Cruz et al., 2016). Growing plants under more natural conditions will greatly facilitate the translation of results from the lab to the field.

Acclimation of photosynthesis to fluctuating irradiance has been reported, at least for Arabidopsis, including thinner leaves with higher nitrogen concentration (Vialet-Chabrand et al., 2017a), upregulation of electron transport (Alter et al., 2012; Vialet-Chabrand et al., 2017a), and photoprotection (Alter et al., 2012). These responses result in higher rates of photosynthesis and growth rates under fluctuating environments compared to nonacclimated leaves (Leakey et al., 2003; Athanasiou et al., 2010; Vialet-Chabrand et al., 2017a). This implies that studies on dynamic photosynthesis using plants grown under constant irradiance could underestimate their capacity to respond to fluctuations due to a lack of acclimation.

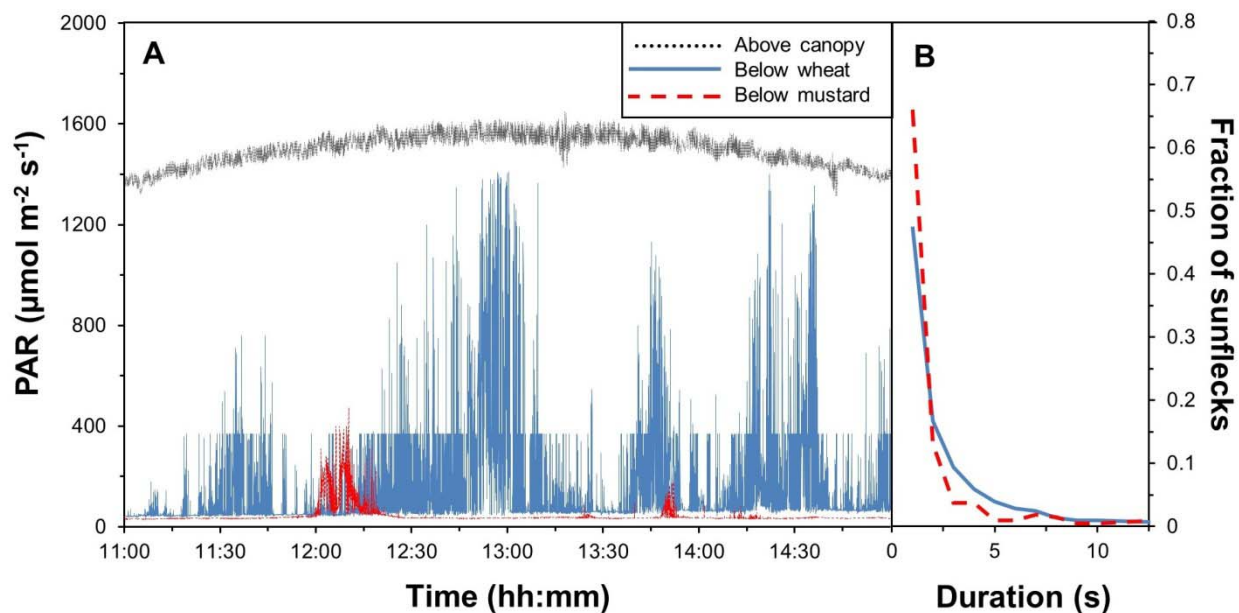
When measuring dynamic responses of photosynthesis to changes in irradiance at the leaf level, it is important to maintain a similar level of illumination for the whole plant. Recent studies suggest that the rate of photosynthetic induction is affected by systemic signals at the plant level (Hou et al., 2015; Guo et al., 2016). Guo et al. (2016) proposed that the signal is auxin generated by the apex in response to red irradiance and that the response in leaves is mediated by accumulation of H<sub>2</sub>O<sub>2</sub> and consequent activation of CEF (Strand et al., 2015).

## 84 **Fluctuating irradiance in canopies**

### 85 *i) Sunflecks*

86 Most studies have focused on irradiance fluctuations at the bottom of canopies or in  
87 forest understories. In these situations, a shade environment with little diurnal variation  
88 prevails, and most incoming irradiance arrives due to transmission and scattering by  
89 leaves higher up in the canopy. Also, gaps in the canopy, which move in response to  
90 wind, allow brief but significant increases in irradiance (Percy, 1990). Smith and Berry  
91 (2013) proposed a detailed classification of these fluctuations, resulting in the terms

92 sunfleck (<8 minutes and peak irradiance lower than above-canopy irradiance), sun  
93 patch (>8 minutes), sun gap (>60 minutes) and clearing (>120 minutes).  
94 In addition to the length of the fluctuation, classifying a fluctuation as a sunfleck  
95 depends on the irradiance increasing above a specific threshold during the fluctuation.  
96 Often, fixed thresholds are used, but their values vary greatly ( $60\text{-}300\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ ;  
97 Pearcy, 1983; Tang et al., 1988; Pearcy et al., 1990; Roden and Pearcy, 1993;  
98 Barradas et al., 1998; Naumburg and Ellsworth, 2002). Thresholds may be adjusted  
99 depending on canopy structure, position within the canopy where measurements are  
100 taken and angle of measurement (Pearcy, 1990; Barradas et al., 1998). An alternative  
101 approach is to use the fraction of irradiance transmitted by the canopy instead of  
102 absolute irradiance to calculate the threshold (Barradas et al., 1998). However, this  
103 approach requires an additional measurement of irradiance above the canopy.  
104 Short-lived sunflecks with low peak irradiance are particularly abundant in the lower  
105 layers of canopies and forest understories. Pearcy et al. (1990) reported that 79% of  
106 sunflecks were  $\leq 1.6\ \text{s}$  long in a soybean (*Glycine max*) canopy, and the same  
107 distribution was reported for aspen (*Populus tremuloides*; Roden and Pearcy, 1993).  
108 Peressotti et al. (2001) reported that most sunflecks in wheat (*Triticum aestivum*), maize  
109 (*Zea mays*) and sunflower (*Helianthus annuus*) were  $\leq 1\ \text{s}$  long. Most sunflecks in bean  
110 (*Phaseolus vulgaris*) and rice (*Oryza sativa*) canopies were  $\leq 5.0\ \text{s}$  long (Barradas et al.,  
111 1998; Nishimura et al., 1998). These results agree with our measurements in durum  
112 wheat (*T. durum*) and white mustard (*Sinapis alba*; Fig. 1).  
113 Canopy structure is assumed to affect sunfleck distribution (Pearcy, 1990), but this has  
114 so far only been systematically tested by Peressotti et al. (2001) who compared  
115 sunflecks in different crop canopies and found only small differences between wheat,  
116 maize and sunflower. Our data, on the other hand, revealed bigger differences between  
117 crops despite similar meteorological conditions (Fig. 1): in durum wheat, 2606 sunflecks  
118 (83% of total irradiance) were detected within six hours, while only 213 (22%) were  
119 observed in white mustard (Fig 1A). In white mustard, sunflecks tended to be shorter  
120 and weaker, though for both crops most sunflecks were  $< 5\ \text{s}$  long (Fig. 1B). For most  
121 sunflecks, the average irradiance increase was  $< 350\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$  and peak irradiance  
122 was always below the irradiance measured above the canopy (Fig. 1A). However, a



123 large proportion of short sunflecks may not always contribute much to integrated  
 124 irradiance, partly because of their short duration and partly because of their low peak  
 125 irradiance (Percy, 1990). For example, in a soybean canopy, the peak irradiance in  
 126 sunflecks less than 1.6 s long was two to three times less than that of longer sunflecks,  
 127 and contributed only 6.7% of the total irradiance, while sunflecks lasting up to 10 s  
 128 contributed only 33% of the total irradiance (Percy et al. 1990).

129 Sunflecks can also be caused by the penumbra effect (Smith et al., 1989), a “soft  
 130 shadow” that occurs when a light source is partially blocked. In canopies, a penumbra is  
 131 produced by small canopy elements that partially obscure the solar disc as viewed from  
 132 a lower leaf. When combined with rapid leaf movements, the penumbra causes  
 133 sunflecks on leaves that are otherwise shaded. Due to the penumbra effect, it was  
 134 estimated that a gap in a canopy must have an angular size greater than  $0.5^\circ$  in order  
 135 for the sunfleck to reach full solar irradiance (Percy, 1990). The frequent, short  
 136 sunflecks discussed above are probably caused by penumbra (Smith and Berry, 2013)  
 137 and contribute to a substantial fraction of total irradiance in forest understories (Percy,  
 138 1990).

139 Due to wind-induced movements the structure of canopies is not static. Wind has two  
 140 effects: (i) movement of the whole plant or “swaying” (de Langre, 2008; Tadrict et al.,  
 141 2014; Burgess et al., 2016) and (ii) fluttering of single leaves, especially in trees (Roden

142 and Pearcy, 1993; Roden, 2003; de Langre, 2008). Plant swaying alters the spatial  
143 distribution of canopy gaps, and the exposure of leaves to these gaps, adding sunflecks  
144 and shadeflecks to the baseline irradiance that would occur in the absence of wind.  
145 Fluttering allows individual leaves to have a more uniform diurnal distribution of  
146 absorbed irradiance and to maintain a high photosynthetic induction state (Roden,  
147 2003). Fluttering further increases the number of sunflecks at the bottom of the canopy  
148 (Roden and Pearcy, 1993). Leaves flutter at a wide frequency range (1-100Hz; Roden  
149 and Pearcy, 1993; Roden, 2003; de Langre, 2008) whereas plant swaying occurs at  
150 0.1-10 Hz (de Langre, 2008; Burgess et al., 2016). Wind thus introduces rapid  
151 irradiance fluctuations in the entire canopy. Without wind, sunflecks and shadeflecks  
152 can still be caused by gaps in the canopy structure and by penumbra, but high wind  
153 speeds have been correlated with increasing irradiance fluctuations (Tang et al., 1988).

154

155 *ii) Shadeflecks*

156 As long as the total irradiance intercepted by a canopy remains the same, the existence  
157 of sunflecks necessitates the existence of shadeflecks (i.e., transient excursions below  
158 a baseline that is the average irradiance (Pearcy, 1990; Pearcy et al., 1990; Barradas et  
159 al., 1998; Lawson et al., 2012). It is important to distinguish between sunflecks and  
160 shadeflecks, as the dynamic responses of photosynthesis are different for increasing  
161 and decreasing irradiance and involve different potentially limiting processes (see  
162 below). A shadefleck should not be seen as a “period between sunflecks”, but rather as  
163 a brief period of low irradiance with respect to a baseline of intermediate or high  
164 irradiance, which tends to occur in the top and middle layers of a canopy. A special type  
165 of shadefleck is a cloudfleck (Box 2; Knapp and Smith, 1988).



## 166 **The regulation of photosynthesis in fluctuating irradiance**

167

### 168 *i) Responses and regulation of electron and proton transport*

169 The shorter term physiological responses of photosynthesis begin with light-driven  
170 redox state and pH changes occurring within and close to the thylakoid membranes.  
171 Photochemistry, the primary chemical event of photosynthesis, provides the redox  
172 driving forces for electron and proton transport, which result in the feed-forward  
173 activation of metabolic processes that produce CO<sub>2</sub> assimilation. Metabolism, when  
174 limiting, will down-regulate electron transport via feed-back mechanisms. This balance  
175 between feed-forward and feed-back regulation is at the heart of photosynthetic  
176 regulation, including responses to changing irradiance.

177 In a leaf initially subject to a sub-saturating irradiance, a sudden increase in irradiance  
178 results in an increase in the rate of photochemistry and then an increase in the rate of  
179 linear electron flow (LEF) from water to ferredoxin within milliseconds. For every  
180 electron passing along the LEF, three protons are translocated from the stroma into the  
181 thylakoid lumen, which changes the electric ( $\Delta\psi$ ) and pH ( $\Delta\text{pH}$ ) gradients across the  
182 thylakoid membrane. Together,  $\Delta\psi$  and  $\Delta\text{pH}$  constitute the proton motive force (pmf).  
183 The pmf is further modulated by cyclic electron flux (CEF) around photosystem I (PSI;  
184 Strand et al., 2015; Shikanai and Yamamoto, 2017) and alternative non-cyclic electron  
185 flux (ANCEF; Asada, 2000; Bloom et al., 2002), making the pmf more flexible to  
186 changing metabolic demands for ATP and NADPH (Kramer and Evans, 2011) and  
187 adjustments in lumen pH resulting in regulatory responses of thylakoid electron  
188 transport and non-photochemical quenching (NPQ). The acidification of the lumen upon  
189 increases in irradiance partially drives the fastest component of NPQ (Fig. 2), qE. This  
190 form of NPQ acts to reduce the lifetime of excited singlet states of chlorophyll a ( $^1\text{chl}^*$ ) in  
191 PSII. When the rate of PSII excitation and  $^1\text{chl}^*$  formation exceeds the potential for  
192 photochemical dissipation of  $^1\text{chl}^*$  via electron transport (e.g. during irradiance  
193 increases), the lifetime of  $^1\text{chl}^*$  in PSII tends to increase, potentially increasing the rate  
194 of formation of triplet chlorophylls in the PSII pigment bed and reaction centre, resulting  
195 in the formation of reactive singlet oxygen (Müller et al., 2001). Upregulating NPQ  
196 activity counteracts the tendency for increased  $^1\text{chl}^*$  lifetime and moderates the

## BOX 2. Cloudflecks

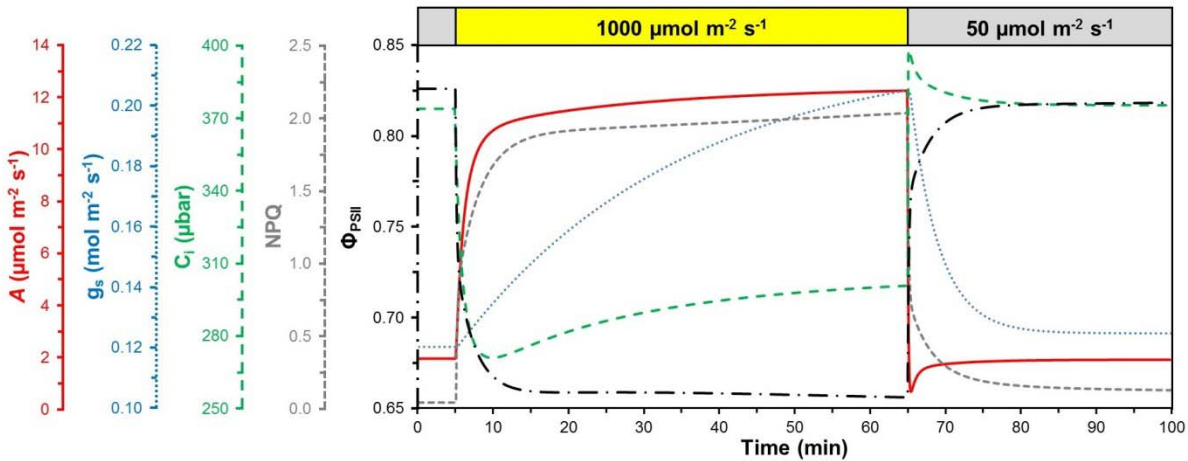
The effects of dynamic shading by clouds are relatively understudied compared to sunflecks and shade flecks within canopies. Analogous to sunflecks, we introduce the term cloudfleck, which denotes the fluctuation of irradiance by a cloud with respect to a clear-sky situation. To our knowledge, this term has not been used previously. The effect of cloudflecks depends on their frequency, duration, and intensity. Knapp and Smith (1988) observed that cloudflecks were on average 3.8 min long, with 9.9-min-long intervals between cloudflecks, during the summer of 1986 at a subalpine meadow (41 °N, 105°W, 2600 m above sea level), averaging 35 cloudflecks per day. Therefore, cloudflecks were generally an order of magnitude longer than sunflecks, which is sufficiently long to affect photosynthetic induction states.

To verify whether such a distribution of cloudflecks applies to other locations, we analyzed 5 years of solar irradiance data that had been gathered once per minute at a meteorological station in Veenkampen, The

Netherlands (51.97 °N, 5.67 °E, 12 m above sea level). The distribution of cloudfleck duration was asymmetrical, with a median duration of 3 min, close to the value reported by Knapp and Smith (1988), but 20% of the cloudflecks were longer than 10 min. On average, there were 15.8 cloudflecks per day (range: 1–81 cloudflecks). The distribution of the time intervals between consecutive cloudflecks was similar to the distribution of cloudfleck duration, with a median of 4 min between consecutive cloudflecks (80% of the cases below 17 minutes), indicating that they tend to be clustered in time. On average, cloudflecks reduced irradiance by 370  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (31% reduction compared to a clear sky). A small fraction (7.9%) actually increased irradiance (<100  $\text{W m}^{-2}$  enhancement). Clouds can locally increase irradiance by scattering light from the side of the cloud onto an area on the ground, thereby adding to the direct irradiance incident on that area (Smith and Berry, 2013).

197 increase in singlet oxygen formation (Müller et al., 2001). The protein PsbS senses the  
198 low pH in the lumen (Li et al., 2000; 2002) and may mediate conformational changes in  
199 trimeric LHCII antenna complexes that allow the LHC to more efficiently dissipate  
200 excitons formed in PSII as heat (Ruban, 2016). The presence of the carotenoid  
201 zeaxanthin further amplifies qE (Niyogi et al., 1998). Zeaxanthin is formed from  
202 violaxanthin via antheraxanthin by the enzyme violaxanthin deepoxidase upon  
203 acidification of the thylakoid lumen, and is reconverted to violaxanthin as lumen pH  
204 increases (Demmig-Adams, 1990).

205 Since after drops in irradiance NPQ relaxes only slowly (Fig. 2), LEF is transiently  
206 limited by an overprotected and quenched PSII, potentially limiting photosynthesis (Zhu  
207 et al., 2004). In *Arabidopsis thaliana*, the  $\Delta\text{pH}$  component of the pmf was increased in  
208 plants overexpressing K<sup>+</sup> efflux antiporter (KEA3) proteins, accelerating NPQ induction  
209 and relaxation kinetics and diminishing transient reductions in LEF and CO<sub>2</sub> assimilation



210 upon transitions from high to low irradiance (Armbruster et al., 2014). In tobacco  
 211 (*Nicotinia tabacum*), the simultaneous overexpression of PsbS, violaxanthin de-  
 212 epoxidase and zeaxanthin epoxidase increased the rate of NPQ relaxation, which  
 213 subsequently increased growth in the field by 14-20% (Kromdijk et al., 2016). These  
 214 results prove that slow NPQ relaxation is an important limitation in naturally fluctuating  
 215 irradiance. Further, the results of Kromdijk et al. (2016) are a powerful testament to the  
 216 fact that irradiance fluctuations strongly diminish growth in the field; they provide a  
 217 glimpse into growth accelerations that would be possible if the rate constants of other  
 218 processes responding to fluctuating irradiance were enhanced.

219

220 *ii) Chloroplast movement*

221 Another potential limitation to electron transport under fluctuating irradiance is the  
 222 movement of chloroplasts in response to blue irradiance. At high blue irradiance,  
 223 chloroplasts move towards the anticlinal walls of the mesophyll cells while at low blue  
 224 irradiance, they move to the periclinal walls (Haupt and Scheuerlein, 1990), resulting in  
 225 decreases and increases of absorptance, respectively (Gorton et al., 2003; Williams et  
 226 al., 2003; Tholen et al., 2008; Loreto et al., 2009). In leaves of some species,  
 227 chloroplast movements can change irradiance absorptance by >10%, although in other  
 228 species the effect is <1% (Davis et al., 2011). The reduction in absorptance in high  
 229 irradiance has a photoprotective effect and significant reductions in photoinhibition have  
 230 been demonstrated for *A. thaliana* (Kasahara et al., 2002; Davis and Hangarter, 2012).

### BOX 3. How Flexible Is Mesophyll Conductance in Variable Irradiance?

In addition to stomatal conductance, mesophyll conductance ( $g_m$ ) places a diffusional limitation on photosynthesis. Whether or not  $g_m$  changes during photosynthetic induction is unclear and under discussion in recent years (Campany et al., 2016; Kaiser et al., 2017; Wachendorf and Küppers, 2017). Changes in  $g_m$  within minutes after changes in irradiance have been described (Flexas et al., 2008; Tholen et al., 2008; Campany et al., 2016), though some responses may be artefacts of the method of estimation used (Tholen et al., 2012; Yin and Struik, 2017).

Which mechanisms could contribute to the apparent flexibility in  $g_m$ ? Inside the leaf,  $CO_2$  diffuses through gaseous, liquid, and protein/lipid (i.e. cell wall and membrane) barriers before reaching the site of carboxylation (Flexas et al., 2012; Kaldenhoff, 2012). Anatomical properties, such as the thickness and porosity of cell walls and chloroplast envelope, will be fixed in the short term. The activity of carbonic anhydrase could

change quickly, but its effects on  $g_m$  remain doubtful (Price et al., 1994; Kaldenhoff, 2012). Two other factors could affect  $g_m$  quickly: chloroplast movement (Williams et al., 2003) and changes in aquaporin activity (Flexas et al., 2006; Uehlein et al., 2008). Chloroplast movement is induced by blue light and can change the surface area of chloroplasts appressed to the cell membrane and thus close to leaf internal air spaces, which can affect  $g_m$  within minutes (Tholen et al., 2008; Loreto et al., 2009; Gorton et al., 2003). Aquaporins are membrane-bound proteins that can facilitate diffusion of small molecules (Kaldenhoff, 2012). There is some experimental evidence (Otto et al., 2010) to suggest that aquaporin permeability to  $CO_2$  diffusion can be triggered within seconds. Altogether,  $g_m$  may adjust rapidly to changes in irradiance, but challenges remain in the interpretation of experimental results. Also, importantly, it is unknown to what extent a variable  $g_m$  could place an additional limitation on photosynthesis to the limitations that have already been described.

231 Furthermore, chloroplast movements alter the area of chloroplasts exposed to the  
232 intercellular spaces, changing mesophyll conductance ( $g_m$ ). Importantly, chloroplasts  
233 move within minutes (Brugnoli and Björkman, 1992; Dutta et al., 2015; Łabuz et al.,  
234 2015), so the effects of their movement on absorptance and  $g_m$  (Box 3) should be  
235 relevant under naturally fluctuating irradiance. In particular, slow chloroplast movement  
236 towards the low irradiance position (time constants of 6-12 minutes; Davis and  
237 Hangarter, 2012; Łabuz et al., 2015), which lead to increased absorptance, would  
238 transiently decrease absorptance after drops in irradiance, thus limiting electron  
239 transport and photosynthesis (i.e., similar to the effect of slow qE relaxation, see  
240 above). However, experimental evidence of this possible limitation is currently lacking.

241

242 *iii) Enzyme activation and metabolite turnover*

243 The activity of several key enzymes in the Calvin Benson cycle (CBC) is regulated in an  
244 irradiance-dependent manner, much of which depends on the thioredoxin (TRX) system  
245 (Geigenberger et al., 2017). There is a multitude of TRX types and isoforms. For  
246 example, *A. thaliana* chloroplasts contain 10 different TRX isoforms (Michelet et al.,  
247 2013). Chloroplastic TRXs may be reduced by ferredoxin-dependent or NADPH-  
248 dependent thioredoxin reductases (Nikkanen et al., 2016; Thormählen et al., 2017). In  
249 the chloroplast, *f*-type TRXs control the activation state of fructose-1,6-bisphosphatase  
250 (FBPase), sedoheptulose-1,7-bisphosphatase (SBPase) and Rubisco activase (Rca;  
251 Michelet et al., 2013; Naranjo et al., 2016). While oxidized FBPase maintains a basal  
252 activity of 20-30%, the oxidized form of SBPase is completely inactive (Michelet et al.,  
253 2013). In *Pisum sativum*, the activities of phosphoribulokinase (PRK) and  
254 glyceraldehyde-3-phosphate dehydrogenase (GAPDH) are controlled by the redox-  
255 regulated protein CP12, which binds the enzymes together in low irradiance and  
256 thereby inactivates them even if they are reduced (i.e. active; Howard et al., 2008).  
257 However, this type of regulation by CP12 is not universal as in several species, the  
258 complex formed by CP12, GAPDH and PRK was mostly absent in darkness or the  
259 enzymes existed both in the bound and free form (Howard et al., 2011). Apart from the  
260 action of CP12, PRK activity is also regulated by TRX *m* and *f* (Schürmann and  
261 Buchanan, 2008).

262 Within the first minute after a switch from low to high irradiance, SBPase, FBPase and  
263 PRK are believed to limit photosynthesis via the slow regeneration of RuBP  
264 (Sassenrath-Cole and Pearcy, 1992; 1994; Sassenrath-Cole et al., 1994; Pearcy et al.,  
265 1996). These enzymes activate and deactivate quickly, with time constants ( $\tau$ ) of ~1-3  
266 minutes for activation and ~2-4 minutes for deactivation (Table S1). Compared to  
267 limitation by either Rubisco or  $g_s$  (see below), which often (co-) limit photosynthetic  
268 induction for 10-60 minutes, the limitation due to activation of SBPase, FBPase and  
269 PRK appears negligible but is relatively understudied. Due to their relatively quick  
270 deactivation in low irradiance, it may be that in the field the activation states of these  
271 enzymes are a stronger limitation of CO<sub>2</sub> assimilation than Rubisco or  $g_s$  (Pearcy et al.,  
272 1996), as the majority of sunflecks in canopies are short and narrowly spaced (see  
273 above). More research into this potentially large limitation is needed, e.g. by using

274 plants with increased concentrations of CBC enzymes (e.g. Simkin et al., 2015), as well  
275 as “always-active” FBPase and PRK (Nikkanen et al., 2016).

276 The dependence of the activation state of Rubisco upon irradiance resembles that of a  
277 irradiance response curve of photosynthesis (Lan et al., 1992). In low irradiance, 30-  
278 50% of the total pool of Rubisco is active (Percy, 1988; Lan et al., 1992; Carmo-Silva  
279 and Salvucci, 2013). The remainder is activated with a  $\tau$  of 3-5 minutes after switching  
280 to high irradiance (Percy, 1988; Woodrow and Mott, 1989; Kaiser et al., 2016; Taylor  
281 and Long, 2017). Activation of Rubisco active sites requires the binding of  $Mg^{2+}$  and  
282  $CO_2$  to form a catalytically competent (carbamylated) enzyme, after which RuBP and  
283 another  $CO_2$  or  $O_2$  molecule have to bind for either carboxylation or oxygenation to  
284 occur (Tcherkez, 2013). Rubisco activates more quickly at higher  $CO_2$  partial pressures,  
285 both *in folio* (Kaiser et al., 2017) and *in vitro* (Woodrow et al., 1996), a phenomenon that  
286 is not well understood and whose kinetics cannot be explained by carbamylation.

287 Several types of sugar phosphates can bind to Rubisco catalytic sites and block their  
288 complete activation (Bracher et al., 2017). Removal of these inhibitors requires the  
289 action of Rca (Salvucci et al., 1985), whose activity depends on thioredoxin and ATP.  
290 Rca light-activates with a  $\tau$  of ~4 minutes in spinach (*Spinacia oleracea*; Lan et al.,  
291 1992). In *A. thaliana*, Rca is present in two isoforms of which the larger,  $\alpha$ -isoform is  
292 redox-regulated and the smaller,  $\beta$ -isoform is regulated by the  $\alpha$ -isoform (Zhang and  
293 Portis, 1999; Zhang et al., 2002). In transgenic plants only containing the  $\beta$ -isoform,  
294 photosynthetic induction after a transition from low to high irradiance was faster than in  
295 the wildtype, as Rca activity was constitutively high and independent of irradiance  
296 (Carmo-Silva and Salvucci, 2013; Kaiser et al., 2016). Modifying the composition of Rca  
297 (Prins et al., 2016) or its concentration, either transgenically (Yamori et al., 2012) or  
298 through classical breeding (Martínez-Barajas et al., 1997), might enhance  
299 photosynthesis and growth in fluctuating irradiance (Carmo-Silva et al., 2015).

300 After the fixation of  $CO_2$  into RuBP, the triose phosphates may be transported out of the  
301 chloroplast and converted into sugars, after which the phosphate is transported back  
302 into the chloroplast and recycled via the chloroplast ATPase and the CBC (Stitt et al.,  
303 2010). The enzyme sucrose phosphate synthase can transiently limit photosynthesis  
304 after a transition from low to high irradiance, but this has so far only been shown in



305 elevated CO<sub>2</sub> (Stitt and Grosse, 1988). After decreases in irradiance, pools of CBC  
306 intermediates can transiently enhance photosynthesis (“post-illumination CO<sub>2</sub> fixation”),  
307 while the turnover of glycine in the photorespiratory pathway may be visible as a  
308 transient decrease in photosynthesis (“post-illumination CO<sub>2</sub> burst”). After very short ( $\leq 1$   
309 s) sunflecks, post-illumination CO<sub>2</sub> fixation enhances total sunfleck carbon gain greatly,  
310 such that the CO<sub>2</sub> fixed directly after a sunfleck exceeds the CO<sub>2</sub> fixed during the  
311 sunfleck (Pons and Pearcy, 1992). The negative effect of post-illumination CO<sub>2</sub> fixation  
312 on the carbon balance of a sunfleck seems less pronounced in comparison (Leahey et  
313 al., 2002). For more details on both phenomena, see Kaiser et al. (2015).

314

315 *vi) CO<sub>2</sub> diffusion into the chloroplast*

316 Diffusion of CO<sub>2</sub> to the site of carboxylation is mediated by  $g_s$  and  $g_m$ . Stomata tend to  
317 decrease their aperture in low irradiance, when evaporative demand and demand for  
318 CO<sub>2</sub> diffusion are small. Vast differences exist between species (15-25 fold) for steady-  
319 state  $g_s$  in low and high irradiance (e.g. McAusland et al., 2016), for rates of stomatal  
320 opening after irradiance increases ( $\tau = 4-29$  minutes) and for rates of stomatal closure  
321 after irradiance decreases ( $\tau = 6-18$  minutes; Vico et al., 2011). Often, initial  $g_s$  after a  
322 switch from low to high irradiance is small enough, and stomatal opening is slow  
323 enough (Fig. 2), to transiently limit photosynthesis (McAusland et al., 2016; Wachendorf  
324 and Küppers, 2017). Manipulating  $g_s$  to respond more quickly to irradiance could greatly  
325 enhance photosynthesis and WUE in fluctuating irradiance (Lawson and Blatt, 2014;  
326 Vialet-Chabrand et al., 2017b). Mesophyll conductance will further affect the CO<sub>2</sub>  
327 available for photosynthesis (Tholen et al., 2012; Yin and Struik, 2017), and steady-  
328 state  $g_m$  affects CO<sub>2</sub> diffusion as strongly as does  $g_s$  (Flexas et al., 2008; 2012).  
329 Mesophyll conductance may be variable under fluctuating irradiance (Campany et al.,  
330 2016), as some of the processes determining  $g_m$  are flexible (Price et al., 1994; Flexas  
331 et al., 2006; Uehlein et al., 2008; Otto et al., 2010; Kaldenhoff, 2012). The possibility  
332 that transient  $g_m$  changes limit photosynthesis in fluctuating irradiance is discussed in  
333 Box 3.

334 Limiting CO<sub>2</sub> diffusion into the chloroplast after a switch from low to high irradiance may  
335 transiently limit photosynthesis in two ways: via a transiently low availability of the

336 substrate CO<sub>2</sub> for carboxylation, and by decreasing the rate of Rubisco activation (Mott  
337 and Woodrow, 1993). While the former limitation is visible through a concomitant  
338 increase in  $A$  and chloroplast CO<sub>2</sub> partial pressure ( $C_c$ ) along the steady-state  $A/C_c$   
339 relationship (Küppers and Schneider, 1993), the latter can be calculated by log-  
340 linearizing CO<sub>2</sub> assimilation after an increase in irradiance, after correcting for changes  
341 in  $C_i$  (Woodrow and Mott, 1989). The apparent  $\tau$  for Rubisco activation calculated from  
342 gas exchange *in folio* correlates well with Rubisco activation *in vitro* (Woodrow and  
343 Mott, 1989; Hammond et al., 1998), and with Rca concentrations (Mott and Woodrow,  
344 2000; Yamori et al., 2012). Additionally, Rubisco activation during photosynthetic  
345 induction can be approximated by “dynamic  $A/C_i$  curves” which are achieved by  
346 measuring the rate of photosynthetic induction at several  $C_i$  levels and plotting  
347 maximum rates of carboxylation ( $V_{cmax}$ ) as a function of time (Soleh et al., 2016). It was  
348 recently shown that the apparent  $\tau_{Rubisco}$  derived from dynamic  $A/C_i$  curves was in  
349 agreement with values derived using the procedure described by Woodrow and Mott  
350 (1989; Taylor and Long, 2017). Apparent  $\tau_{Rubisco}$  decreases with increases in  $C_i$  (Mott  
351 and Woodrow, 1993; Woodrow et al., 1996) and with relative air humidity (Kaiser et al.,  
352 2017) during photosynthetic induction. The latter phenomenon was caused by humidity  
353 effects in initial  $g_s$ , leading to faster depletion of  $C_c$  and transiently lower  $C_c$  after an  
354 increase in irradiance (Kaiser et al., 2017). The mechanism behind this slowing down of  
355 Rubisco activation due to lower  $C_c$  is of yet unresolved.



356 **Phenotyping for faster photosynthesis in fluctuating irradiance**

357 High throughput phenotyping for natural variation (including mutant screens, e.g. Cruz  
358 et al., 2016) gained importance following the analyses of Lawson et al. (2012; Lawson  
359 and Blatt, 2014) and Long et al. (2006). These studies highlighted the response times of  
360 photosynthesis to changing irradiance as limitations to carbon gain, including the slow  
361 response of  $g_s$  (Tinoco-Ojanguren and Pearcy, 1993), which can also diminish WUE  
362 (Lawson and Blatt, 2014), stressing their value as routes for improving assimilation.  
363 Kromdijk et al. (2016) consequently showed that improved relaxation of qE type NPQ  
364 improved tobacco yield under field conditions. While they used transgenics, the  
365 modifications used - increased amounts of PsbS, violaxanthin de-epoxidase and  
366 zeaxanthin epoxidase - could have occurred naturally. In fact, altering gene expression  
367 patterns has been a major route to improving the usefulness of plants for agriculture  
368 (Swinnen et al., 2016), either through natural variation in the gene pool of natural  
369 ancestors, or through mutations occurring during domestication. Naturally occurring  
370 variation in a trait can be used to analyse the genetic architecture of the trait, and this  
371 can be used to increase the efficiency of improving the trait by breeding. Knowing how a  
372 trait is genetically determined increases the options for its improvements by breeding  
373 beyond those emerging from the physiological or biochemical approaches of the kind  
374 used by Kromdijk et al. (2016). Variation for the kinetics of photosynthetic responses to  
375 changing irradiance is also another resource for further conventional physiological and  
376 biochemical analyses of the regulation and limitations acting on photosynthesis under  
377 these conditions.

378 If variation for a quantitative trait, such as photosynthetic responses, is identified in a  
379 genetically diverse population, and the genetic diversity has been mapped by means of  
380 e.g. single nucleotide polymorphisms, it is possible to correlate genetic with phenotypic  
381 variation (e.g. Harbinson et al., 2012; Rungrat et al., 2016) and to identify the QTL  
382 (quantitative trait loci) whose variation correlates with phenotypic variation. Different  
383 types of mapping populations can be used for QTL identification: genome-wide  
384 association study (GWAS) and linkage mapping using recombinant inbred lines. These  
385 strategies have their own advantages and disadvantages (Bergelson and Roux, 2010;  
386 Harbinson et al., 2012; Korte and Farlow, 2013; Rungrat et al., 2016). Once identified,

387 QTL are invaluable as markers for conventional plant breeding approaches, and as a  
388 starting point for identifying the causal gene for the QTL. It is obviously advantageous to  
389 maximise the chances of finding an association by including as much genetic diversity  
390 as possible in a mapping population. In the case of crop plants domestication results in  
391 a loss of genetic diversity (Doebley et al., 2006; Shi and Lai, 2015), so there is much to  
392 be gained by including field races and wild types in the construction of mapping  
393 populations or RILs. The phenotypic data required for QTL mapping requires  
394 measurements upon hundreds or thousands of individuals depending on the mapping  
395 approach adopted, the precision of the phenotyping procedure compared to the  
396 variability of the trait and the heritability of the trait. In photosynthesis, which even in  
397 stable environments can change diurnally, quick measurements are needed (Flood et  
398 al., 2016). Measuring this many plants quickly places considerable demands on the  
399 design of high-throughput systems. Currently, the measuring technologies that are best  
400 suited to automated high throughput phenotyping of plant photosynthetic traits, including  
401 those in unstable irradiance, are chlorophyll fluorescence imaging (Barbagallo et al.,  
402 2003; Furbank and Tester, 2011; Harbinson et al., 2012; Rungrat et al., 2016) and  
403 thermal imaging for measuring stomatal responses (Jones, 1999; Furbank and Tester,  
404 2011; McAusland et al., 2013). While it is based on fluorescence from PSII, chlorophyll  
405 fluorescence allows the measurement of many useful photosynthetic parameters such  
406 as the electron transport efficiency of PSII, NPQ and its components (of which qE is  
407 most commonly reported),  $F_v/F_m$ ,  $q_P$ ,  $F_v'/F_m'$  and similar parameters (Baker et al., 2007;  
408 Furbank and Tester, 2011; Harbinson et al., 2012; Murchie and Harbinson, 2014).  
409 Chlorophyll fluorescence procedures are well developed and the phenomenology and  
410 correlations of fluorescence-derived physiological parameters are well understood (e.g.  
411 Baker et al., 2007; Baker, 2008; Murchie and Harbinson, 2014). Biomass accumulation  
412 can also be used as a measure of plant fitness, and while this is not high-throughput nor  
413 specific for a photosynthetic process, it is simple to apply, requires no specific  
414 technology, and gives a useful measure of the extent to which a plant can successfully  
415 adapt to fluctuating irradiance.

416 While the technologies and procedures for phenotyping and QTL identification are  
417 promising, the application of this approach to photosynthesis is still limited, especially in

418 the case of photosynthetic responses to fluctuating irradiance. QTL for qE have been  
419 identified using low throughput phenotyping (Jung and Niyogi, 2009). van Rooijen et al.  
420 (in press) have identified a gene (*YS1*) underlying longer term responses to an  
421 irradiance change using a GWAS analysis of an *A. thaliana* mapping population (Li et  
422 al., 2010). This work demonstrates that phenotyping combined with further genetic  
423 analysis can be used for identifying QTLs and genes linked to variation in a  
424 photosynthetic trait, opening the door to a new approach to understanding  
425 photosynthetic responses to fluctuating irradiance. If a QTL can be found for a trait,  
426 such as faster responses to fluctuating light, then by implication there is an association  
427 with genetic markers. This association can be used in marker-assisted breeding to  
428 accelerate the transfer of the QTL into a genotype which lacks the trait but which has  
429 otherwise desirable properties.

## 430 **Concluding remarks**

431 Average rates of photosynthesis decrease under fluctuating irradiance when compared  
432 to a constant environment. Whereas part of this decrease is explained by the non-linear  
433 response of photosynthesis to irradiance, further decreases are the result of slow  
434 changes in enzyme activities, stomatal conductance and NPQ. Changes in mesophyll  
435 conductance and irradiance absorbance (caused by chloroplast movements) may add  
436 to these limitations, but this awaits experimental verification. Whereas much of the  
437 earlier research focused on Rubisco activity and dynamic stomatal conductance, recent  
438 experimental and modelling studies suggest other processes (and enzymes) to be  
439 limiting (Hou et al., 2014; Guo et al., 2016). Therefore, both models and experiments  
440 should widen their scope. This requires extending the toolbox of the dynamic  
441 photosynthesis experimentalist to include rapid gas exchange systems, chlorophyll  
442 fluorescence and spectroscopic techniques and the design of new measurement  
443 protocols and mathematical models to provide the necessary parameters. There is also  
444 the realization that the growth environment of plants should approximate that  
445 experienced in the field (Poorter et al., 2016). Recent developments of lighting  
446 technology (LEDs) enable this. Increasingly, plants are grown under more fluctuating  
447 conditions (Külheim et al., 2002; Leakey et al., 2003; Athanasiou et al., 2010; Alter et  
448 al., 2012; Violet-Chabrand et al., 2017a), but the complex nature of natural irradiance  
449 fluctuations and the scarcity of measurements in the field mean that to date no standard  
450 exists for defining relevant fluctuating growth conditions in the laboratory.

451 Our review of the literature indicates that the fluctuating regime strongly depends on  
452 whether fluctuations are caused by wind and gaps in the canopy (i.e., sunflecks) or by  
453 intermittent cloudiness (i.e., cloudflecks; Box 2). Whereas the former consists of  
454 fluctuations at the scale of seconds over a low irradiance background, cloudflecks are  
455 fluctuations at the scale of minutes over a high irradiance background. Furthermore, the  
456 variation across species, canopy structure and location seems to be small, but further  
457 characterization of cloudflecks and sunflecks is needed. Both fluctuating regimes are  
458 relevant to crops in the field, but the relative importance of processes limiting  
459 photosynthesis could depend on the specific irradiance pattern.

460 **Figure captions:**

461

462 **Figure 1.** Sunflecks in two crop canopies. A) Irradiance fluctuations above and below a  
463 durum wheat and white mustard canopy, logged at 1 s resolution. B) Fraction of the  
464 total number of sunflecks as a function of sunfleck duration; calculations based on data  
465 displayed in panel A. Photosynthetically active irradiance (PAR; 400-700 nm) was  
466 logged using two LI-190R quantum sensors (Li-Cor Biosciences, Lincoln, Nebraska,  
467 USA) and a LI-1400 (Li-Cor) data logger. Data were recorded 10 cm above the ground  
468 for measurements below canopies and just above canopies for 6 h (11:00-17:00) on two  
469 consecutive days (May 26 and 27, 2017) in Wageningen, the Netherlands (51.97 °N,  
470 5.67 °E, 12 m above sea level). The two days were cloudless with average wind speeds  
471 of 3.5 m s<sup>-1</sup> and 4.2 m s<sup>-1</sup>, respectively. In the absence of sunflecks, the irradiance  
472 measured below the canopy was 2.4% and 3.7% of above-canopy PAR, for white  
473 mustard and wheat, respectively, indicating full canopy closure. To detect sunflecks, a  
474 baseline was constructed by interpolating PAR values in the absence of sunflecks and  
475 defining a sunfleck as the absolute change in PAR with respect to the baseline >10  
476  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (this was larger than the measurement error).

477 **Figure 2.** Schematic depiction of dynamic reactions of leaf photosynthetic processes to  
478 irradiance fluctuations. The leaf is initially adapted to shade (50  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), then  
479 exposed to strong irradiance (1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for 60 minutes, after which it is shaded  
480 again for 35 minutes. Displayed are net photosynthesis rate ( $A$ ; red line, continuous),  
481 stomatal conductance ( $g_s$ ; blue line, dots), substomatal CO<sub>2</sub> partial pressure ( $C_i$ ; green  
482 line, long dashes), non-photochemical quenching (NPQ; grey line, short dashes) and  
483 the electron transport efficiency of photosystem II ( $\Phi_{\text{PSII}}$ ; black line, long dashes and  
484 dots). These values are representative of *Arabidopsis thaliana* Col-0, grown in climate  
485 chambers at a constant irradiance of 170  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

486 **Supplemental material**

487 **Table S1.** Time constants of irradiance-dependent activation and deactivation of  
488 FBPase, PRK, and SBPase, based on fits to published data.



## ADVANCES

- For a long time, irradiance fluctuations have been considered to be important mainly in forest understory plants. Now, it is increasingly accepted that they affect photosynthesis in all plant systems, including crops.
- Studying the regulation of processes underlying photosynthesis in fluctuating irradiance provides a key tool to improving crop photosynthesis, growth, and ultimately yield
- Enhancing the rate of NPQ relaxation after decreases in irradiance boosts photosynthesis and crop growth in the field.
- Imaging of plant photosynthetic responses to irradiance fluctuations can reveal phenotypes not visible under constant irradiance.
- High-throughput phenotyping, using chlorophyll fluorescence and/or thermography, can help identify the genetic basis for fast responses of photosynthesis and  $g_s$  to changes in irradiance



## OUTSTANDING QUESTIONS

- To what extent does the dynamic regulation of enzyme activity in the Calvin cycle (besides Rubisco) limit photosynthesis in a naturally fluctuating irradiance?
- Could a variable  $g_m$  limit photosynthesis in fluctuating irradiance?
- To what extent can chloroplast movements limit crop photosynthesis in fluctuating irradiance?
- Which factors limit photosynthesis under fluctuating irradiance in  $C_4$  and CAM plants? Do the specific mechanisms in  $C_4$  and CAM pathways increase the efficiency at which photosynthesis responds to fluctuating irradiance?
- How does plant morphology affect the frequency and intensity of sunflecks in canopies?

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