A mechanistic view of the reduction in photosynthetic protein abundance under diurnal light fluctuation

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Leaves adapted to diurnal fluctuating light (FL) tend to have reduced photosynthetic parameters in comparison with those grown under constant light but intercepting the same daily photon integral (DPI). This reduction may result from a non-linear relationship between photosynthetic protein synthesis rate (PPSR) and incident photosynthetically active radiation (PAR). Models incorporating the PPSR–PAR relationship have quantitatively predicted the effects of FL reported in the literature. Further simulations suggest that the degree of this reduction varies with the FL pattern, DPI level and parameters describing the PPSR–PAR relationship.

Obtaining an understanding of the physiological responses of the plant to a FL regime has gained increasing attention in the past few years since FL reflects a more realistic situation for plants growing under natural conditions (Kaiser et al., 2018; Matsubara, 2018; Burgess et al., 2019). By hypothesizing that photosynthetic capacity (\(A_{\text{max}}\)) is determined by a mechanism leading towards maximal carbon assimilation, a higher \(A_{\text{max}}\) would be expected under FL (Retkute et al., 2015). However, this hypothesis leads to an overestimation of \(A_{\text{max}}\) by more than 50% under frequent light fluctuation, suggesting a more complex underlying mechanism. Recently, Vialet-Chabrand et al. (2017) have experimentally demonstrated that the daily carbon assimilation of plants grown under FL was lower in comparison with plants grown under a square wave light (SQ) regime but intercepting the same DPI (mol m\(^{-2}\) d\(^{-1}\)). They highlighted the influence of diurnal light fluctuations on photosynthetic acclimation and photosynthetic capacity. One of their findings is that plants grown under FL had reduced photosynthetic parameters, particularly maximal electron transport rate (\(J_{\text{max}}\)) and leaf absorptance of incident PAR. Biochemically, this reduction is due to a decrease in the photosynthetic protein abundance by 3–15%. However, the physiological mechanisms resulting in this difference in protein abundance between FL and SQ remain unknown. Here, we seek explanations for this reduction in photosynthetic proteins under FL by applying an hourly based dynamic model for photosynthetic acclimation.

Protein abundance is regulated by the orchestration of multiple mechanisms and is the outcome of protein turnover: the continuous dynamics of protein synthesis and degradation (Kristensen et al., 2013; Nelson and Millar, 2015). Based on the concept of protein turnover, we have recently presented a mechanistic model describing photosynthetic acclimation (Pao et al., 2019) in which the experimental data suggested a non-linear relationship between the PPSR and PAR (see Supplementary Fig. S1 at JXB online). PPSR increases almost linearly with PAR under low light conditions (up to 200 µmol PAR m\(^{-2}\) s\(^{-1}\) for Rubisco and electron transport proteins), and then the slope of the PPSR–PAR curve decreases and the protein synthesis rate approaches a saturation level at high PAR (around 900 µmol PAR m\(^{-2}\) s\(^{-1}\)). This form of a non-linear relationship is not surprising since it has been observed in the cause–effect relationships of many other biological phenomena. Of note is its implication that protein synthesis rate under FL conditions (ranging between 0 and 1500 µmol PAR m\(^{-2}\) s\(^{-1}\) in Vialet-Chabrand et al., 2017) is saturated occasionally during the course of the day and the protein synthesis per day per unit DPI is consequently less than that under SQ, the non-saturating condition (constantly at 460 µmol PAR m\(^{-2}\) s\(^{-1}\) for 12 h). By applying this PPSR–PAR relationship (Fig. 1A), it is possible to assess the differences in photosynthetic protein abundance between plants grown under FL and SQ.
To simulate the effect of the diurnal light fluctuation, we first converted the parameters in the model of Pao et al. (2019) to an hourly basis by assuming a 12 h photoperiod and zero protein synthesis in the dark. Then, three FL patterns (Fig. 1B) and SQ with DPI between 1 and 60 mol m\(^{-2}\) d\(^{-1}\) were used as light input to simulate the abundance of Rubisco, electron transport, and light harvesting proteins (Pao et al., 2019), which were then converted to maximal Rubisco carboxylation rate (\(V_{\text{cmax}}\)), \(J_{\text{max}}\), and leaf PAR absorptance, respectively. Constants converting the amount of nitrogen in each functional protein pool into the corresponding capacities are used according to Buckley et al. (2013). Under natural diurnal light fluctuation (FL\(_N\) in Fig. 1B) and light intensity (DPI = 10 and 20 mol PAR m\(^{-2}\) d\(^{-1}\)) similar to the FL experiment in Vialet-Chabrand et al. (2017), the model predicted the effects of FL on photosynthetic parameters: \(V_{\text{cmax}}\) and \(J_{\text{max}}\) were reduced by 21–22% (Fig. 1C, D) and leaf PAR absorptance by 2–4% (Fig. 1E). This prediction is within the range reported for leaf PAR absorptance (3–5%) but is different from that for the \(V_{\text{cmax}}\) (8–10%) and \(J_{\text{max}}\) (11–15%) found in Arabidopsis (Vialet-Chabrand et al., 2017). These differences could be due to the lack of protein synthesis in the dark assumed in the simulations (see below) or due to the fact that their model was parameterized using greenhouse cucumber (\(Cucumis sativus\)), which might have different PPSR–PAR responses from Arabidopsis. However, both experimental and model studies suggest that \(V_{\text{cmax}}\) and \(J_{\text{max}}\) were more affected by FL than leaf PAR absorptance. This can be explained by the fact that the synthesis rate of light harvesting proteins reaches saturation at a lower PAR level than Rubisco and electron transport proteins (Fig. 1A). Therefore, the effects of FL on light harvesting proteins under high DPI were almost negligible.

The different effects of FL on \(V_{\text{cmax}}, J_{\text{max}}\), and leaf absorptance (Fig. 1C–E) imply that the characteristics of the PPSR–PAR curve determine the impact of light fluctuation on the abundance of photosynthetic proteins. Hence, we further examined the extent to which the PPSR–PAR curve parameters, the maximum protein synthesis rate (\(S_{\text{mm}}\), equal to 0.1, 0.5, or 2.5) and the curvature (\(k_1\), equal to 0.5 or 5), affect the photosynthetic acclimation under natural diurnal light fluctuation (FL\(_N\) in Fig. 1B) with DPI levels between 1 and 60 mol m\(^{-2}\) d\(^{-1}\) in combinations with nitrogen supply levels (2–10 mM) and leaf吸光度.
age (5–45 d). Age and nitrogen levels had no influence (<1%) on the impact of FLs (data not shown). The reduction of protein abundance due to FL was up to 22%, depending on the combinations of DPI, $S_{\text{mm}}$, and $k_I$ (Fig. 2). Three types of response curves can be identified: (i) the combination of high $k_I$ and low $S_{\text{mm}}$ results in the strongest reduction under low light and this reduction decreases with DPI, resembling the light harvesting proteins (Fig. 1A); (ii) combining high $k_I$ and $S_{\text{mm}}$ or low $k_I$ and $S_{\text{mm}}$ shows the strongest reduction under low–intermediate DPI, resembling Rubisco and electron transport proteins (Fig. 1A); (iii) combining low $k_I$ and high $S_{\text{mm}}$, the reduction in protein abundance increases with DPI. The third type of these response curves indicates that the PPSR will not be saturated even under high light conditions, probably an unfavorable strategy under natural selection. Altogether, these results suggest that variations in the parameters of the PPSR–PAR curve can form an explanation of the different acclimatory responses to FL between plant functional types, as reported by Watling et al. (1997).

Mathematically, the hyperbolic characteristics of the PPSR–PAR response (Fig. 1A) suggest that the strongest impact of light fluctuation can be expected if the incident PAR fluctuates largely across the vertex of the PPSR–PAR curve and the impact of FL becomes smaller when it mostly fluctuates within the nearly linear range of the PPSR–PAR curve. This non-linear characteristic has two biological implications. Firstly, the influence of FL can be expected to be small under low light (DPI < 10 mol m$^{-2}$ d$^{-1}$, Fig. 1C, D). This result is similar to the observation in Arabidopsis that the impact of FL on the electron transport rate is stronger under a DPI of 5.1 than one of 3.6 mol m$^{-2}$ d$^{-1}$ (Alter et al., 2012). Also, in Alcatesia macrorhiza no reduction in $A_{\text{max}}$ was observed under FL at a very low DPI level (1.4 mol m$^{-2}$ d$^{-1}$; Sims and Peary, 1993) while $A_{\text{max}}$ tended to be 15% lower than SQ when DPI was 7 mol m$^{-2}$ d$^{-1}$ (Watling et al., 1997). Secondly, photosynthetic protein abundance will be more strongly affected by the large fluctuation (FLs in Fig. 1B) than by the small fluctuation (FLs in Fig. 1B, C–E). This agrees with the observations in Arabidopsis that, in comparison with SQ (85 µmol PAR m$^{-2}$ s$^{-1}$), FLs (ranging between 50 and 1250 µmol PAR m$^{-2}$ s$^{-1}$) reduces electron transport rate by 28%, while FLs (ranging between 50 and 650 µmol PAR m$^{-2}$ s$^{-1}$) reduces electron transport rate by only 8% (Alter et al., 2012). Grown under the FLs pattern (ranging between 50 and 525 µmol PAR m$^{-2}$ s$^{-1}$), $A_{\text{max}}$ and nitrogen per unit leaf area ($N_{\text{area}}$, a proxy of photosynthetic protein abundance) of Shorea leprosula leaves were not different from those of leaves grown under SQ (170 µmol PAR m$^{-2}$ s$^{-1}$; Leakey et al., 2002), but in their following study Leakey et al. (2003) showed that $A_{\text{max}}$ and $N_{\text{area}}$ of the same species grown under FLs (ranging between 0 and 1700 µmol PAR m$^{-2}$ s$^{-1}$) were 20–30% lower than those of their counterparts grown under FLs (ranging between 0 and 750 µmol PAR m$^{-2}$ s$^{-1}$).

As with any other model, this model is a simplification of the real system. For example, it assumes zero protein synthesis rate under darkness, which is unlikely for Rubisco (Ishihara et al., 2015). If a low rate of Rubisco synthesis during the dark period under FL and SQ is assumed (as suggested by Ishihara et al., 2015), the relative impact of FL will be lower than our prediction and thus closer to the reduction measured by Vialet-Chabrand et al. (2017). The current model also assumed the same degradation rate constants for different PAR levels although this does not hold true in planta especially under high light (Li et al., 2018). The available information is so far restricted for parameterizing this effect (Nelson et al., 2014; Li et al., 2017). Theoretically, if the degradation is enhanced under excess light while the synthesis rate remains stable, it can be expected that the reduction in protein abundance under FL would be even more severe. However, if the synthesis rate is coordinated with the degradation rate as reported for photosystem II subunit D1 protein (Aro et al., 1993), similar results to our simulation could be expected due to restored balance in the net rate of change. In addition, there are still unknown mechanisms involved in the acclimation to FL that are not considered in the model. The effects of the frequency of light fluctuations and the length of individual light events on photo-acclimation, as shown in previous studies (Yin and Johnson, 2000; Alter et al., 2012) and implying that protein synthesis does not react to a light signal instantaneously (e.g. Rerkut et al., 2015), cannot be reproduced by our model (data not shown). Besides photosynthetic proteins, many physiological processes are also involved in the acclimation mechanism to FL, especially when tackling excess light energy. Photo-oxidative damage caused by the excess light events under FL may increase the need for photoprotection, photosynthesis, and cyclic electron flow, which together alter the metabolism and partitioning of nitrogen and carbon (Matsubara, 2018; Annunziata et al., 2018; Schneider et al., 2019). Also, our model does not account for any photoperiodic regulation, which is also known to affect long-term acclimation (Seaton et al., 2018).

In summary, the hyperbolic PPSR–PAR response provides a mechanistic explanation of the reported reduction in photosynthetic protein abundances caused by diurnal light.
fluctuation. Our results suggest that the differences in protein abundances between FL and SQ conditions are determined by three components: the pattern of FL, the DPI level, and the species-specific PPSR–PAR curve parameters. Although a model cannot account for all details of the acclimation response under all environmental scenarios, our model delivers a systematic view of this phenomenon and thus can be a useful tool for designing FL scenarios for future experiments (see Supplementary Dataset S1 for the R script of the model). Our analyses point out the avenues for further investigations in the interspecific and genotypic variations of the PPSR–PAR relationship and in the response time to the light signal, as well as photoperiodic regulation and the combined effects of different environmental factors on photosynthetic protein turnover.

Supplementary data

Supplementary data are available at JXB online. Dataset S1, R script of the protein turnover model and input file of light fluctuation patterns.

Fig. S1. Non-linear relationship between photosynthetic protein synthesis rate and light intensity.

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