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Commentary

Modelling photosynthesis in highly dynamic environments: the case of sunflecks

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The impacts of rapid fluctuations in solar energy on photosynthesis were first recognized almost a century ago (Lundegarth 1921 as reviewed by Pearcy 1990), yet major advancements in understanding the underlying physiological processes and their environmental controls were made only in the 1980s. In his 1990 review of the environmental and physiological controls on the utilization of transient sunfleck light, Pearcy called attention to two reviews published in the late 1980s, one on the regulatory aspects of photosynthetic carbon metabolism, playing an important role in the dynamic responses of CO₂ assimilation (Woodrow and Berry 1988), and the other on the role of sunflecks in the physiological ecology of understory plants (Chazdon 1988). Although most research on sunfleck photosynthesis concentrated on understory plants, for which prevailing light intensities below 20% of full sunlight are the main factors limiting growth (Chazdon 1988), sunflecks are also critical in the lower parts of dense canopies, where light is a limiting factor. Thus, the effects of spatial and temporal variation in sunfleck activity are likely to manifest on plant growth and reproduction in canopies or in understory seedlings, where diffuse radiation punctuated by sunflecks becomes the dominant source of energy to drive photosynthesis (Roden and Pearcy 1993). A photosynthetic machinery optimized for performance in highly dynamic light environments will thus be crucial in these conditions.

Photosynthetic processes of higher plants are continuously adjusted to match the complex changes of the environment. From an eco-evolutionary perspective, plants must decide how to optimally allocate available resources to maximize net carbon gain while minimizing expenditure in terms of new tissue

construction, maintenance and repair costs. This already intricate optimization problem is complicated even further by the highly dynamic character of resource availability (i.e., nutrients, water, and light and thermal energies). Resource availability fluctuates at time-scales that may range from the subsecond domain (e.g., variation in light energy input caused by leaf fluttering or sunflecks) to years (e.g., slow soil nutrient depletion), or even millennia (e.g., changing climate producing varying combinations of temperature and precipitation patterns and atmospheric CO₂ concentrations). Consequently, plants make 'decisions' aimed to optimize photosynthetic response to the dynamics of the available resources; decisions that are only meaningful at the time-scale for which they were made, and that typically present little plasticity at shorter time-scales. For instance, species-specific wood anatomical properties and general leaf morphology are traits adjusted at an evolutionary time-scale, whereas sun-shade leaf morphology or leaf biochemical properties can be adjusted at annual or diurnal time-scales, respectively. This decision-making process underlies the adaptive dichotomy between pioneer species (optimized for high performance in sunny environments) and shade-tolerant species capable of thriving in the shade, the intraspecific plasticity in leaf morphological properties between sun and shade leaves, or the biophysical adjustments at the leaf-level to fine-tune photosynthesis for optimal performance at the diurnal and seasonal time-scales. In this context, leaves of plants dwelling in shaded environments face one of the most challenging photosynthetic decision-making processes: how to utilize and cope with sunflecks. This is the subject of a review paper in the current issue where Way and Pearcy evaluate the

recent developments in sunfleck photosynthesis since the classic review of [Percy \(1990\)](#), putting special emphasis on current topics of relevance.

Sunflecks are rapid and momentary increases in light intensity of variable duration (seconds to minutes) superimposed on the background diffuse light. For plants in shaded environments, such as seedlings or understory species, light energy received during sunflecks can represent a critical source of energy (or potential damage) that may tip the balance between survival and death. Indeed, relative growth rates for understory tree saplings have been found to correlate with the occurrence of sunflecks ([Percy 1983](#)), evidencing the critical role of sunflecks under light-limited environments. Similarly, analysis of $\delta^{13}\text{C}$ of biomass reveals that the annual contribution of carbon fixed during sunflecks can be close to 50% for certain understory species ([Percy and Pfitsch 1991](#)). Consequently, optimization of photosynthetic responses to fluctuating light will be crucial for survival in these environments. But what is so special about living in the shade? In this issue, [Way and Percy \(2012\)](#) comprehensively review the principal leaf traits that control the optimal utilization of sunfleck energy (summarized

in Box 1), discussing the potential implications that climate change-induced increases in atmospheric CO_2 , temperature or occurrence of drought may have on the performance of photosynthesis in shaded environments.

Upon a sunfleck, a leaf that has been in the shade undergoes a process of photosynthetic induction that lasts for several minutes and includes different phases of biochemical and stomatal limitations (e.g., Rubisco activation, stomatal opening; Box 1). Similarly, following a sunfleck an induction loss phase takes place involving gradual Rubisco deactivation and stomatal closure. Typically, the induction loss phase is slower, increasing the probability that photosynthesis is readily induced in subsequent sunflecks. The photosynthetic response to sunflecks is thus a combination of a number of highly dynamic processes that involve different time constants, which differ among species and depend on other environmental factors. [Way and Percy \(2012\)](#) introduce a number of trade-offs that exemplify the photosynthetic decision-making process. For example, keeping the stomata open during sunflecks will greatly enhance photosynthetic gain in subsequent sunflecks, but if atmospheric vapor pressure deficit (VPD) is high or soil

Box 1 Adaptive leaf traits in sunfleck environments (for more details see [Way and Percy 2012](#))

A. *Traits to maximize CO_2 assimilation.* A rapid photosynthetic induction gain during a sunfleck and a slow induction loss after it are traits that enhance CO_2 assimilation in shaded environments.

1. Rapid activation of Rubisco	When light intensity increases during a sunfleck, Rubisco is activated as part of the photosynthetic induction process. A fast activation of Rubisco enhances the amount of carbon that can be photosynthetically assimilated during the sunfleck. To speed up the Rubisco activation process, leaves of sunfleck-dominated environments increase the allocation of nitrogen to Rubisco activase (the enzyme that catalyzes the activation of Rubisco) and away from Rubisco
2. Rapid opening of stomata	As in Rubisco activation, stomata also open in response to light, enhancing stomatal conductance (g_s). The dynamics of g_s increase depend on species and environment conditions, where, e.g., shade-tolerant species tend to increase g_s to a greater extent compared with pioneer species. Furthermore, initial g_s immediately before the sunfleck differs during the course of the day or the passing of the seasons, most likely the result of a dynamic optimization of water use. Rapid stomatal opening leads to increasing intercellular CO_2 concentration, which enhances photosynthesis directly through c_i but probably also indirectly by speeding up the activation of Rubisco, a step that requires CO_2 binding to its active site
3. Slow deactivation of Rubisco	After a sunfleck, photosynthesis undergoes a process of induction loss that depends, among other things, on the rate of de-activation of Rubisco. Deactivation is typically slower than activation, which enhances the probability of a high level of photosynthetic induction in subsequent sunflecks
4. Slow stomatal closure	Keeping up high g_s during the inter-sunfleck period enhances the photosynthetic carbon gain of subsequent sunflecks by keeping a high c_i . As in the stomatal opening dynamics, stomatal closure seems also to take place more slowly in shade-tolerant species growing in sunfleck-dominant environments compared with pioneer species. In addition, high VPD also speeds up stomatal closure

B. *Traits to minimize damage.* The sudden increase in light and temperature upon a sunfleck may also lead to photodamage or heat damage to the leaf, which necessitates special protective mechanisms

5. Ability to adjust physical properties	In some species, leaves implement light avoidance strategies to reduce the energy input during sunflecks and minimize photodamage risks. These strategies include restructuring of thylakoids via grana stacking, chloroplast movements or changes in leaf orientation to minimize light interception
6. Ability to adjust biochemical properties	Accumulation of protective pigments such as carotenoids or anthocyanins plays a double protective role by promoting the thermal dissipation of excess light energy (mainly via the xanthophyll cycle), or as antioxidants by scavenging reactive oxygen species (ROS) that could otherwise damage the photosynthetic machinery
7. Thermotolerance	Isoprene emission is known to improve thermotolerance and reduce heat damage. Interestingly, isoprene-emitting capacity is mainly present in species that thrive in sunfleck-prone environments, whereas pioneer species are rarely (e.g., poplars) isoprene emitters, a functional role that perhaps could help explaining the still unclear taxonomic prevalence of isoprene emission capacity

water availability is low, the potential cost of water lost in the process (in terms of additional carbon needed to expand fine roots into less exploited soil volume, or lost potential of subsequent CO₂ uptake due to drought-induced stomatal closure) might surpass the benefits of the expected carbon gain; and a tendency to close the stomata faster after the sunfleck will develop. This is a common trade-off that can be quantified with the help of a mathematical optimization function.

Complex processes such as photosynthesis cannot be fully understood in terms of controlling factors and trade-offs without the use of mathematical models. Mathematical models of photosynthesis have been classified as steady-state models (where the state of the system at t_1 is not affected by the state at t_0), or dynamic (where the state of the system at t_1 depends on that at t_0 and its interaction with a number of dynamic processes). However, the response of photosynthesis to environmental stimuli does not always upscale across time and photosynthetic performance will vary not only along the course of the day (e.g., in response to photosynthetic induction gain and loss) but also during the season (due to seasonal up-/down-regulation processes). These adjustments present a serious challenge to steady-state models. At the seasonal time-scale, the dynamic variation in photosynthetic parameters must be incorporated in photosynthetic models to successfully reproduce the seasonality of photosynthesis in species with marked patterns (Mäkelä et al. 2004, Bauerle et al. 2012). Similarly, steady-state models are incapable of reproducing photosynthesis in the highly dynamic conditions of sunflecks, where these models tend to overestimate carbon assimilation because they do not integrate the slow photosynthetic induction response of the leaf (reviewed in Way and Pearcy 2012). In these shaded and highly dynamic environments, photosynthetic models that account for the slow induction gain and loss upon a sunfleck represent a great improvement of accuracy in predicting photosynthetic carbon gain (Percy et al. 1997). In summary, the idealized representation of steady state in photosynthetic models carries an intrinsic bias-producing error. Hence, it is necessary to inquire, does the magnitude of the bias matter at the spatiotemporal scale for which a model is used?

Emphasis on upscaling of photosynthesis from leaf to canopy and landscape level is growing in response to the increasing demand for answers to global questions. While dynamic models present a substantial improvement compared to steady-state models, their parameterization remains a challenge for upscaling activities because parameters change across time and space, and the more complex structure (number of parameters) in dynamic models may decrease overall model precision (Rastetter et al. 1992). Upscalable models would require fewer parameters that either remain stable and can be taken from look-up tables, or that can be estimated by upscale-friendly means (for example by assimilating remotely

sensed data), taking into account corrections for non-linearity across space (Rastetter et al. 1992). In this context, a potential approach to reduce the number of parameters and improve their robustness is the integration of plant decision-making logic into model construction, where plants are considered as a whole during model development, because decisions are also taken at the plant level. A classic example of integration of plant decision-making logic into a model is that of the theory of optimal control of stomata (Cowan and Farquhar 1977, Hari et al. 1986). For instance, the same optimal control theory could be applied to the dynamic sunfleck model of Percy et al. (1997) to introduce changes in the time constants for the stomatal response along with varying plant water status. Likewise, the model of Mott and Woodrow (2000) predicting the allocation of protein between Rubisco and Rubisco activase depending on the light environment could be applied to the parameterization of the time constants of Rubisco activation (a function of Rubisco activase) and maximum photosynthetic capacity (a function of Rubisco) in Percy's sunfleck model. These are just two examples of how integrating plant decision-making knowledge into modelling could facilitate the development of models that are more robust, have fewer parameters and are eventually driven by environmental variables only.

Although 'Integrated organismal responses to changing light conditions make it exceedingly difficult to quantify the significance of sunflecks *per se* for growth, survivorship, and reproduction...' (Chazdon 1988), advances have been made. Percy and his collaborators were the earliest to link results from experiments on transient photosynthetic response, including photoinhibition, to transient light with a three-dimensional radiation transfer model, assessing both the bias introduced through steady-state modelling and the contribution of sunfleck light to the carbon economy of individual plants (Naumburg et al. 2001, Percy et al. 2005). Percy's work and the aforementioned reviews have been highly cited since their appearance. And yet, the review by Way and Percy (2012) demonstrates that some of the questions brought up by Percy (1990) are still unanswered, hindering our ability to accurately estimate carbon uptake of plants lower in the canopy. Furthermore, most ecosystem models, including those that are used for predicting regional and global vegetation-atmosphere carbon exchange, central to addressing climate change questions, are still driven by steady-state approaches to photosynthesis, despite the indications that such simplification may introduce substantial bias, and although tools to reduce this bias are available. With the large amount of knowledge accumulating on the dynamics of photosynthesis and the interplay between different plant physiological processes, the time is ripe to move into dynamic models of photosynthesis that, hand in hand with dedicated observational studies and experiments, address the increasingly complex questions we face.

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