Tree Physiology review

Sunflecks in trees and forests: from photosynthetic physiology to global change biology

Danielle A. Way[1,2,4] and Robert W. Pearcy[3]

[1]Nicholas School of the Environment, Duke University, Durham, NC 27708, USA; [2]Department of Biology, University of Western Ontario, London, ON, Canada N6A 5B8; [3]Section of Evolution and Ecology, Division of Biological Sciences, University of California, Davis, CA 95616, USA; [4]Corresponding author (danielle.way@duke.edu)

Sunflecks are brief, intermittent periods of high photon flux density (PFD) that can significantly improve carbon gain in shaded forest understories and lower canopies of trees. In this review, we discuss the physiological basis of leaf-level responses to sunflecks and the mechanisms plants use to tolerate sudden changes in PFD and leaf temperature induced by sunflecks. We also examine the potential effects of climate change stresses (including elevated temperatures, rising CO_2 concentrations and drought) on the ability of tree species to use sunflecks, and advocate more research to improve our predictions of seedling and tree carbon gain in future climates. Lastly, while we have the ability to model realistic responses of photosynthesis to fluctuating PFD, dynamic responses of photosynthesis to sunflecks are not accounted for in current models of canopy carbon uptake, which can lead to substantial overestimates of forest carbon fixation. Since sunflecks are a critical component of seasonal carbon gain for shaded leaves, sunfleck regimes and physiological responses to sunflecks should be incorporated into models to more accurately capture forest carbon dynamics.

Keywords: induction gain, induction loss, isoprene, light stress, photosynthetic induction, xanthophyll.

Introduction

Sunflecks create a continually changing pattern of sun and shade patches, both within a tree canopy and on understory forest plants. Despite being present in any given location in these environments <10% of the time, sunflecks contribute 10–80% of the photon flux density (PFD) available for photosynthesis by understory plants (Chazdon 1988, Pfitsch and Pearcy 1989a, Leakey et al. 2005). Thus, factors that affect sunfleck utilization can be important determinants of the carbon balance of understory plants, such as establishing tree seedlings and saplings, as well as of leaves within the canopy itself.

Here, we review the responses of photosynthetic physiology to sunflecks and the ecological relevance of sunflecks, concentrating on tree species and forest ecosystems. The emphasis of this paper is to survey the sunfleck literature published since Pearcy (1990) reviewed the field, and to emphasize the

potential implications of sunflecks on trees and forests in the light of global change pressures, such as rising CO_2, increasing temperatures and drought.

The nature of sunfleck light regimes

Quantifying sunflecks is somewhat arbitrary since they are typically defined as a continuous excursion above some threshold just above the background diffuse light level or some physiologically relevant level. The threshold therefore varies depending on the species or canopy conditions. The characteristics of sunfleck light regimes in an understory or in a tree canopy depend on attributes such as the canopy height, and canopy structural characteristics such as the clumping of foliage, the flexibility of branches and petioles, and leaf size. Overcast skies block direct beam radiation and can be important in determining the daily or seasonal pattern of sunfleck occur-

rence, while intermittent clouds add to light regime dynamics. Penumbral effects, where leaves in the canopy partially block direct sun from reaching lower leaves, cause sunflecks to have a numbra with full direct beam solar irradiance surrounded by a penumbra where irradiances are gradually reduced towards the diffuse light background (or umbra). At any given point in the penumbra, the sunfleck PFD is a function of the fraction of the solar disk that is obscured by canopy; small gaps in tall canopies create sunflecks that are entirely penumbral, but as gap size increases, a larger and larger fraction is numbra. Due to the slight (0.5°) divergence of the solar beam, sunflecks are spread over a larger area as height to the canopy gap increases. This spreading of the penumbra, while causing the PFD at any given point within it to be dimmer, increases the probability that a given plant or canopy leaf will be in a sunfleck, significantly enhancing photosynthesis (Stenberg 1998, Palmroth et al. 1999). And because the response of photosynthesis to PFD is non-linear, canopy photosynthesis is enhanced when penumbral effects redistribute the PFD from high PFD sunflecks more evenly throughout the canopy, ensuring more leaves receive PFD below the light saturation point of photosynthesis (Stenberg 1998, Palmroth et al. 1999). Simulations show that this enhancement in photosynthesis due to spreading of the PFD of a sunfleck over a larger area can vary from 15 to 140% with depth in a single conifer canopy, or by as much as 200–500% in model systems with varying proportions of numbra and penumbra as compared with simulations with no penumbral effects (Stenberg 1998; H. Tong and R. W. Pearcy, unpublished results). This effect of canopy structure is an important but poorly studied aspect of sunfleck use.

The temporal nature of sunfleck regimes in understories is determined in part by the earth's rotation and by wind-driven canopy movements. Frequently, sunflecks in forest understories are clustered into periods of multiple sunflecks separated by longer periods with few or no sunflecks (Vierling and Wessman 2000). On a clear day, a leaf in the understory may receive only a few sunflecks in the most shaded microsites or up to 300 or more sunflecks. Most of these are shorter than 10 s and only 1–2% are typically large enough to approach full sunlight PFDs because of penumbral effects (Pearcy 1983, Chazdon 1988, Singsaas et al. 2000). However, sunflecks longer than 120 s, which represent only 5% of all sunflecks in forest understories, contribute >75% of the total daily sunfleck PFD (Pearcy et al. 1994). In a recent paper, Miyashita et al. (2012) characterized sunfleck distributions in a Japanese temperate deciduous and coniferous forest understory, as well as in gap sites in each forest type, over an entire year. Unsurprisingly, the evergreen forest understory had the lowest daily accumulated PFD over the year, but also many fewer sunfleck events (PFD > 50 μmol m^{-2} s^{-1}) than the deciduous or gap plots, since evergreen plots had high leaf area indices year-round. All of the high-intensity sunflecks (PFD > 1000 μmol m^{-2} s^{-1}) that did occur in the evergreen plot

were in the growing season (May to October), while the deciduous plot experienced high-intensity light events as early as February (Miyashita et al. 2012).

Sunfleck regimes within forest canopies have not been well studied because of access problems, and some high-frequency measurements of PFD on individual leaves throughout a canopy are only presented as a daily integrated light regime (Posada et al. 2009). From the limited measurements available, strong gradients in sunfleck activity occur through tree canopies: there are many short duration sunflecks reaching full direct-beam PFDs because of canopy movements in the upper layers, but few sunflecks with much lower maximum PFDs (because of penumbral effects) in the bottom layers (Küppers et al. 1996, Vierling and Wessman 2000). The small leaf size in coniferous canopies causes penumbral PFD to be a significant component of the light regime (Stenberg 1998, Palmroth et al. 1999), more so than in broad-leaved evergreen or deciduous canopies (Baldocchi and Collineau 1994). Models have shown that this diffuse light caused by penumbral effects in conifers can improve canopy photosynthesis by up to 40% (Stenberg 1998). In *Populus fremontii* S. Watson and *Populus tremuloides* Michx. canopies, the flattened petioles allow for leaf flutter even at low wind speeds, which creates rapidly varying PFD both on the fluttering leaf surfaces themselves as well as deeper in the canopy (Roden and Pearcy 1993a).

The physiology of sunfleck utilization

Responses of CO_2 assimilation rates to sunflecks are complex because several components of the photosynthetic apparatus with markedly different time constants (τ, the time to reach 63% of the full response) are involved. Light harvesting and energy transfer essentially occur instantaneously relative to the timescales usually considered in physiology, while the initial adjustments in photosynthetic carbon reduction cycle metabolites following a change in PFD take no more than a second or so. Regulation of energy dissipation via non-photochemical quenching of photosystem II does exhibit a dynamic behavior on timescales of seconds to minutes (Porcar-Castell et al. 2006). It is unclear as to whether these regulatory processes play a direct role in the dynamics of photosynthetic CO_2 exchange during the sunfleck itself. However, the slow relaxation of non-photochemical quenching following a sunfleck could transiently limit carbon gain following an intense sunfleck.

In response to a sunfleck, a rapid buildup of high-energy metabolites consisting of ribulose-1,5-bisphosphate (RuBP) and its immediate precursors in the carbon reduction cycle occurs, forming a pool that is available to support a few seconds of continued CO_2 assimilation after the sunfleck. Electron transport initially becomes uncoupled from CO_2 fixation, as evidenced by a burst of O_2 evolution that exceeds CO_2 assimilation

rates at the beginning of a sunfleck (Kirschbaum and Pearcy 1988c). Within a few seconds, however, electron transport and carbon fixation become coupled as metabolite pools become filled. After the sunfleck, CO_2 assimilation supported by this high-energy pool can continue at a decreasing rate for a few seconds, while O_2 evolution decreases almost instantaneously. For short sunflecks (<10 s), this post-lightfleck CO_2 fixation (region 2 in Figure 1) can significantly enhance total carbon gain attributable to a sunfleck by 150–200% as compared with a hypothetical case where the responses to step changes in PFD are instantaneous. However, for longer sunflecks, carbon assimilation during the sunfleck itself dominates, so the additional contribution of post-lightfleck CO_2 assimilation is insignificant.

At timescales of minutes, the utilization of sunflecks is limited by the induction requirement of CO_2 assimilation. Photosynthetic induction in leaves has been shown to involve light regulation of key photosynthetic enzymes and stomatal opening which requires 20 or more minutes for completion and in effect limits the maximum assimilation rate that can be achieved during a sunfleck. Following a long period of shade,

the maximum CO_2 assimilation rates achieved during a sunfleck will be strongly limited by the induction state of the leaf (Figure 1a). However, if the leaf is first exposed to saturating PFD before being briefly shaded, then the response to a subsequent sunfleck will be much greater than that in an uninduced leaf (Figure 1b and c). Similarly, assimilation will increase during a series of sunflecks as induction limitations relax. In effect, induction during one sunfleck primes the leaf so that it is better able to utilize subsequent sunflecks.

The induction requirement consists of two phases. First, when an uninduced leaf is exposed to a light increase there is an initial, almost instantaneous increase in assimilation to a low rate allowed by the metabolite pool sizes and enzyme activation state present in the low light (Figure 1). This is not part of the induction response per se, but it is followed by a fast induction phase lasting 1–1.5 min that is due to the rapid light activation of enzymes in the RuBP regeneration pathway (Kirschbaum and Pearcy 1988b, Sassenrath-Cole and Pearcy 1992). The fast induction phase is most apparent when a fully induced leaf is shaded for a few minutes before the light is increased again (Figure 1b and c). Under these conditions, the
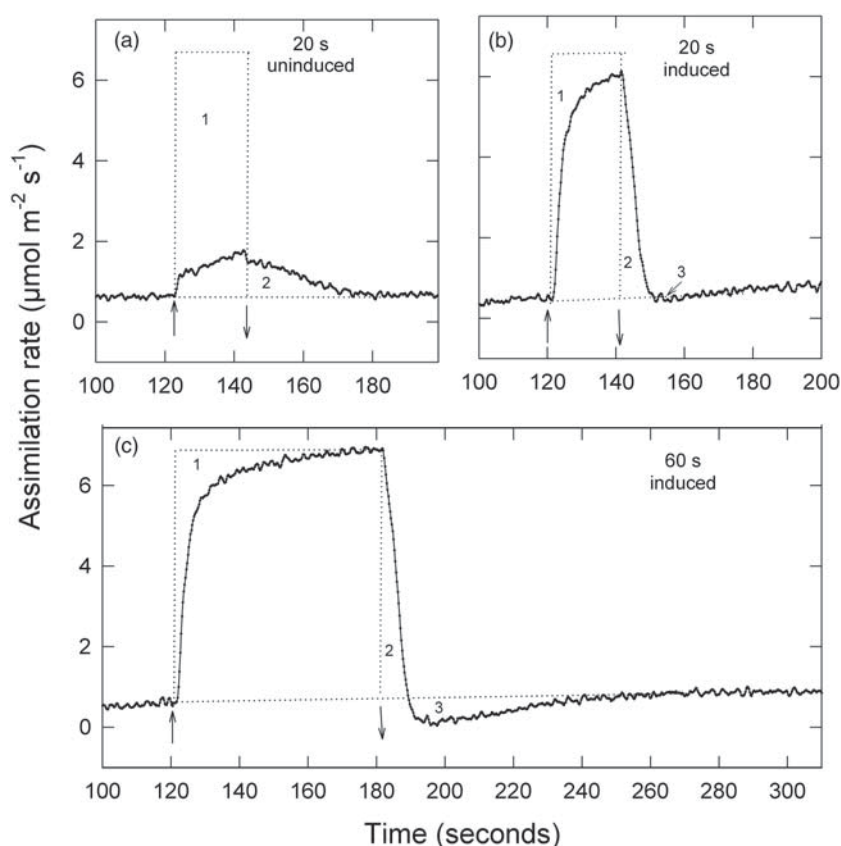

Figure 1. Representative responses of the net CO_2 assimilation rate of *A. macrorrhiza* to 20 s lightflecks (a,b) and to a 60 s lightfleck (c) as measured in a fast-response gas exchange apparatus that completely responded to a step change in CO_2 concentration in 2 s (Kirschbaum and Pearcy 1988c). Panel a is for an uninduced leaf while panels b and c are for an induced leaf. The areas bounded by the dotted lines and the response itself are: (1) the assimilation lost because of induction limitations; (2) the net assimilation gained because of post-lightfleck CO_2 assimilation; and (3) the photorespiratory post-illumination CO_2 burst. (From Pearcy et al. 1996, with permission.)

initial concentration of RuBP available to RuBP carboxylase/oxygenase (Rubisco) is low, but it builds up to saturating levels over ~1 min. With longer periods in the shade, deactivation of Rubisco and stomatal closure become more limiting and the fast induction phase becomes less apparent.

The second, much slower phase of induction is due to the light activation requirement of the primary carboxylating enzyme, Rubisco, combined with an increase in stomatal conductance (g_s). Light activation of Rubisco is relatively slow, with a τ of 4–5 min. Maximum activation is reached within ~10 min, while deactivation following a light decrease is much slower and more variable, with a τ of 20 to 28 min (Seemann et al. 1988, Woodrow and Mott 1989). The reason for the down-regulation being slower than up-regulation is not clear, but this hysteresis is important in the carryover and enhancement of induction from one sunfleck to another. Light regulation of Rubisco involves a reversible addition of Mg^+ and CO_2 to the active site that causes a conformational change in Rubisco (carbamylation) and by the binding of sugar phosphates, especially RuBP, to the inactive enzyme. An auxiliary enzyme, Rubisco activase (that is itself light activated), is necessary for Rubisco activation (Portis 1995) via its facilitation of sugar phosphate removal from Rubisco. Experiments with antisense-mediated reductions of Rubisco activase in tobacco (Mate et al. 1996, Mott et al. 1997) reveal much slower rates of induction that are proportional to leaf activase content. This observation has formed the basis of an interesting model that predicts the optimum allocation of protein between Rubisco and Rubisco activase in different light environments (Mott and Woodrow 2000). In constant light, the distribution of protein between Rubisco and Rubisco activase that maximizes steady-state photosynthetic rates will be the optimum. The increase in CO_2 assimilation rate that can be achieved by allocating more to activase and less to Rubisco is less than that achieved by allocating more to Rubisco, even though Rubisco will not be fully activated because of limiting activase content. In fluctuating light, the optimal allocation predicted by the model is more complex. Shorter sunflecks should favor greater allocation to Rubisco activase at the expense of Rubisco, increasing the rate of activation and hence induction. On the other hand, shorter low-light periods between sunflecks should favor greater allocation to Rubisco. This model awaits empirical tests in sun versus shade plants and in plants acclimated to different light environments.

The role of g_s in the dynamics of induction is quite variable, depending on species, growth conditions and the environment. Increases in g_s during induction typically exhibit a short lag before increasing to a maximum over another 10–60 min (Kirschbaum and Pearcy 1988a, Tinoco-Ojanguren and Pearcy 1993b). When g_s is high, the limitation to induction shifts mostly to Rubisco regulation and the induction response is hyperbolic in shape. Conversely, when g_s is low and more limit-

ing, induction follows a more sigmoidal increase. Studies of the relative role of stomatal versus Rubisco limitations revealed the important role of initial g_s in the shade (Tinoco-Ojanguren and Pearcy 1993b, Valladares et al. 1997, Allen and Pearcy 2000b). The initial g_s, and hence the induction response, has been shown to differ between the morning and afternoon (Pfitsch and Pearcy 1989b, Allen and Pearcy 2000a) and between the wet and dry season (Allen and Pearcy 2000a). The reasons for the daily variation were not clear since there were no obvious environmental correlates, and leaf water potentials (Ψ) and relative humidity hardly differed between the early wet season and the early dry season when measurements were made in these studies. Calculation of the limitations imposed by biochemistry (RuBP regeneration and Rubisco) showed little change over a wide range of initial g_s values, but then showed a sharp increase over a small range of low initial g_s (Figure 2). Thus, in cases where initial g_s was low, and therefore intercellular CO_2 concentrations (c_i) were low during induction, biochemical limitations also relaxed slowly. This is consistent with a co-ordination between Rubisco activation and stomatal conductance at low c_i. Mott and Woodrow (1993) observed a strong dependence of Rubisco activation time on c_i, probably because low c_i slows the rate of CO_2 and Mg^{2+} binding to the Rubisco active site.

In response to a sunfleck, stomata exhibit a distinct pulse response (Kirschbaum et al. 1988, Assmann 1988). This pulse response consists of an initial lag followed by an increase in g_s that continues in low light long after the sunfleck itself (Figure 3). An often slower closing response is then initiated that returns g_s back to the initial levels measured prior to the sunfleck. Tinoco-Ojanguren and Pearcy (1992) compared a pioneer tree, *Piper auritum* Kunth, and a shade-tolerant shrub,
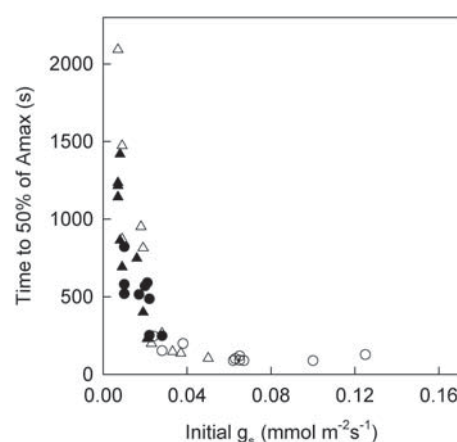

Figure 2. Relationship between initial stomatal conductance (g_s) of *P. marginata* leaves in low PFD before induction and the time required to reach 50% of the fully induced photosynthetic rate. Circles show morning measurements while triangles are for afternoon measurements. Filled symbols are wet-season measurements while open symbols are for dry-season measurements. (From Allen and Pearcy 2000a, with permission.)
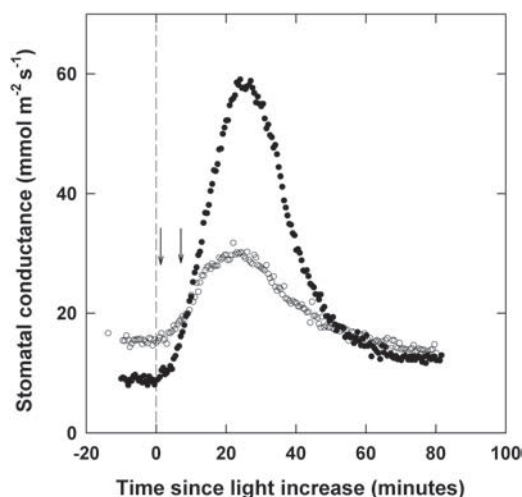
Figure 3. The pulse response of stomatal conductance of leaves of a tropical forest understory shrub to a 1 min (open circles) and an 8 min (filled circles) lightfleck. The dashed line shows the time when the PFD was increased while the down-arrows show when it was decreased. Note that the maximum stomatal conductances were not achieved until 21 min after the 1 min lightfleck and 16 min after the 8 min lightfleck. (From Tinoco-Ojanguren et al. 1992, with permission.)

Piper aequale Vahl., acclimated to high and low light and found that despite essentially identical steady state responses of g_s when both were grown in the shade, the pulse responses were markedly different. Although the opening response in both species continued after a sunfleck for 20–40 min, the pulse response was much lower and more symmetrical in *P. auritum* than *P. aequale*. Conversely, when grown in high light the pulse response was much greater in *P. auritum* than *P. aequale*. The large and hysteretic pulse response in *P. aequale* was shown to improve carbon gain by 30–200%, depending on sunfleck duration. In contrast, the small stomatal response to sunflecks in *P. auritum* shade plants resulted in no significant improvement in the use of subsequent sunflecks. High vapor pressure deficit (VPD) caused stomatal closing in *P. aequale* to be faster and the pulse response to become more symmetrical than what was observed at low VPD, which is consistent with greater water conservation (Tinoco-Ojanguren and Pearcy 1993a). While a pulse response would seem to be wasteful in terms of water, the resulting water loss would be quite low at the high humidity characteristic of tropical forest understories.

The past 25 years have yielded many studies of induction responses comparing plants with different ecological preferences such as shady understories versus sunny gaps, and also for plants grown under different environmental conditions. The pattern that emerges from these studies is that plants in shady understories or grown under low-light conditions usually have, with some exceptions (Rijkers et al. 2000, Naumberg and Ellsworth 2000), faster rates of induction and reach 90% of full induction in a shorter time than plants in more open habitats

or grown in high-light environments (Tang et al. 1994, Küppers et al. 1996, Ogren and Sundin 1996, Chen and Klinka 1997, Valladares et al. 1997, Urban et al. 2007, Montgomery and Givnish 2008). Similar comparisons of early, mid- and late successional species reveal generally faster induction and slower induction loss in the latter groups, while induction was also faster in Panamanian tropical forest understory species with short as compared with long leaf longevities (Kursar and Coley 1993, Zhang et al. 2012). Much of the faster induction response appears to be explained by the higher initial g_s prior to a light increase (Figure 2) (Valladares et al. 1997, Han et al. 1999, Allen and Pearcy 2000a, 2000b, Wong et al. 2012). Meta-analyses, however, have mostly failed to reveal consistent differences related to successional status or growth conditions. Vico et al. (2011) compiled a database of τ for increases and decreases in g_s from over 60 published studies and found smaller values for increases than decreases, but also found that values for increases and decreases were strongly correlated. Time constants were smaller for graminoids and for species from drier habitats, but otherwise there was no consistent factor explaining the variation in τ. A somewhat smaller database compiled by Naumberg and Ellsworth (2000) revealed no consistent relationship between shade tolerance and induction times; the only apparent trend was for gymnosperms to exhibit slower induction than angiosperms. However, comparisons between studies are not straightforward because of differences in methodology and environment. For example, leaves that were in darkness prior to induction exhibit slower induction responses than those that were in shade light (Naramoto et al. 2001). As discussed earlier, the time of day and season can affect the rate of induction and the partitioning of limitations to stomata versus biochemistry. Additionally, induction has been found to be faster in plants in situ in the understory than in potted plants in a growing house (Kursar and Coley 1993) and to vary with leaf age (Urban et al. 2008).

How much do sunflecks contribute to carbon gain?

The daily contribution of sunfleck utilization by leaves can be determined by integrating the diurnal course of photosynthesis and PFD and separating carbon gain due to sunflecks from that due to background diffuse PFD. The carbon gain can then be compared with a steady-state model to address the question of how limitations or enhancements to sunfleck use influence carbon gain. The few available studies of this type reveal wide variation, with sunflecks contributing from 30 to 60% of the daily carbon gain in tropical forest understories (Björkman et al. 1972, Pearcy and Calkin 1983, Pearcy 1987) but as little as 10–20% for deciduous forest tree seedlings (Schulze 1972, Weber et al. 1985). The low contributions in the deciduous forest may be due to the higher diffuse light level in this habitat

and also the low photosynthetic capacity of the seedlings. The contribution of sunfleck utilization to the diurnal carbon gain of *Adenocaulon bicolor* Hook. on clear days in different microsites in a redwood forest understory revealed a wide variation from 30 to 65% (Pfitsch and Pearcy 1989a); this variation was more due to differences in sunfleck PFD ($r^2 = 0.81$) and less to differences in diffuse PFD ($r^2 = 0.54$) among the microsites. Of course, cloudy days reduce the annual contribution of sunflecks. Pearcy and Pfitsch (1991) assessed the annual contribution for *A. bicolor* in a redwood forest understory by measuring $\delta^{13}C$ ratios of the biomass that depend on the intercellular CO_2 pressure at the time the carbon was fixed (Farquhar et al. 1982). Intercellular CO_2 pressures are lower and $\delta^{13}C$ are higher for carbon fixed during sunflecks as compared with carbon fixed during diffuse light. The annual contribution of photosynthesis during sunflecks derived in this way ranged from 9% in sites with the least annual sunfleck PFD to 46% for sites with the greatest sunfleck PFD. Thus, sunflecks can be a significant driver of carbon gain on both a daily and annual basis.

Comparisons of the diurnal course of leaf level carbon assimilation to the predictions of a steady-state model can provide insights into the physiological and biochemical limitations to sunfleck utilization. The steady-state model is parameterized from a light response curve and then applied to the diurnal course of PFD (e.g., Posada et al. 2009, Miyashita et al. 2012). Several different equations describing the light response of photosynthesis have been used, but the essential point is that step change in PFD yields an instantaneous step change in assimilation in a model of this type. Using this approach, Pfitsch and Pearcy (1989a) found that the steady-state model overestimated daily carbon assimilation by 20 to 30% on clear days with substantial sunfleck activity, but by only 3% on cloudy days when there was no sunfleck activity, which is consistent with a significant induction limitation to sunfleck use in the understory. A similar overestimation by a steady-state model as compared with measurements was found for *Fagus sylvatica* L. seedlings in a deciduous forest understory (Schulte et al. 2003).

Further insights into the contribution of sunfleck utilization can be gained by the application of dynamic models of photosynthesis (Figure 4). Several dynamic models directed at understanding sunfleck use have been developed that start with the widely used Farquhar et al. (1980) model. This model is then modified to make it dynamic by including relevant metabolite pool sizes and light regulation of key enzymes and coupling it to a dynamic stomatal model (Kirschbaum et al. 1988). The models of Pearcy et al. (1997), Kirschbaum et al. (1998) and Naumberg and Ellsworth (2002) are all derived from the model of Gross et al. (1991). The model of Stegemann et al. (1999) is more empirical, focusing on differential equations to simulate induction gain and loss. These models have all been used to reveal large dynamic limitations to daily carbon
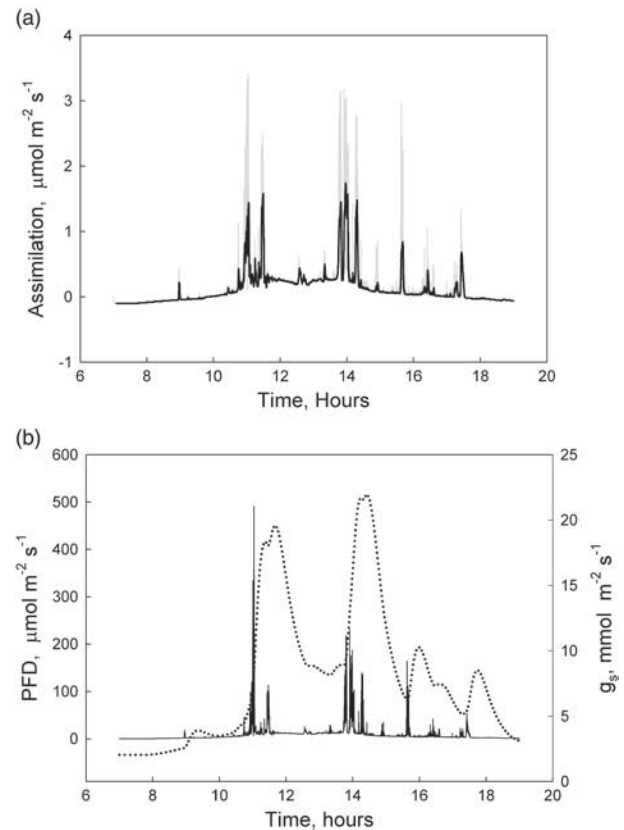

Figure 4. Simulated diurnal course of net CO_2 assimilation and stomatal conductance of *Psychotria marginata* in response to a PFD time series recorded at 1-s intervals in the understory of an Australian tropical forest. Panel a shows the dynamic simulation (black line) with the Pearcy et al. (1997) model and the steady-state simulation (gray line) with the same model. Panel b shows the measured PFD input (black line) and the dynamic simulation of stomatal conductance (dotted line).

assimilation in understories, and thus offer a cautionary note regarding reliance on the much simpler steady-state models for understanding carbon budgets of understory plants; similar caveats are likely to apply to tree canopies. Application of the Pearcy et al. (1997) model to simulate assimilation and stomatal conductance of an understory herb, *Alocasia macrorrhiza* (L.) G. Don, predicted a daily carbon gain 1 to 25% lower than a steady-state output of the model, with the greatest difference occurring when sunflecks contributed more than 50% of the PFD (Pearcy 2007). Changing parameters to selectively eliminate different dynamic limitations showed that dynamic stomatal responses (Figure 4b) imposed the greatest limitation, followed by limitations on sunfleck use imposed by light regulation of Rubisco. In contrast, post-lightfleck CO_2 assimilation made no contribution to carbon gain because short sunflecks, for which it is a significant contributor, made up only a small fraction of the sunfleck PFD. Naumberg and Ellsworth (2002) compared the simulated dynamic and steady-state carbon gain for four tree species and found similar overestimations by the steady-state model that also depended on species-specific

dynamic responses. Thus, the fast induction gain and slow loss found for *Liriodendron tulipifera* L. resulted in closer agreement between the steady-state and dynamic simulations than that found in *Acer rubrum* L., which had lower steady-state g_s and also faster induction loss. Montgomery and Givnish (2008) utilized the Naumburg and Ellsworth model to predict the crossover point in daily carbon gain for two Hawaiian *Lobelia* species occurring along a light gradient and showed that the crossover point, where carbon gain in one species became superior to that of the other, was close to the observed crossover in the relative dominance of the two species along the light gradient. Overall, these studies show that ignoring dynamic responses could yield misleading inferences about the performance of understory plants. And as sunflecks can contribute a substantial portion of daily light and carbon fixation in forest canopies, it is not surprising that incorporating sunfleck processes into models of forest carbon fluxes improves their performance. Alton et al. (2007) found that adding functions for both leaf orientation within forest canopies and a probability distribution for sunfleck occurrence to the land-surface scheme JULES improved its ability to predict how gross primary productivity responded to light in three different forest types.

Despite the importance of incorporating dynamic light responses into models of forest carbon gain (as seen in Alton et al. 2007), to date there has been relatively little attention given to the role of sunflecks in tree canopies. While there has been recognition of the importance of how canopy structure alters penumbral effects in tree canopies (Stenberg 1998, Palmroth et al. 1999), these models and those that account for detailed PFD regimes in various canopy layers (Kim et al. 2008, Sterck and Schieving 2011) or high-frequency light intensity data (Posada et al. 2009, Miyashita et al. 2012) do not incorporate dynamic photosynthetic responses, instead relying on simpler static models of photosynthesis that are likely to overestimate forest carbon gain. Küppers et al. (1996) have shown with arrays of multiple quantum sensors that there are strong gradients of sunfleck activity from the upper to lower crown, both in an understory tree and within a tree crown in a canopy gap; similar results were obtained by Vierling and Wessman (2000) for a tropical forest tree canopy. Thus, it could be expected that the dynamic responses of photosynthesis to PFD changes would impact on crown carbon gain. Aspen (*P. tremuloides*) and cottonwood (*P. fremontii*) canopies present interesting cases because leaf fluttering occurs at a threshold wind speed of only ~1 m s^{-1}. Leaf fluttering creates a highly dynamic light environment in aspen canopies, both at the top of the crown and deeper due to increased direct beam penetration (Roden and Pearcy 1993a). Fluttering leaves at the top of the canopy intercepted less light, whereas lower canopy leaves intercepted more light as compared with still conditions. Simulations of the fluttering of individual leaves with the Pearcy et al. (1997) model with PFDs recorded at 10 Hz revealed that post-lightfleck CO_2 fixation increased photosynthesis by 10–15% in fluttering versus fixed leaves (Roden 2003). Overall canopy carbon gain was estimated to be increased by 10% due to increased light penetration and post-lightfleck CO_2 fixation as compared with still conditions (Roden and Pearcy 1993b). Further studies are needed within tree canopies to understand the role of the dynamic light environment in determining forest carbon gain and of the effects of crown structure and leaf morphology on creating these dynamic light environments.

Sunfleck tolerance mechanisms

While sunflecks can be critical to the survival of understory plants, they can be a mixed blessing. At the two ends of the continuum of leaf responses to light are shade and sun leaves (Boardman 1977, Givnish 1988). The characteristics of a shade leaf maximize light capture, but reduce the costs of maintaining excess photosynthetic machinery: shade leaves have a high specific leaf area with few layers of palisade mesophyll cells and high chlorophyll concentrations per unit dry mass, but low concentrations of Rubisco and nitrogen (table 1 in Givnish 1988). Sun leaves generally have the opposite traits to maintain a high maximum photosynthetic rate. Because the relatively low investment in photosynthetic proteins yields a low light-saturated photosynthetic rate, a classic shade leaf risks photoinhibition and damage from the high PFD of sunflecks, while a classic sun leaf will be ill-suited to shade conditions, overinvesting in photosynthetic proteins that cannot be fully utilized. The sudden and large variations in PFD mean that understory leaves exposed to sunflecks must not only be able to regularly function as shade leaves, but also be able to minimize the potential for damage associated with these crucial, brief bouts of bright light. For example, a recent study of three woody species found a significant reduction in the quantum efficiency of photosystem II (i.e., dark-adapted F_v/F_m) after exposure to a PFD of 2000 µmol m^{-2} s^{-1}, with the most photoinhibition occurring in leaves grown at 10% of full sunlight (Wong et al. 2012). And this type of damage appears to have ecological consequences for seedling recruitment. Exposure to high-PFD sunflecks has been correlated with reduced survival of *Abies magnifica* A. Murray seedlings, whereby recruitment was high in plots that received short sunflecks in the morning, but establishment was inhibited in plots with gaps overhead that produced midday sunflecks of high PFD (Ustin et al. 1984).

The ability to tolerate sunflecks can involve numerous mechanisms. Physical movement to avoid excess PFD is one option that operates on multiple scales. Inside chloroplasts, there can be restructuring of the thylakoid grana size and stacking within 10 min of exposure to a high PFD (Rozak et al. 2002). Work on the understory species *Alocasia brisbanensis* (F.M. Bailey) Domin has shown that chloroplasts are positioned periclinally

(parallel to the leaf surface) at low PFD to optimize absorption (Williams et al. 2003); when the same leaf is exposed to a high PFD, chloroplasts reposition themselves anticlinally (perpendicular to the leaf surface) to minimize absorption within as little as two minutes of the change in PFD. The rapidity of this change makes it a viable mechanism for leaves to reduce excess PFD interception during sunflecks, while allowing a return to the previous state soon after the sunfleck disappears. At the whole leaf level, a change in leaf angle at the onset of a sunfleck would reduce PFD absorption, although the default angle for understory leaves may be horizontal to maximize PFD absorption (Valladares and Pearcy 2002). The same appears to hold true within a tree canopy: Posada et al. (2009) reported that leaves with a lower daily PFD were oriented nearly horizontal, while leaves of the same tree receiving higher daily PFD were more steeply angled. For most species, these changes are fixed during development with little later plasticity. However, in a few species, such as *Oxalis oregana* Nutt., leaves can rapidly fold from a horizontal to a vertical position during a sunfleck and then recover in a few minutes after the sunfleck (Powles and Björkman 1981). For those species incapable of rapid leaf movements, other tolerance mechanisms come into greater prominence. A second mechanism for increasing sunfleck tolerance is high g_s, to allow for substantial latent heat loss and rapid diffusion of CO_2 into the leaf (Young and Smith 1979). While this strategy can reduce heat stress and support higher photosynthetic rates, it necessitates access to abundant water, making it unsuitable when water is limiting.

Leaf pigments (including anthocyanins and carotenoids) constitute another set of mechanisms for tolerating the light stress that accompanies sunflecks. In a detailed analysis of the localization of anthocyanins within the canopy of the tree species *Quintinia serrata* A. Cunn., Gould et al. (2000) found evidence for a primary role of anthocyanins in protecting photosynthesis during sunflecks. Within a leaf, anthocyanins were preferentially located in photosynthetic mesophyll tissue, with leaf anthocyanin concentrations increasing with expected annual PFD exposure from nearby gaps (Gould et al. 2000). This likely represents a relatively static response to the sunfleck exposure environment of a specific leaf, but other pigment-based defenses, such as the xanthophyll cycle, are more dynamic.

If intercepted light levels are too great to process through photosynthesis, leaves must safely dissipate excess light energy through mechanisms such as electron channeling through photorespiration (Niinemets et al. 1999) or up-regulation of antioxidants to offset the formation of damaging reactive oxygen species (Grace and Logan 1996, Posch et al. 2008). While these topics have received considerable attention in studies examining responses to different light environments, the most well-studied sunfleck tolerance mechanism in tree species involves a group of carotenoids known as xanthophylls, including lutein and neoxanthin (Demmig-Adams and

Adams 1996, Logan et al. 1997, Königer et al. 1998, Adams et al. 1999, Demmig-Adams and Adams 2006). Sunfleck stress tolerance often involves the xanthophyll cycle, which consists of conversions between three xanthophyll pigments. Under low light, violaxanthin is the predominant xanthophyll cycle representative in leaves. When PFD increases above the light saturation point of photosynthesis, the resulting acidification of the thylakoid lumen leads to the successive removal of two epoxy groups from violaxanthin (V), generating the intermediate molecule antheraxanthin (A), and then zeaxanthin (Z), in a process called de-epoxidation. Zeaxanthin absorbs energy from excited chlorophyll molecules and dissipates it as heat. When PFD declines again, zeaxanthin is epoxidized and the pools of violaxanthin are reformed, preventing wasteful dissipation of light energy through the xanthophyll cycle. A similar cycle, involving the xanthophyll lutein and lutein epoxidase, has been found in some species (including woody plants), and is thought to also facilitate light energy dissipation under high-PFD conditions (García-Plazaola et al. 2007).

Within a tree canopy, concentrations of xanthophyll cycle pigments increase with canopy height, reaching their greatest concentrations in the upper canopy where PFDs are highest (Posch et al. 2008). The xanthophyll cycle ($V + A + Z$) fraction of total leaf carotenoids is positively correlated with daily integrated PFD intercepted, rather than the maximum PFD, such that leaves exposed to sunflecks have intermediate values to deep-shade and sun leaves (Logan et al. 1997, Adams et al. 1999, Tausz et al. 2005). While the proportion of xanthophyll cycle pigments in the de-epoxidized state does not fall to zero overnight in leaves that experience sunflecks during the growing season, pre-dawn values of de-epoxidation (given as the ratio $(A + Z)/(V + A + Z)$) range from as low as 0.04 to as high as 0.50 depending on the individual leaf and species (Logan et al. 1997, Adams et al. 1999, Tausz et al. 2005). The percentage of de-epoxidized xanthophylls rises after a sunfleck, with higher post-sunfleck percentages in leaves that had higher overnight percentages: in *A. brisbanensis*, up to a third of the xanthophyll cycle pool was de-epoxidized after the first day's sunfleck (Logan et al. 1997) and *Nothofagus cunninghamii* (Hook.) Oerst leaves had half of their xanthophyll pool de-epoxidized (Tausz et al. 2005), while in two vine species (*Stephania japonica* (Thunb.) Miers and *Smilax australis* R.Br.), between 70 and 80% of the pool was de-epoxidized (Adams et al. 1999). Despite these differences, relatively little epoxidation occurred between sunflecks in *A. brisbanensis* and the vines, or after 10 min of shade in *N. cunninghamii*, such that the protective capacity of the xanthophyll cycle developed after a single sunfleck tended to remain through the day (Logan et al. 1997, Adams et al. 1999, Tausz et al. 2005). While the retention of de-epoxidized xanthophylls between sunflecks might be expected to reduce the efficiency of light-energy transfer to photosynthesis and hence possibly limit carbon gain in these

low-light periods, the thermal dissipation of light energy by the xanthophyll cycle is dependent not only on $Z + A$, but also on the trans-thylakoid pH gradient (Logan et al. 1997, Adams et al. 1999). Thus, although these changes are not instantaneous, rapid increases in electron transport during transient high PFDs acidify the thylakoid lumen and engage the xanthophyll cycle, while sudden decreases in electron transport after a sunfleck inhibit energy dissipation via the xanthophyll cycle, allowing high photosynthetic light use efficiency instead. Differences in de-epoxidation may also correlate with life history strategies: late-successional tree species had higher values of xanthophyll cycle pool de-epoxidation than early-successional species, which may reflect an adaptation to regenerating in shaded understories with frequent sunflecks (Zhang et al. 2012).

Safely dissipating excess light is critical for preventing damage from sunflecks to leaves, but it does little to protect plants from the direct effects of the rise in leaf temperature that occurs during sunflecks. Leaf temperature increases rapidly during sunflecks as the radiative load on the leaf rises, with temperature increases of up to 10 °C in both tree canopies and understory seedlings (Young and Smith 1979, Singsaas and Sharkey 1998, Leakey et al. 2003). In some species, tolerance of photosynthesis to these temperature increases is provided by isoprene emission. Isoprene (2-methyl-1,3-butadiene) is the most abundant biogenic, volatile organic compound emitted by vegetation, and emissions can account for up to 5–10% of net carbon gain (Sharkey et al. 2001). The benefit of isoprene production to plants appears to be primarily in improving abiotic stress tolerance, particularly the types of stress imposed by sunflecks.

The support for isoprene as a sunfleck tolerance mechanism that protects photosynthetic function comes from a number of lines of evidence. Emission rates are stimulated by both high-light levels and leaf temperatures, such that isoprene emission ramps up rapidly during sunflecks and declines when the sunfleck ends (Figure 5a; Singsaas et al. 1997, Singsaas and Sharkey 1998, Behnke et al. 2010, Way et al. 2011). Blocking isoprene synthesis with inhibitors lowers the temperature at which irreversible heat damage to photosynthesis occurs, while resupplying it exogenously restores the original thermotolerance level (Sharkey and Singsaas 1995, Singsaas et al. 1997, Sharkey et al. 2001), indicating that isoprene emission improves photosynthetic thermotolerance. Similarly, studies using transgenically modified poplars have shown that photosynthesis is less inhibited by repeated sunfleck stresses in naturally isoprene-emitting lines than in lines where isoprene synthesis has been suppressed using RNAi technology (Behnke et al. 2010, Way et al. 2011). Lastly, many of the species that emit isoprene are trees and woody plants that experience sunflecks in their canopy or in forest understories, while isoprene production is rare in plant species that experience chronic, constant high

temperatures and irradiances in their environment (Sharkey et al. 2001).

Isoprene appears to function by protecting photosynthesis during transient heat stress and alleviating oxidative damage during high-light and high-temperature events. An early hypothesis was that isoprene stabilizes chloroplast membranes at supraoptimal temperatures, minimizing leakiness across the thylakoid membrane (Singsaas et al. 1997). Isoprene is lipophilic and extremely volatile, and modeling of the molecule's behavior in lipid bilayers supports a role for increasing membrane stability during high temperatures (Siwko et al. 2007). Recently, Velikova et al. (2011) found the first direct evidence for isoprene's role in improving the thermal stability of thylakoid
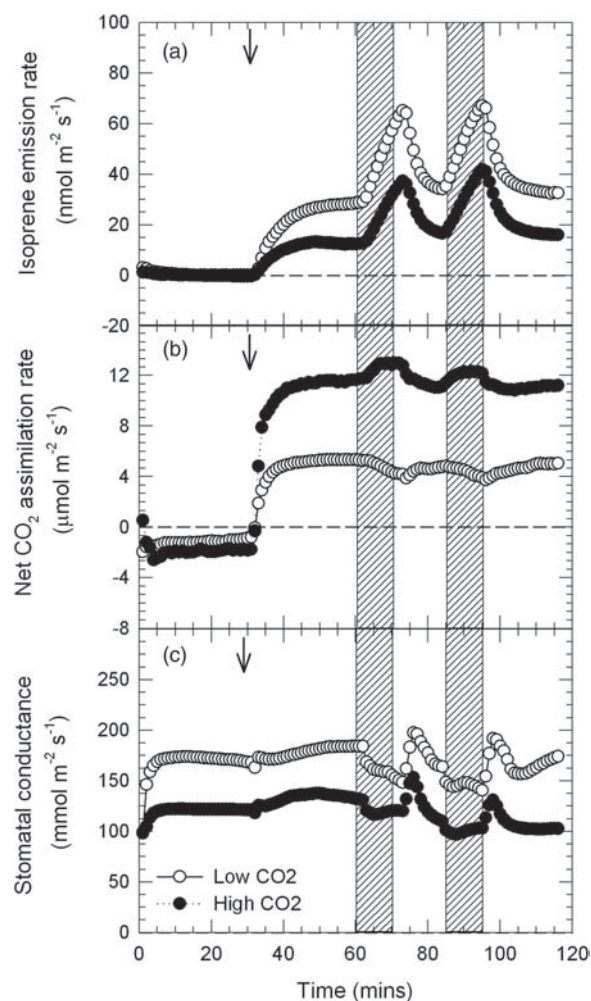

Figure 5. Average response of (a) isoprene emission rates; (b) net CO_2 assimilation rates and; (c) stomatal conductance in *Populus × canescens* (Aiton.) Sm. leaves to fluctuations in PFD and leaf temperature when grown and measured at either low (290 ppm, open circles, solid lines) or high (590 ppm, filled circles, dashed lines) CO_2 concentrations. Leaves were dark acclimated for 30 min at 30 °C; arrows indicate when light was applied (700 µmol photons m^{-2} s^{-1}). Hatched bars indicate when light and heat flecks were applied (1600 µmol photons m^{-2} s^{-1}, 39 °C) before being allowed to recover to pre-fleck levels. Figure 5a and data for Figure 5b and c used with permission from Way et al. 2011.

membranes, using three independent methods. In comparing both wild-type, non-isoprene-emitting *Arabidopsis thaliana* L. Heynh with *A. thaliana* that was genetically modified to produce isoprene and naturally emitting *Platanus orientalis* L. with *P. orientalis* where isoprene emissions were suppressed, Velikova et al. (2011) found thylakoid membranes were more stable and photosynthesis was enhanced at high temperatures when isoprene was present compared to when it was suppressed. The second way that isoprene can increase sunfleck tolerance is by preventing oxidative damage from reactive oxygen species and ozone through its antioxidant properties (Loreto and Velikova 2001, Affek and Yakir 2002, Velikova et al. 2004, Vickers et al. 2009). While these roles for isoprene are often advocated separately, there is no a priori reason to think that they are mutually exclusive, and both are likely to play a role in sunfleck tolerance in woody species that emit isoprene.

How will global change factors interact with sunflecks?

Heat and drought stress

Anthropogenic activities, such as land use change and fossil fuel use, are already increasing air temperatures, with a projected global average warming of ~3 °C by the year 2100 (IPCC 2007). Associated with rising temperatures are changes in precipitation patterns, such that droughts are expected to become more frequent and severe (IPCC 2007). High temperatures and water stress can both limit photosynthesis, and since carbon assimilation during sunflecks is necessary to maintain positive carbon gain in many understory plants and shaded leaves, the effect of these stresses on sunfleck use could alter plant survival and forest succession.

A need to conserve water during drought periods should correlate with tighter stomatal regulation and lower g_s to prevent unnecessary evaporative losses (Valladares and Pearcy 2002). With regard to stomatal movements during sunflecks, water stress might be expected to reduce the speed of stomatal opening during induction gain, reduce the lag times evident in the pulse responses (see Figure 3), and increase stomatal closure during induction loss to minimize transpiration, but these effects would also limit carbon gain during sunflecks (Vico et al. 2011). However, across a wide-range of plant species and functional types, species from dry climates tend to open their stomata faster during sunflecks than species from wet climates, although both groups have similar rates of stomatal closure (Vico et al. 2011). This unexpected result may have to do with the initial g_s pre-sunfleck in xeric and mesic conditions. During dry periods, g_s in shaded leaves usually declines (Valladares and Pearcy 2002, Allen and Pearcy 2000a). Compared with wet season measurements, dry season g_s in the shade was reduced in each of four woody Rubiaceae species, imposing a greater induction limitation on

sunfleck use (Allen and Pearcy 2000a). But this low g_s in the shade during dry periods would necessitate a greater degree of stomatal opening to sunflecks (and thus a faster stomatal response time) if leaves are to reach the same maximum g_s they achieve in the wet season and thus reduce stomatal limitations to photosynthesis compared with the wet season.

In a recent meta-analysis, Vico et al. (2011) found that the stomata of trees and shrubs have longer response times (i.e., higher τ) to step changes in PFD than grasses (consistent with the results of Knapp and Smith 1989), with woody gymnosperms having especially high values of τ. While there is little information on stomatal behavior to sunflecks in gymnosperms, the available data show that they are the only functional group that takes longer to open their stomata when exposed to high PFD than to close them when re-exposed to shade (Vico et al. 2011). Interestingly, the τs of gymnosperms from wet climates are more similar to those of woody angiosperms from dry climates than those from wet climates (Vico et al. 2011). Although the link between stomatal response times to light and tree xylem structure has not been investigated, this is consistent with a hypothesis that plants with high hydraulic conductivity (such as ring-porous trees from mesic climates) might have faster stomatal responses to changes in PFD than diffuse-porous or tracheid-bearing trees with lower hydraulic conductivity (Zhang et al. 2012), since tighter g_s regulation may be needed to prevent excessive transpiration when water transport is rapid. Figure 6 plots τ for stomatal opening and closure for woody species from Vico et al. (2011) against stem-specific hydraulic conductivity rates (k_s) taken from various studies in the literature for the same species (compiled in Manzoni et al. 2012). In cases where τ could not be estimated in Vico et al. (2011) because it was much larger than the time allowed for sun or shade flecks, we used a conservative estimate of τ (three times the duration of the sunfleck in the original study). In general, gymnosperms inhabit the left top corner of the graphs with relatively low k_s and large τ values, while angiosperms have faster stomatal movements and higher k_s (Figure 6). However, *P. tremuloides* (open circle in Figure 6) has much slower stomatal responses than expected from these general trends, which is consistent with the lack of g_s response to PFD changes seen in *Populus* species in recent studies (Tang and Liang 2000, Tomimatsu and Tang 2012; Robert W. Pearcy, personal observation). Studies explicitly linking the rate of stomatal responses to the hydraulic capacity of trees within the same individual could more clearly address this hypothesis.

Because low light levels reduce radiant heat loads and the need for latent heat loss through transpiration, water stress may be expected to be lessened in shaded understory environments, but studies on woody species often find the opposite (Abrams and Mostoller 1995, Valladares and Pearcy 2002). While both shade- and sun-grown *Heteromeles arbutifolia* (Lindl.) M. Roem. had similar pre-dawn Ψ of −0.5 MPa during a moist spring and the shaded shrubs exhibited less negative midday Ψ than the
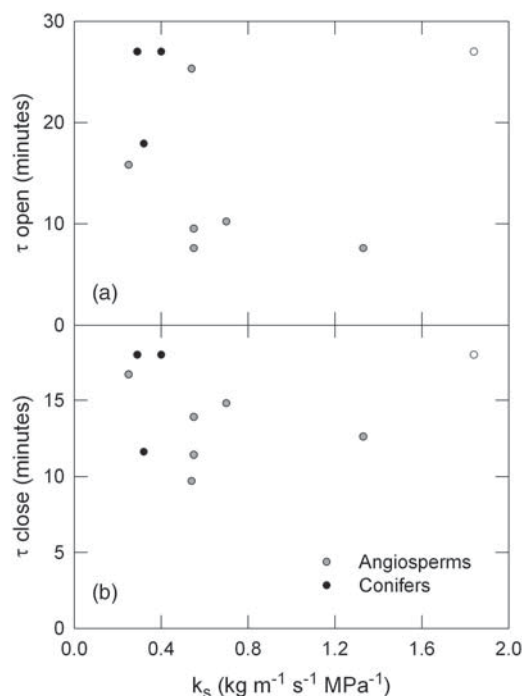
Figure 6. Relationship between stem specific hydraulic conductivity (k_s) and the time constant (τ, from Vico et al. 2011) for (a) stomatal opening; and (b) stomatal closing in response to changes in light in both woody angiosperms (grey circles) and woody conifers (black circles). *Populus tremuloides* is indicated by an open circle; note the different y-axes values.

exposed plants, this pattern was reversed during an exceptionally dry summer (Valladares and Pearcy 2002). Leaf water status decreased in both groups, but significantly more in the shaded plants: both pre-dawn and midday Ψ dropped to −4 MPa in understory *H. arbutifolia*, compared with remaining above −2 and −3 MPa, respectively, in sun plants (Valladares and Pearcy 2002). Similarly, pre-dawn Ψ was lower in shaded, understory leaves than in exposed leaves from six species of temperate tree saplings, although midday measurements were lower in exposed leaves (Abrams and Mostoller 1995). These patterns may be related to the lower root-to-shoot ratio in shade plants as compared with sun plants, a strategy that maximizes leaf area and hence potential carbon gain: this reduction in the root-to-shoot ratio occurs in oak seedlings grown under increasing sunfleck conditions (Holmes 1995). But a lower root-to-shoot ratio also lowers potential drought tolerance (Givnish 1988, Valladares and Pearcy 2002). Since open-grown tree species are better able to recover from low midday Ψ than shaded conspecifics (Abrams and Mostoller 1995), understory plants may be particularly vulnerable to droughts. This is also consistent with data showing that plots with long, intense sunflecks have lower tree seedling densities than plots with shorter, lower-intensity sunflecks on south-facing slopes in North America, which may reflect either cumulative light stress or increased water stress from high radiation loads (Ustin et al. 1984).

The stronger drought stress imposed on understory woody plants compared with full-sun individuals is also reflected in their ability to fix carbon. The sharp decline in Ψ during drought in both sun and shade *H. arbutifolia* coincided with a reduction in g_s, but while sun-exposed leaves maintained substantial daily carbon gain during the drought, understory leaves that depended on sunflecks were barely capable of achieving positive daily carbon balance (Valladares and Pearcy 2002). Reductions in photosynthesis were attributable to stomatal closure, but also to reduced carboxylation efficiency during the drought, severely limiting the carbon gain of understory *H. arbutifolia* in comparison with sun plants (Valladares and Pearcy 2002). Initial g_s is strongly correlated with induction gain time (Figure 2, see also Wong et al. 2012), so leaves that close their stomata during low PFD due to water stress will be less capable of using sunflecks. This is supported by work from Tang and Liang (2000) who showed that in a poplar species with stomata that were relatively insensitive to changes in PFD, drought stress increased the induction time for low-light, but not for high-light, leaves.

While drought can affect leaves that depend on sunflecks more than leaves grown in open light, so can heat. As discussed above, sudden increases in radiation during sunflecks lead to concomitant rises in leaf temperature (Young and Smith 1979, Singsaas and Sharkey 1998, Leakey et al. 2003), a combination of stresses that can be particularly damaging to leaves (Königer et al. 1998). Large leaf sizes, horizontal orientations and low wind speeds in the understory are conducive to achieving high leaf temperatures during sunflecks. In one of the few studies to investigate how high temperatures modify sunfleck use, Leakey et al. (2003) found that carbon gain in forest seedlings during a series of sunflecks was 59% lower in leaves measured at 38 versus 28 °C. This was partly due to enhanced photorespiration rates, but steady-state measurements of net photosynthesis predicted a 40% inhibition in carbon gain by the higher temperatures, indicating that heat stress was less deleterious under continuous light. The extra effect of heat stress on plants experiencing fluctuating light was caused by a 14% inhibition of light use efficiency at high measurement temperatures, due to a faster induction loss (Leakey et al. 2003). After 10 min of shade, leaves at 38 °C retained only 16% of their induction state and had reduced g_s by ~60%, compared with the 83% retention of induction state and 18% reduction in g_s in the cooler leaves. An increase in the rate of induction loss was also found between 15 and 25 °C in *F. sylvatica* seedlings (although there was evidence for a decline in the rate of induction loss at 35 °C), but induction gain was generally enhanced by increasing temperatures (Küppers and Schneider 1993). However, leaves that receive naturally fluctuating light and temperature may be better able to handle changes imposed by sunflecks: leaf temperature would normally decline between sunflecks, which would help offset the decrease in light use

efficiency caused by enhanced photorespiration when leaf temperatures remain elevated during post-irradiance periods. Thus, while many sunfleck experiments are done with step changes in irradiance but constant or only slightly varying leaf temperatures, a more realistic approach may be to vary both irradiance and temperature (as in Figure 5).

Elevated CO₂

Elevated CO_2 concentrations increase carbon fixation by raising c_i and also cause lower g_s (Ainsworth and Rogers 2007). Both of these effects could improve sunfleck use since high c_i could enhance Rubisco activation (Mott and Woodrow 1993), reducing the time needed for biochemical induction gain, while lower maximum g_s could reduce the time needed to open the stomata fully during a sunfleck (Kosvancova et al. 2009). Studies examining sunfleck utilization in tree species find that, as expected, growth at elevated CO_2 (from ambient + 200 ppm CO_2 to as much as a 1000 ppm CO_2 growth environment) increases steady-state photosynthetic rates (Naumberg and Ellsworth 2000, Leakey et al. 2002, Kosvancova et al. 2009, Tomimatsu and Tang 2012). But there is more variability in the findings regarding how CO_2 concentrations affect induction gain and loss. While high CO_2 did not affect induction gain (measured after 1 min) in four temperate species (Naumberg and Ellsworth 2000), F. sylvatica, Picea abies (L.) H. Karst. and two different Populus species all reached a higher induction state after 50–60 s of high light when grown at elevated CO_2 (Kosvancova et al. 2009, Tomimatsu and Tang 2012). Populus euramericana Guinier and P. abies also took less time to reach 90% of maximum steady-state photosynthetic rates (A_{max}) when grown at high CO_2 than at ambient CO_2, but CO_2 effects were not significant in F. sylvatica or Populus koreana × trichocarpa (Kosvancova et al. 2009, Tomimatsu and Tang 2012). Leakey et al. (2002) found that the shape of the photosynthetic response to a sunfleck was altered in Shorea leprosula Miq., a tropical dipterocarp, such that the time to reach 50% of A_{max} was increased, but the time to reach 90% of A_{max} was decreased, by growth at elevated CO_2. Thus, while high CO_2 increases induction gain in some species, it appears to have little effect in others; variation in the elevated CO_2 concentration used is unlikely to explain these differences, since different species within a given study responded in opposite manners. Part of this difference may be due to species-specific variation in stomatal behavior. By comparing two Populus species with varying stomatal responses to light intensity, Tomimatsu and Tang (2012) showed that the effect of elevated CO_2 on induction gain was stronger in the species with greater light-induced regulation of g_s. When light levels were increased sharply, g_s rose markedly in P. koreana × trichocarpa and quickly reached a maximum regardless of growth CO_2, effectively minimizing stomatal limitations and promoting fast induction gain. However, P. euramericana took longer to gain full induction at ambient CO_2 than high CO_2

because slower stomatal opening at ambient CO_2 led to a longer duration where both stomatal and biochemical limitations reduced carbon fixation (Tomimatsu and Tang 2012).

In contrast, there seems to be general agreement that high CO_2 growth conditions decrease the rate of induction loss (Naumberg and Ellsworth 2000, Leakey et al. 2002). The slower loss of induction also increases photosynthesis in subsequent sunflecks in high CO_2-grown saplings, compounding the 1.4–1.6 times direct enhancement of maximum photosynthetic rates derived from elevated CO_2 (Naumberg and Ellsworth 2000, Leakey et al. 2002). Species-specific differences in induction loss have also been reported, whereby A. rubrum lost induction more rapidly than L. tulipifera (Naumberg and Ellsworth 2000).

The effects of elevated CO_2 on leaf sunfleck use can also alter seedling growth by increasing carbon gain. Leakey et al. (2002) showed that while elevated CO_2 increased seedling carbon gain and growth under both constant light and a shade/sunfleck treatment, the relative enhancement of carbon gain by high CO_2 compared with ambient CO_2 was much greater in the sunfleck treatment (89%) than under uniform light (59%), as was growth, where the relative enhancement by high CO_2 was 60% in sunflecks and only 25% under constant irradiance. The greater response to high CO_2 in the dynamic light regime was caused by two factors. First, elevated CO_2 increased net photosynthesis most significantly at low light levels, thus providing more of a benefit to the leaves experiencing long periods of deep shade (Leakey et al. 2002). Secondly, high CO_2 increased post-lightfleck CO_2 assimilation (region 2 in Figure 1) and almost completely erased the post-illumination CO_2 burst caused by photorespiration (region 3 in Figure 1), increasing the ability of the high CO_2-grown seedlings to maximize sunfleck use for CO_2 fixation (Leakey et al. 2002). Thus, the benefit of rising CO_2 for increasing tree seedling growth may be greatest in dynamic light environments, such as forest understories and lower canopy layers.

Elevated CO_2 also feeds back onto traits that increase sunfleck tolerance. Isoprene emissions in leaves are negatively correlated with atmospheric CO_2 concentrations (Wilkinson et al. 2009): high CO_2 suppresses isoprene production (Figure 5a) and therefore could reduce the ability to tolerate sunflecks in isoprene-emitting species. Instead, elevated CO_2 suppresses photorespiration and increases the thermal optimum for photosynthesis, so high leaf temperatures and PFDs during sunflecks increase net photosynthesis (Figure 5b), even as the sunfleck reduces g_s (Figure 5c); the opposite response in net photosynthesis is seen at low CO_2 concentrations (Figure 5b). Because of these effects, plants with suppressed isoprene emission capability recover photosynthetic capacity from sunfleck-induced stress equally well as isoprene-emitting lines when grown at high CO_2, since photosynthesis is already more heat tolerant (Way et al. 2011). However, the ability to

Table 1. Patterns of response in sunfleck physiological parameters to various climate change stresses. Arrows indicate the direction of the response of the parameter (up = increase, down = decrease), a dash represents no change in the parameter, a question mark shows that we have insufficient data to establish a pattern.

	Elevated CO_2	High temperatures	Drought
g_s	↓	–	↓
Induction gain	↑/–	↑	?
Induction loss	↓	↑	?

produce isoprene has a protective function on photosynthetic sunfleck tolerance when plants develop at low CO_2 concentrations, implying that isoprene-based sunfleck tolerance will be less effective in a future high CO_2 climate (Way et al. 2011).

Because increases in atmospheric CO_2 will happen concurrently with increases in temperature and drought stress, predicting the effects of climate change on sunfleck physiology requires thinking about these changes together. Other global change factors may also be influenced by physiological responses to sunflecks. The ability to use sunflecks or alter the sunfleck regimes experienced by competitors appears to facilitate invasive species success in some studies (Horton and Neufeld 1998, Brantley and Young 2009), which may in turn affect forest community composition and tree seedling survival (Flory and Clay 2009, Marshall et al. 2009). Unfortunately, there are no multi-factor global change experiments addressing sunfleck use. We can, however, search for commonalities where responses to individual drivers may reinforce each other (Table 1). Both CO_2 and drought reduce g_s, while warming effects on g_s are less certain and are often related to associated increases in VPD. Lower initial g_s could mean greater stomatal limitations in the future, unless there are also offsetting τ decreases. The rate of induction gain tends to increase in both elevated CO_2 and temperature studies, implying that if stomatal limitations do not dominate, leaves may be able to make more efficient use of sunflecks in a future climate. In contrast, induction loss responses to CO_2 and temperature appear to be opposing, making it difficult to predict whether post-lightfleck CO_2 assimilation will be altered in a consistent manner. As well, the impacts of drought on changes in induction gain and loss are not clear, and could override physiological responses to warming and high CO_2.

Conclusions

Despite the prevalence of sunflecks in tree canopies and forest understories, the use of sunfleck dynamics and dynamic photosynthetic responses to changing PFD in models of forest carbon fluxes has lagged. Since assuming static responses of photosynthesis to sunflecks can overestimate carbon gain by over 20%, incorporating realistic photosynthetic responses to

variable PFD should be a research priority. However, to accomplish this, we also need a much better understanding not only of how to generalize these dynamic responses (such as by shade tolerance or functional group), but also of how climate change will alter these dynamics. Given the importance of the capacity to use sunflecks for the establishment and growth of forest understory species, addressing these uncertainties should be a goal for both modelers and physiologists.

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.

Adams WW III, Demmig-Adams B, Logan BA, Barker DH, Osmond CB (1999) Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II efficiency in two vines, *Stephania japonica* and *Smilax australis*, growing in the understory of an open Eucalyptus forest. Plant Cell Environ 22:125–136.

Affek HP, Yakir D (2002) Protection by isoprene against singlet oxygen in leaves. Plant Physiol 129:269–277.

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. Plant Cell Environ 30:258–270.

Allen MT, Pearcy RW (2000*a*) Stomatal behavior and photosynthetic performance under dynamic light regimes in a seasonally dry tropical rain forest. Oecologia 122:470–478.

Allen MT, Pearcy RW (2000*b*) Stomatal versus biochemical limitations to dynamic photosynthetic performance in four tropical rainforest shrub species. Oecologia 122:479–486.

Alton PB, North PR, Los SO (2007) The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Global Change Biol 13:776–787.

Assmann SM (1988) Enhancement of the stomatal response to blue light by red light, reduced intercellular concentrations of CO_2, and low vapor pressure differences. Plant Physiol 87:226–231.

Baldocchi D, Collineau S (1994) The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In: Caldwell MM, Pearcy RW (eds) Exploitation of environmental heterogeneity by plants. Academic Press, San Diego, pp 21–71.

Behnke K, Loivamaki M, Zimmer I, Rennenberg H, Schnitzler JP, Sandrine L (2010) Isoprene emission protects photosynthesis in sunfleck exposed grey poplar. Photosynth Res 104:5–17.

Björkman O, Ludlow M, Morrow P (1972) Photosynthetic performance of two rain-forest species in their habitat and analysis of their gas exchange. Carnegie Institution of Washington Yearbook 71:94–102.

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28:355–377.

Brantley ST, Young DR (2009) Contribution of sunflecks is minimal in expanding shrub thickets compared to temperate forest. Ecology 90:1021–1029.

Chazdon R (1988) Sunflecks and their importance to forest understory plants. Adv Ecol Res 18:1–63.

Chen HYH, Klinka K (1997) Light availability and photosynthesis of *Pseduotsuga menziesii* seedlings grown in the open and in the forest understory. Tree Physiol 17:23–29.

Demmig-Adams B, Adams WW III (1996) The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci 1:21–26.

Demmig-Adams B, Adams WW III (2006) Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol 172:11–21.

Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90.

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol 9:121–137.

Flory SL, Clay K (2009) Invasive plant removal method determines native plant community responses. J Appl Ecol 46:434–442.

García-Plazaola JI, Matsubara S, Osmond CB (2007) The lutein epoxide cycle in higher plants: its relationship to other xanthophyll cycles and possible functions. Funct Plant Biol 34:759–773.

Givnish TJ (1988) Adaptation to sun and shade: a whole plant perspective. Aust J Plant Physiol 15:63–92.

Gould KS, Markham KR, Smith RH, Goris JJ (2000) Functional role of anthocyanins in the leaves of *Quintinia serrata* A. Cunn. J Exp Bot 51:1107–1115.

Grace SC, Logan BA (1996) Acclimation of foliar antioxidant systems to growth irradiance in three broad-leaved evergreen species. Plant Physiol 112:1631–1640.

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.

Holmes TH (1995) Woodland canopy structure and the light response of juvenile *Quercus lobata* (Fagaceae). Am J Bot 82:1432–1442.

Horton JL, Neufeld HS (1998) Photosynthetic responses of *Microstegium vimineum* (Trin.) A. Camus, a shade-tolerant, C4 grass, to variable light environments. Oecologia 114:11–19.

IPCC. 2007. Climate Change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, 996 pp.

Kim HS, Oren R, Hinkley TM (2008) Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation. Tree Physiol 28:559–577.

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.

Kirschbaum MUF, Gross LJ, Pearcy RW (1988) Observed and modelled stomatal responses to dynamic light environments in the shade plant *Alocasia macrorrhiza*. Plant Cell Environ 11:111–121.

Kirschbaum MUF, Küppers M, Schneider H, Giersch C, Noe S (1998) Modelling photosynthesis in fluctuating light with inclusion of stomatal conductance biochemical activation and pools of key photosynthetic intermediates. Planta 204:16–26.

Knapp AK, Smith WK (1989) Influence of growth form on ecophysiological responses to variable sunlight in subalpine plants. Ecology 70:1069–1082.

Königer M, Harris GC, Pearcy RW (1998) Interaction between photon flux density and elevated temperatures on photoinhibition in *Alocasia macrorrhiza*. Planta 205:214–222.

Kosvancova M, Urban O, Sprtova M, Hrstka M, Kalina J, Tomaskova I, Spunda V, Marek MV (2009) Photosynthetic induction in broad-leaved *Fagus sylvatica* and coniferous *Picea abies* cultivated under ambient and elevated CO_2 concentrations. Plant Sci 177:123–130.

Küppers M, Schneider H (1993) Leaf gas exchange of beech (*Fagus sylvatica* L.) seedlings in lightflecks: effects of fleck length and leaf temperature in leaves grown in deep and partial shade. Trees Struct Funct 7:160–168.

Küppers M, Timm H, Orth F, Stegemann J, Stober R, Sneider 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.

Kursar TA, Coley PD (1993) Photosynthetic induction times in shade-tolerant species with long and short-lived leaves. Oecologia 93:165–170.

Leakey ADB, Press MC, Scholes JD, Watling JR (2002) Relative enhancement of photosynthesis and growth at elevated CO_2 is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. Plant Cell Environ 25:1701–1714.

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.

Leakey ADB, Scholes JD, Press MC (2005) Physiological and ecological significance of sunflecks for dipterocarp seedlings. J Exp Bot 56:469–482.

Logan BA, Barker DH, 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.

Loreto F, Velikova V (2001) Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. Plant Physiol 127:1781–1787.

Manzoni S, Vico G, Porporato A, Katul GG (2012) Biological constraints on water transport in the soil-plant-atmosphere system. Adv Water Resour. doi:10.1016/j.advwatres.2012.03.016.

Marshall JM, Buckley DS, Franklin JA (2009) Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods. J Torrey Bot Soc 136:342–349.

Mate CJ, von Caemmerer S, Evans JR, Hudson GS (1996) The relationship between CO_2-assimilation rate, Rubisco carbamylation

and Rubisco activase content in activase-deficient transgenic tobacco suggests a simple model of activase action. Planta 198:604–613.

Miyashita A, Sugiura D, Sawakami K, Ichihashi R, Tani T, Tateno M (2012) Long-term, short-interval measurements of the frequency distributions of the photosynthetically active photon flux density and net assimilation rates of leaves in a cool-temperate forest. Agric For Meteorol 152:1–10.

Montgomery RA, Givnish TJ (2008) Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: dynamic photosynthetic responses. Oecologia 155:455–467.

Mott KA, Woodrow IE (1993) Effects of O_2 and CO_2 on nonsteady-state photosynthesis. Plant Physiol 102:859–866.

Mott KA, Woodrow IE (2000) Modelling the role of Rubisco activase in limiting non-steady-state photosynthesis. J Exp Bot 51:399–406.

Mott KA, Snyder GW, Woodrow IE (1997) Kinetics of Rubisco activation as determined from gas-exchange measurements in antisense plants of *Arabidopsis thaliana* containing reduced levels of Rubisco activase. Aust J Plant Physiol 24:811–818.

Naramoto M, Han Q, Kakubari Y (2001) The influence of previous irradiance on photosynthetic induction in three species grown in the gap and understory of a *Fagus crenata* forest. Photosynthetica 39:545–552.

Naumberg E, Ellsworth DS (2000) Photosynthesis sunfleck utilization potential of understory saplings growing under elevated CO_2 in FACE. Oecologia 122:163–174.

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.

Niinemets U, Bilger W, Kull O, Tenhunen JD (1999) Responses of foliar photosynthetic electron transport, pigment stoichiometry, and stomatal conductance to interacting environmental factors in a mixed species forest canopy. Tree Physiol 19:839–852.

Ogren E, Sundin U (1996) Photosynthetic response to dynamic light: a comparison of species from contrasting habitats. Oecologia 106:18–27.

Palmroth S, Palva L, Stenberg P, Kotisaari A (1999) Fine scale measurement and simulation of penumbral radiation formed by a pine shoot. Agric For Meteorol 95:15–25.

Pearcy RW (1983) The light environment and growth of C_3 and C_4 tree species in the understory of a Hawaiian forest. Oecologia 58:19–25.

Pearcy RW (1987) Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory microenvironments. Funct Ecol 1:169–178.

Pearcy RW (1990) Sunflecks and photosynthesis in plant canopies. Annu Rev Plant Physiol Plant Mol Biol 41:421–453.

Pearcy RW (2007) Responses of plants to heterogeneous light environments. In: Pugnaire FI, Valladares F (eds) Functional plant ecology. CRC Press, Boca Raton, pp 213–257.

Pearcy RW, Calkin HW (1983) Carbon dioxide exchange of C_3 and C_4 tree species in the understory of a Hawaiian forest. Oecologia 58:26–32.

Pearcy RW, Pfitsch WA (1991) Influence of sunflecks on the $\delta^{13}C$ of *Adenocaulon bicolor* plants occurring in contrasting forest understory microsites. Oecologia 86:457–462.

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.

Pearcy RW, Krall JP, Sassenrath-Cole GF (1996) Photosynthesis in fluctuating light. In: Baker NR (ed.) Photosynthesis and the environment. Kluwer Academic Publishers, New York, NY, USA, pp 321–346.

Pearcy RW, Gross LJ, He D (1997) An improved dynamic model of photosynthesis for estimation of carbon gain in sunfleck light regimes. Plant Cell Environ 20:411–424.

Pfitsch WA, Pearcy RW (1989a) Daily carbon gain by *Adenocaulon bicolor* (Asteraceae), a redwood forest herb, in relation to its light environment. Oecologia 80:465–470.

Pfitsch WA, Pearcy RW (1989b) Steady-state and dynamic photosynthetic response of *Adenocaulon bicolor* (Asteraceae) in its redwood forest habitat. Oecologia 80:471–476.

Portis AR (1995) Regulation of Rubisco by Rubisco activase. J Exp Bot 46:1285–1291.

Porcar-Castell A, Back J, Juurola E, Hari P (2006) Dynamics of energy flow through photosystem II under changing light conditions: a model approach. Funct Plant Biol 33:229–239.

Posada JM, Lechowicz MJ, Kitajima K (2009) Optimal photosynthetic use of light by tropical tree crowns achieved by adjustment of individual leaf angles and nitrogen content. Ann Bot 103:795–805.

Posch S, Warren CR, Adams MA, Guttenberger H (2008) Photoprotective carotenoids and antioxidants are more affected by canopy position than by nitrogen supply in 21-year-old *Pinus radiata*. Funct Plant Biol 35:470–482.

Powles SB, Björkman O (1981) Leaf movement in the shade species *Oxalis oregana*. II. Role in protection against injury by intense light. Carnegie Institution of Washington Yearbook 63–66.

Roden JS (2003) Modeling the light interception and carbon gain of individual fluttering aspen (*Populus tremuloides* Michx) leaves. Trees 17:117–126.

Rijkers T, de Vries PJ, Pons TL, Bongers F (2000) Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. Oecologia 125:331–340.

Roden JS, Pearcy RW (1993a) Effect of leaf flutter on the light environment of poplars. Oecologia 93:201–207.

Roden JS, Pearcy RW (1993b) Photosynthetic gas exchange response of poplars to steady-state and dynamic light environments. Oecologia 93:208–214.

Rozak PR, Seiser RM, Wacholtz WF, Wise RR (2002) Rapid, reversible alterations in spinach thylakoid appression upon changes in light intensity. Plant Cell Environ 25:421–429.

Sassenrath-Cole GF, Pearcy RW (1992) The role of ribulose-1,5-biscposphate regeneration in the induction requirement of photosynthetic CO_2 exchange under transient light conditions. Plant Physiol 99:227–234.

Schulze ED (1972) Die wirking von Licht und Temperatur auf den CO_2-gaswechel verschiedener Lebensformen aus der Kractschicht eines montanen Buchenwaldes. Oecologia 9:223–234.

Schulte M, Offer C, Hansen U (2003) Induction of CO_2-gas exchange and electron transport: comparison of dynamic and steady-state responses in *Fagus sylvatica* leaves. Trees Struct Funct 17:153–163.

Seemann JR, Kirschbaum MUF, Sharkey TD, Pearcy RW (1988) Regulation of ribulose-1,5-bisphosphate carboxylase activity in response to step changes in irradiance. Plant Physiol 88:148–152.

Sharkey TD, Singsaas EL (1995) Why plants emit isoprene. Nature 374:769.

Sharkey TD, Chen X, Yeh S (2001) Isoprene increases thermotolerance of fosmidomycin-fed leaves. Plant Physiol 125:2001–2006.

Singsaas EL, Sharkey TD (1998) The regulation of isoprene emission responses to rapid leaf temperature fluctuations. Plant Cell Environ 21:1181–1188.

Singsaas EL, Lerdau M, Winter K, Sharkey TD (1997) Isoprene increases thermotolerance of isoprene-emitting species. Plant Physiol 115:1413–1420.

Singsaas EL, Ort DR, DeLucia EH (2000) Diurnal regulation of photosynthesis in understory saplings. New Phytol 145:39–49.

Siwko ME, Marrink SJ, de Vries AH, Kozubek A, Schoot Uiterkamp AJM, Mark AE (2007) Does isoprene protect plant membranes from thermal shock? A molecular dynamics study. Biochim Biophys Acta 1768:198–206.

Stenberg P (1998) Implications of shoot structure on the rate of photosynthesis at different levels in a coniferous canopy using a model incorporating grouping and penumbra. Funct Ecol 12:82–91.

Stegemann J, Timm HC, Küppers MF (1999) Simulation of photosynthetic plasticity in response to highly fluctuating light: an empirical model integrating dynamic photosynthetic induction and capacity. Trees 14:145–160.

Sterck F, Schieving F (2011) Modelling finctional trait acclimation for trees of different height in a forest light gradient: emergent patterns driven by carbon gain maximization. Tree Physiol 31:1024–1037.

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.

Tausz M, Warren CR, Adams MA (2005) Dynamic light use and protection from excess light in upper canopy and coppice leaves of *Nothofagus cunninghamii* in an old growth, cool temperate rainforest in Victoria, Australia. New Phytol 165:143–156.

Tang Y, Hiroshi K, Mitsumasa S, Izumi W (1994) Characteristics of transient photosynthesis in *Quercus serrata* seedlings grown under lightfleck and constant light regimes. Oecologia 100:463–469.

Tinoco-Ojanguren C, Pearcy RW (1992) Dynamic stomatal behavior and its role in carbon gain during lightflecks of a gap phase and an understory species acclimated to high and low light. Oecologia 92:222–228.

Tinoco-Ojanguren C, Pearcy RW (1993a) Stomatal dynamics and its importance to carbon gain in two rainforest *Piper* species. 1. VPD effects on the transient stomatal response to lightflecks. Oecologia 94:388–394.

Tinoco-Ojanguren C, Pearcy RW (1993b) Stomatal dynamics and its importance to carbon gain in two rainforest *Piper* species: II. Stomatal versus biochemical limitations during photosynthetic induction. Oecologia 94:388–394.

Tomimatsu H, Tang Y (2012) Elevated CO_2 differentially affects photosynthetic induction response in two *Populus* species with different stomatal behavior. Oecologia 169:869–878.

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, Sprtova 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.

Ustin SL, Woodward RA, Barbour MG, Hatfield JL (1984) Relationships between sunfleck dynamics and red fir seedling distribution. Ecology 65:1420–1428.

Valladares F, Pearcy RW (2002) Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Nino year. Plant Cell Environ 25:749–759.

Valladares F, Allen MT, Pearcy RW (1997) Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. Oecologia 111:505–514.

Velikova V, Edreva A, Loreto F (2004) Endogenous isoprene protects *Phragmites australis* against singlet oxygen. Physiol Plant 122:219–225.

Velikova V, Varkonyl Z, Szabo M et al. (2011) Increased thermostability of thylakoid membranes in isoprene-emitting leaves probed with three biophysical techniques. Plant Physiol 157:905–916.

Vickers CE, Possell M, Cojocariu Cl, Laothawornkitkul J, Ryan A, Mullineaux PM, Hewitt CN (2009) Isoprene synthesis protects tobacco plants from oxidative stress. Plant Cell Environ 32:520–531.

Vierling LA, Wessman CA (2000) Photosynthetically active radiation heterogeneity within a monodominant Congolese rain forest canopy. Agric For Meteorol 103:265–278.

Vico G, Manzoni S, Palmroth S, Katul GG (2011) Effects of stomatal delays on the economics of leaf gas exchange under intermittent light regimes. New Phytol 192:640–652.

Way DA, Schnitzler JP, Monson RK, Jackson RB (2011) Enhanced isoprene-related tolerance of heat- and light-stressed photosynthesis at low, but not high, CO_2 concentrations. Oecologia 166:273–282.

Weber JA, Jurik TW, Tenhunen JD, Gates DM (1985) Analysis of gas exchange in seedlings of *Acer saccharum*: integration of field and laboratory studies. Oecologia 65:338–347.

Wilkinson MJ, Monson RK, Trahan N, Lee S, Brown E, Jackson RB, Polley HW, Fay PA, Fall R (2009) Leaf isoprene emission rate as a function of atmospheric CO_2 concentration. Glob Change Biol 15:1189–1200.

Williams WE, Gorton HL, Witiak SM (2003) Chloroplast movements in the field. Plant Cell Environ 26:2005–2014.

Wong SL, Chen CW, Huang HW, Weng JH (2012) Using combined measurements for comparison of light induction of stomatal conductance, electron transport rate and CO_2 fixation in woody and fern species adapted to different light regimes. Tree Physiol 32:535–544.

Woodrow IE, Mott KA (1989) Rate limitation of non-steady-state photosynthesis by ribulose 1,5-bisphosphate carboxylase in spinach. Aust J Plant Physiol 16:487–500.

Young DR, Smith WK (1979) Influence of sunflecks on the temperature and water relations of two subalpine understory congeners. Oecologia 43:195–205.

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.