

## Supplementary material

### Exploiting heterogeneous environments: does photosynthetic acclimation optimise carbon gain in fluctuating light?

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#### A Quasi-steady net photosynthetic rate model

The relationship between the net photosynthetic rate  $P$  and light intensity  $L$  (Fig. 1) possesses the following properties:  $P \rightarrow P_{\max}$  for large  $L$  (saturation);  $P(0, P_{\max}) = R_D < 0$  where  $-R_D = \alpha P_{\max}$  for some  $\alpha > 0$ ;  $P(L_c, P_{\max}) = 0$ , where  $L_c$  is the light compensation point; and  $\frac{\partial P}{\partial L}(L_c, P_{\max}) = \phi$ . In this study, baseline parameters are  $\alpha = 0.1$  and  $\phi = 0.0124$  mol  $CO_2$  per mol photons.

Two simple models for  $P$  versus  $L$  are

$$P^{(1)}(L, P_{\max}) = \begin{cases} -\alpha P_{\max} + \phi L & \text{if } 0 < L \leq \frac{(1+\alpha)P_{\max}}{\phi}, \\ P_{\max} & \text{if } L > \frac{(1+\alpha)P_{\max}}{\phi}, \end{cases} \quad (1a)$$

$$P^{(3)}(L, P_{\max}) = \frac{\phi L + (1 + \alpha)P_{\max} - \sqrt{(\phi L + (1 + \alpha)P_{\max})^2 - 4\theta\phi(1 + \alpha)LP_{\max}}}{2\theta} - \alpha P_{\max}. \quad (1b)$$

The parameter  $\theta$  determines the curvature of the response curve (1b). For  $\theta = 1$ , (1b) becomes  $P^{(3)}(L, P_{\max}) = \frac{1}{2}(P_{\max}(1 - \alpha) + L\phi - |P_{\max}(1 + \alpha) - L\phi|)$ , which is equivalent to (1a).

The value of  $P_{\max}$ , which we denote  $P_{\max}^*$ , that maximises  $P$  for given  $L$  satisfies

$$P_{\max}^{*(1)}(L) = \frac{\phi L}{1 + \alpha}; \quad (2a)$$

$$P_{\max}^{*(3)}(L) = \frac{L\phi \left( \alpha(-1 + \alpha(\theta - 1))(2\theta - 1) - (1 + \alpha - 2\alpha\theta) \sqrt{\alpha(-1 + \alpha(\theta - 1))(\theta - 1)} \right)}{\alpha(1 + \alpha)(-1 + \alpha(\theta - 1))}. \quad (2b)$$

Here  $\frac{\partial P}{\partial P_{\max}} = 0$  defines  $P_{\max}^*$  in (2b); (2a) is then determined from the limit  $\theta \rightarrow 1$ .

#### B Light intensity regime under alternation between two light levels

Suppose that the light intensity  $L(t)$  switches with period  $T$  between two different intensities  $L_{\pm}$ , where  $L_- \leq L_+$ . For  $0 \leq t \leq kT$ ,  $L(t) = L_-$ , where  $0 \leq k \leq 1$ ;  $L(t) = L_+$  otherwise.

The net carbon assimilation rate for such an  $L(t)$  is

$$C(k, L_-, L_+) = \frac{1}{T} \int_0^{kT} P(L_-, P_{\max}) dt + \frac{1}{T} \int_0^{(1-k)T} P(L_+, P_{\max}) dt, \quad (3)$$

giving

$$C^{(1)}(k, L_-, L_+) = \begin{cases} -\alpha P_{\max} + \phi(kL_- + (1-k)L_+), & \text{if } L_+ \leq \frac{(1+\alpha)P_{\max}}{\phi}, \\ k(-\alpha P_{\max} + \phi L_-) + (1-k)P_{\max}, & \text{if } L_- \leq \frac{(1+\alpha)P_{\max}}{\phi} < L_+, \\ P_{\max}, & \text{if } \frac{(1+\alpha)P_{\max}}{\phi} < L_-, \end{cases} \quad (4a)$$

$$C^{(3)}(k, L_-, L_+) = k \frac{L_- \phi - \sqrt{-4L_- P_{\max}(1+\alpha)\theta\phi + (P_{\max}(1+\alpha) + L_- \phi)^2}}{2\theta} \\ + (1-k) \frac{L_+ \phi - \sqrt{-4L_+ P_{\max}(1+\alpha)\theta\phi + (P_{\max}(1+\alpha) + L_+ \phi)^2}}{2\theta} \\ - P_{\max}\alpha + \frac{P_{\max}(1+\alpha)}{2\theta}. \quad (4b)$$

According to (4a), the maximum net carbon assimilation rate is attained for  $P_{\max} = \phi L_{\pm}/(1+\alpha)$  (depending on the value of  $k$ ), with the transition between the two states arising for  $\partial C/\partial P_{\max} = 0$ , with

$$k = \frac{1}{1+\alpha}. \quad (5)$$

Thus for  $0 < k < 1/(1+\alpha)$ ,  $P_{\max}^{opt} = P_{\max}^*(L_-) > \bar{P}_{max}$ , whereas for  $1/(1+\alpha) < k < 1$ ,  $P_{\max}^{opt} = P_{\max}^*(L_+) < \bar{P}_{max}$ . This step-like property remains evident in Figure 3, for which  $\theta = 0.99$ , although in this case  $P_{\max}^{opt}$  is typically larger than  $\bar{P}_{max}$ , indicating that  $P_{max}$  must be elevated in order to attain an optimised response in fluctuating light conditions.

## C Small amplitude light fluctuations

Light in nature is much more heterogeneous and unpredictable than that considered in previous sections. Here we consider how to maximise  $C$  when  $L$  is a fluctuating quantity. Specifically, suppose that  $L = \bar{L} + \hat{L}$ , where the bar denotes a time average and by definition  $\overline{\hat{L}} = 0$ . If the fluctuations are infinitesimal, we anticipate that  $C$  is maximised by  $\bar{P}_{\max} = P_{\max}^*(\bar{L})$ . We now determine how  $P_{\max}^{opt}$  must change in order to accommodate the fluctuations. We write the change as the constant  $\hat{P}_{\max}$ . For clarity of notation we express the response curve as  $P = F(L, P_{\max})$  for some function  $F$ .

Setting  $P_{\max} = \bar{P}_{\max} + \hat{P}_{\max}$ , where  $\hat{P}_{\max}$  is to be determined, we Taylor expand  $F$ , treating  $\hat{P}_{\max}$  as being of comparable magnitude to  $\hat{L}^2$ :

$$P = F(\bar{L}, \bar{P}_{\max}) + F_L(\bar{L}, \bar{P}_{\max})\hat{L} + F_P(\bar{L}, \bar{P}_{\max})\hat{P}_{\max} + \frac{1}{2}F_{LL}(\bar{L}, \bar{P}_{\max})\hat{L}^2 + \dots \quad (6)$$

where  $F_P \equiv \partial F/\partial P_{\max}$ . Evaluating  $C$  for large  $T$ , so that  $C$  is the time-average of  $P$ , it follows that

$$C = F + F_P \hat{P}_{\max} + \frac{1}{2}F_{LL} \overline{\hat{L}^2} + \dots \quad (7)$$

Maximising  $C$  over  $P_{\max}$  requires  $C_P = 0$ , i.e.  $F_P + F_{PP}\hat{P}_{\max} + \frac{1}{2}F_{PLL}\overline{\hat{L}^2} + \dots = 0$ . However derivatives are evaluated at  $L = \bar{L}$ ,  $P_{\max} = \bar{P}_{\max}$  and  $F_P(\bar{L}, \bar{P}_{\max}) = 0$ , implying that

$$\hat{P}_{\max} = -\overline{\hat{L}^2} \frac{F_{PLL}}{2F_{PP}}, \quad (F_{PP} \neq 0). \quad (8)$$

For the light saturation model given by (1b), (8) gives

$$P_{\max}^{opt} = \bar{P}_{\max} + \frac{\overline{\hat{L}^2} \bar{P}_{\max} \left( \bar{P}_{\max}^2 (1+\alpha)^2 + \bar{L} \bar{P}_{\max} (1+\alpha) (2\theta - 1) \phi - 2\bar{L}^2 \phi^2 \right)}{2 \bar{L}^2 \left( \bar{P}_{\max}^2 (1+\alpha)^2 - 2\bar{L} \bar{P}_{\max} (1+\alpha) (2\theta - 1) \phi + \bar{L}^2 \phi^2 \right)}. \quad (9)$$

Numerical calculations over range of parameter values show that second term in the above expression is positive, therefore  $P_{\max}^{opt} > \bar{P}_{\max}$  if  $\overline{\hat{L}^2} > 0$ . This is illustrated in Fig. 4. Thus  $P_{\max}^{opt}$  must increase in the presence of fluctuations as a consequence of the shape of the underlying light-response surface.