



Editorial

Two decades of sunfleck research: looking back to move forward

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The study of how plants make use of sunflecks, relatively short duration but high-intensity patches of light in the understory and shaded tree canopy, has been of interest for decades. The potential ecological significance of sunflecks was recognized early in the 20th century (Allee 1926, Evans 1956), and the first few studies attempting to quantify the contribution of sunflecks to carbon gain in understories were undertaken at this time (Lundegårdh 1922). However, the lack of suitable methodologies for measuring photosynthetic responses or even quantifying sunfleck light regimes hampered progress. Gradually, techniques were developed for quantifying the nature of sunfleck light regimes both in forest understories and in crop canopies (Reifsnnyder et al. 1971, Norman 1971). But studies of the photosynthetic response to sunflecks lagged because the plant response was confounded with the much slower instrument response times: indeed, until the early 1980s, nearly all the focus was on steady-state photosynthetic responses of understory plants to light. The instrument response limitations were first overcome by mathematically deconvoluting the plant response from the instrument response (Pearcy et al. 1985). Later, the development of fast-responding CO₂/H₂O analyzers greatly accelerated research on the mechanisms underlying sunfleck utilization.

Although the phenomena underlying dynamic responses of photosynthesis to sunflecks (such as induction requirements) were studied by physiologists and biochemists from the early part of the 20th century (Osterhout and Hass 1918), their role in sunfleck utilization was not recognized until the early 1980s. Evidence for a role for the light activation requirement of the primary carboxylating enzyme, Rubisco, in photosynthetic induction was first uncovered in the 1960s (see Walker 1973). Since induction was evident in algae and aquatic plants lacking

stomata, their role in the induction response of terrestrial plants was initially questioned. This led to research on the relative roles of stomatal versus Rubisco limitations for induction gain (Kirschbaum and Pearcy 1988a). In the course of these studies, a fast induction requirement not directly related to Rubisco regulation was identified (Kirschbaum and Pearcy 1988b), and subsequent physiological/biochemical studies identified this as a limitation imposed by the light regulation of enzymes in the ribulose biphosphate regeneration pathway (Sassenrath-Cole and Pearcy 1992). Other studies revealed the contribution of post-illumination CO₂ fixation to sunfleck utilization and its relationship to the buildup and utilization of metabolite pools (Kirschbaum and Pearcy 1988c). These mechanistic studies provided the basis for the development of dynamic models applicable for understanding the limitations to sunfleck utilization in contrasting environments and with contrasting dynamic responses (Gross et al. 1991). In turn, application of the models revealed the strong limitation imposed by the induction requirement, but also that post-lightfleck CO₂ assimilation makes no significant contribution to carbon gain in understories (Pearcy et al. 1994).

From the mid-1990s to the present, attention has shifted from laboratory-based mechanistic studies to more field-oriented studies designed to elucidate the significance of sunflecks to the carbon gain of plants in forest understories and in plant canopies (Ogren and Sundin 1996). Comparative work sought to identify species differences in induction gain and loss, and to relate these differences to successional status, habitat preferences and growth conditions. Additionally, research has increasingly focused on environmental limitations constraining sunfleck use, such as excessive light (Barker et al. 1997) and leaf temperatures (Leakey et al. 2003) and the

photo- and thermal-protective mechanisms that are important in coping with these stresses.

The accompanying virtual issue consists of 12 sunfleck-themed papers published in *Tree Physiology* over the past 17 years. One (Way and Pearcy 2012) is a recent review that briefly covers research on the mechanism of sunfleck utilization, modeling of sunfleck use and stress effects, and the physiological traits that facilitate coping with high temperatures and excess light occurring in sunflecks. A main conclusion of the review is that canopy models should incorporate dynamic responses to photosynthesis to accurately estimate forest carbon uptake. This point is illustrated in the paper by Naumberg and Ellsworth (2002) who show that using static photosynthetic light responses to predict daily tree carbon fixation yields overestimations of carbon gain by as much as 42%. Porcar-Castell and Palmroth (2012) expand on the need to move from steady-state models to dynamic models for addressing large-scale questions and advocate using plant decision-making logic to make this happen.

A recurring theme in the literature is that shade leaves (either from species adapted to shaded habitats or from shade-acclimated leaves in understories or within tree canopies) should be more dependent on sunflecks to maintain a positive carbon balance than sun leaves. Therefore, shade leaves could be hypothesized to have mechanisms that enhance sunfleck use, such as faster induction gain and/or slower induction loss. Some studies in this virtual issue, such as Küppers et al. (1996), have found support for this hypothesis with comparisons of late successional tree species that reproduce in the shaded understory versus early successional species that regenerate in more open, disturbed habitats. Wong et al. (2012) also found that an early successional species had longer induction times than a late successional tree, which could reduce the use of sunflecks in an understory environment, limiting the early successional species to a high light niche. In a third paper, Zhang et al. (2012) grew early, mid- and late successional subtropical Chinese tree seedlings at low light and then characterized their ability to use sunflecks. The early successional species had the slowest induction gain and showed rapid induction loss, while the mid-successional species showed the fastest induction gain times. Lastly, Chen and Klinka (1997) characterized photosynthetic traits in *Pseudotsuga menziesii* (Mirb.) Franco seedlings in an understory forest plot and an open clear-cut site and found that, as predicted, shade branches had shorter induction times than sun branches.

However, the story told by the papers collected here is not as tidy as it may first appear. In contrast to the above studies, Urban et al. (2007) found no clear correlation between shade tolerance and induction gain times between sun and shade leaves or across shade-tolerant, mid-shade-tolerant and shade-intolerant trees from a temperate European forest site. Similarly, responses of induction kinetics to shade environment

can be species dependent. Han et al. (1999) measured naturally occurring seedlings in a gap and a shaded understory site and found that shade leaves of one species had shorter induction periods than gap leaves, another had similar induction rates in both habitats, while a third had longer induction times in shade than in gap sites. Taken together, these papers reveal that there is no simple relationship between the speeds of induction gain and loss, and either species or conditions where efficient sunfleck use should be favored.

The components underlying induction, especially stomatal behavior, are complex and are dependent on environmental and developmental factors besides transient light changes. Tang and Liang (2000) found that water stress reduced stomatal conductance in shade, but not sun, leaves of a *Populus* species; drought also led to faster induction gain in shade-grown, but not sun-grown leaves during simulated sunflecks. Similarly, drought led to a greater reduction in photosynthesis and leaf water status in leaves from shaded sites than those in open sites (Abrams and Mostoller 1995). Another factor that might affect our ability to detect generalizations across species in sunfleck physiology is leaf age. Using three species of *Populus*, Urban et al. (2008) showed that transient stomatal limitations to sunflecks were more pronounced in older leaves, highlighting the importance of considering physiological variation within a single tree.

While progress has been made in understanding the nature and significance of sunfleck utilization it is also clear that many questions remain. The limitations on sunfleck use imposed by induction are a consequence of the regulatory properties of the photosynthetic apparatus that appear to match supply and demand among the various processes. Aside from the stomata, whose role in meeting the compromise between water loss and carbon gain is well documented, the advantage provided by the other regulatory steps is little understood. Modeling experiments in which time constants for the components are varied could help to elucidate how each influences sunfleck use in light regimes with different sunfleck frequencies and durations. A better understanding of the role of sunflecks within tree canopies is also needed, as most research has concentrated on understory plants and tree seedlings, despite the importance of fluctuating light in the canopy itself. The role of other environmental constraints such as high temperatures, reduced water potentials and excessive irradiance in sunflecks needs to be better understood. Finally, we need to understand how changes in the environment due to global climate change will impact sunfleck use, and whether including sunfleck dynamics will improve mechanistic models of ecosystem carbon gain. By bringing these papers together, we hope to stimulate research on these questions among tree physiologists and to emphasize the importance of incorporating realistic, dynamic photosynthetic responses into current models of forest systems.

References

- Abrams MD, Mostoller SA (1995) Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. *Tree Physiol* 15:361–370.
- Allee WC (1926) Measurement of environmental factors in the tropical rain forest of Panama. *Ecology* 7:273–302.
- Barker DH, Logan BA, Adams WW III, Demmig-Adams B (1997) The response of xanthophyll cycle-dependent energy dissipation in *Alocasia brisbanensis* to sunflecks in a subtropical rainforest. *Aust J Plant Physiol* 24:27–33.
- Chen HYH, Klinka K (1997) Light availability and photosynthesis of *Pseudotsuga menziesii* seedlings grown in the open and in the forest understory. *Tree Physiol* 17:23–29.
- Evans GC (1956) An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks. *J Ecol* 44:391–428.
- Gross LJ, Kirschbaum MUF, Pearcy RW (1991) A dynamic model of photosynthesis in varying light taking account of stomatal conductance, C₃-cycle intermediates, photorespiration and RuBisCO activation. *Plant Cell Environ* 14:881–893.
- Han Q, Yamaguchi E, Odaka N, Kakubari Y (1999) Photosynthetic induction responses to variable light under field conditions in three species grown in the gap and understory of a *Fagus crenata* forest. *Tree Physiol* 19:625–634.
- Kirschbaum MUF, Pearcy RW (1988a) Gas exchange analysis of the relative importance of stomatal and biochemical factors in photosynthetic induction in *Alocasia macrorrhiza*. *Plant Physiol* 86:782–785.
- Kirschbaum MUF, Pearcy RW (1988b) Gas exchange analysis of the fast phase of photosynthetic induction in *Alocasia macrorrhiza*. *Plant Physiol* 87:818–821.
- Kirschbaum MUF, Pearcy RW (1988c) Concurrent measurements of oxygen and carbon dioxide exchange during lightflecks in *Alocasia macrorrhiza* (L.) G. Don. *Planta* 174:527–533.
- Küppers M, Timm H, Orth F, Stegemann J, Stober R, Schneider H, Paliwal K, Karunaichamy KSTK, Ortiz R (1996) Effects of light environment and successional status on lightfleck use by understory trees of temperate and tropical forests. *Tree Physiol* 16:69–80.
- Leakey ADB, Press MC, Scholes JD (2003) High-temperature inhibition of photosynthesis is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant Cell Environ* 26:1681–1690.
- Lundegårdh H (1922) Zur Physiologie und Ökologie der Kohlen-säureassimilation. *Biol Zentralbl* 42:337–358.
- Naumberg E, Ellsworth DS (2002) Short-term light and leaf photosynthetic dynamics affect estimates of daily understory photosynthesis in four tree species. *Tree Physiol* 22:393–401.
- Norman JM, Miller EE, Tanner CB (1971) Light intensity and sunfleck-size distributions in plant canopies. *Agronomy J* 75:481–488.
- Ogren E, Sundin U (1996) Photosynthetic response to dynamic light: a comparison of species from contrasting habitats. *Oecologia* 106:18–27.
- Osterhout WJV, Haas ARC (1918) On the dynamics of photosynthesis. *J Gen Physiol* 1:1–16.
- Pearcy RW, Osteryoung K, Calkin HW (1985) Photosynthetic responses to dynamic light environments by Hawaiian trees. *Plant Physiol* 79:896–902.
- Pearcy RW, Chazdon RL, Gross LJ, Mott KA (1994) Photosynthetic utilization of sunflecks: a temporally patchy resource on a time scale of seconds to minutes. In: Caldwell MM, Pearcy RW (eds) *Exploitation of environmental heterogeneity by plants*. Academic Press, San Diego, pp 175–208.
- Porcar-Castell A, Palmroth S (2012) Modelling photosynthesis in highly dynamic environments: the case of sunflecks. *Tree Physiol* 32:1062–1065.
- Reifsnnyder WE, Furnival GM, Horowitz JL (1971) Spatial and temporal distribution of solar radiation beneath forest canopies. *Agric Meteorol* 9:21–37.
- Sassenrath-Cole GF, Pearcy RW (1992) The role of ribulose-1,5-bisphosphate regeneration in the induction requirement of photosynthetic CO₂ exchange under transient light conditions. *Plant Physiol* 99:227–234.
- Tang Y, Liang NS (2000) Characterization of the photosynthetic induction response in a *Populus* species with stomata barely responding to light changes. *Tree Physiol* 20:969–976.
- Urban O, Kosvancova M, Marek MV, Lichtenthaler HK (2007) Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. *Tree Physiol* 27:1207–1215.
- Urban O, Sptova M, Kosvancova M, Tomaskova I, Lichtenthaler HK, Marek MV (2008) Comparison of photosynthetic induction and transient limitations during the induction phase in young and mature leaves from three poplar clones. *Tree Physiol* 28:1189–1197.
- Walker DA (1973) Photosynthetic induction phenomena and the light activation of ribulose diphosphate carboxylase. *New Phytol* 72:209–235.
- Way DA, Pearcy RW (2012) Sunflecks in trees and forests: from photosynthetic physiology to global change biology. *Tree Physiol* 32:1066–1081.
- Wong S-L, Chen C-W, Huang HW, Weng JH (2012) Using combined measurements for comparison of light induction of stomatal conductance, electron transport rate and CO₂ fixation in woody and fern species adapted to different light regimes. *Tree Physiol* 32:535–544.
- Zhang Q, Chen YJ, Song LY, Liu N, Sun LL, Peng CL (2012) Utilization of lightflecks by seedlings of five dominant tree species of different subtropical forest successional stages under low-light growth conditions. *Tree Physiol* 32:545–553.