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Commentary

Sunflecks?

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The term 'sunfleck' has been used frequently in the literature to describe the effects of understory sunlight regimes on understory species, and less often for leaves in individual plant crowns or plant canopies (the term 'canopy' will be used here onwards to describe both). Pearcy and Way (2012) and Way and Pearcy (2012) provide recent, comprehensive reviews of over three decades of studies describing the nature and importance of sunflecks to plant ecophysiology. The authors point out the common occurrence of sunflecks in natural environments, as well as the need for more documentation on sunfleck dynamics and utilization, including the modeling of future CO_2 exchange for different plant communities under current scenarios of climate change (Porcar-Castell and Palmroth 2012).

Our motivation for writing this Commentary is to provide a broader, but more definitive, perspective on the intensity and temporal dynamics of the variable sunlight regimes characteristic of virtually all habitats (Figure 1). To begin with, a precise quantitative definition of the frequently used term 'sunfleck', based on the sunlight intensity and duration of a single exposure, is unclear. Although additional terms have been suggested previously (e.g., sunpatch) based on the intensity and temporal dynamics of direct-beam sunlight measured in forest understories (see reviews by Smith et al. 1989, Chazdon and Pearcy 1991), these have not been adopted and the discussion remains imprecise. Thus, a recent review (Way and Pearcy 2012) has generally stated in its opening sentence, 'Sunflecks create a continually changing pattern of sun and shade patches, both within a tree canopy and on understory forest plants'. Is the term 'sunfleck' synonymous with 'sunpatch', or do we need a more definitive view of sun exposure episodes? Even though sunflecks are most often perceived as brief and spatially smaller sun exposures compared with sunpatches, little quantitative information about intensity or duration is available to more precisely define one versus the other. We suggest here that a more quantitative categorization of variable sunlight dynamics, along with the corresponding nomenclature, would provide a more effective approach for interpreting and predicting the ecophysiological impacts of variable sunlight.

Sunlight passing through openings

There are many sources, types and occurrences of variable sunlight patterns in the natural environment (Figure 1). A photon traveling from the sun to a plant leaf must pass through the atmosphere (often polluted), through or between clouds, and through or between plants before being absorbed, reflected or transmitted by a single leaf. Passage of the sun's direct rays through any of the above openings can generate numbra and penumbra that can be predicted according to the size of the opening and distance to the incident surface (e.g., Smith et al. 1989, Cescatti and Niinemets 2004), while reflectance from any surface (except mirror-like) will generate non-collimated, diffuse sunlight from the surroundings. Thus, two general types of sunlight occur—direct-beam (including full-sun numbra and partial-direct beam penumbra) and diffuse light transmitted or reflected from the sky, clouds and surroundings. The word 'numbra' refers here to direct-beam, full sunlight passing through an opening (Smith et al. 1989), not the shade numbra projected by an intercepting object such as a sunlit leaf (Miller and Norman 1971, Cescatti and Niinemets 2004). Generally speaking, direct-beam sunlight will always combine with a diffuse component to give total solar irradiance. As reviewed by Way and Pearcy (2012), sunlight originating from openings in canopies (or even clouds) can project a bright numbra (full sun) surrounded by a less intense penumbral ring, and their absolute and relative sizes are directly proportional to the size of the opening and are inversely related to the distance from the incident surface (Smith et al. 1989). A smaller canopy

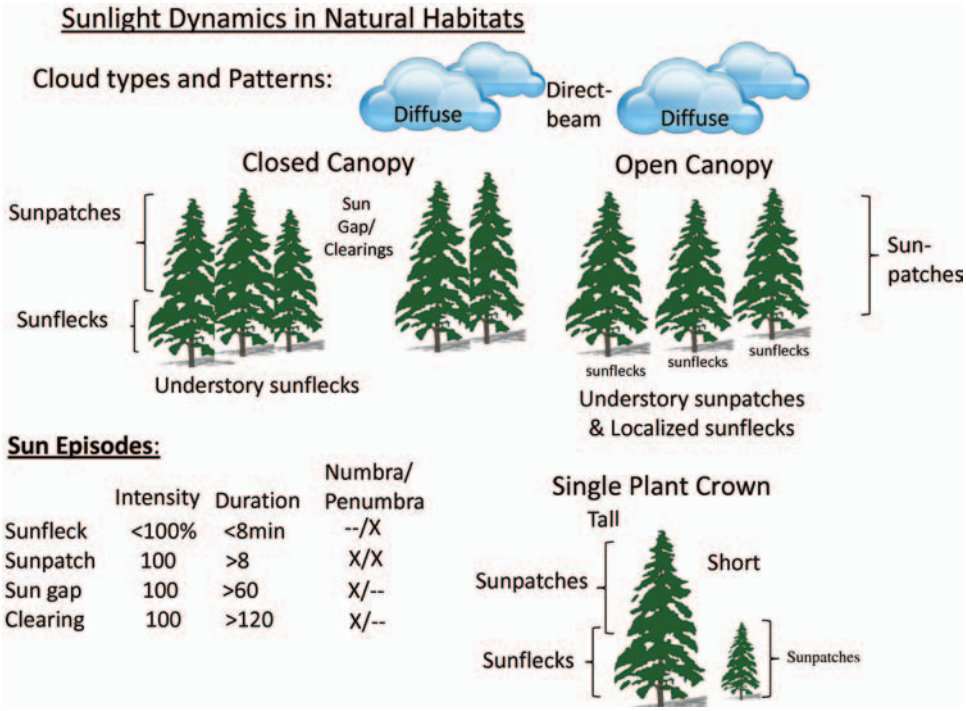

Figure 1. Generalized schematic showing the occurrence of different forms of variable sunlight generated by clouds and vegetation (i.e., sunflecks, patches, gaps and clearings). The intensity of each exposure type is expressed in percent of full sunlight; the occurrence of numbra and penumbra sunlight is indicated by X. The spatial occurrence of sunflecks and sunpatches in both understories and canopies is indicated. Possible changes in photon wavelengths are not indicated. See the text for more details.

opening and a greater distance to the incident surface results in a smaller, more transient full-sun numbra (if present at all) that diminishes until completely absent at a great enough distance (regardless of the opening size) due to the expanding (spreading) penumbral ring of less intense, but still direct-beam sunlight. Also, the numbra and their penumbral rings can overlap in an understory or within a leaf canopy due to adjacent canopy openings. Within plant canopies, a more dense canopy (the number of leaves per m^3) will generate, in general, smaller canopy openings and greater amounts of penumbra closer to the top of the canopy, or adjacent branch layers in conifer trees (Stenberg 1990), although leaf size and aggregation will also be influential. Branch layering in clusters can enhance sunlight entry into canopies at lower solar angles, e.g., forest trees at higher latitudes (Smith and Brewer 1989). Changes in the spectral composition of sunlight can also change when sunlight is transmitted through mediums, e.g., the atmosphere, clouds or leaves, but not through openings.

Variable sunlight: intensity and duration are linked

Overall, little is known comprehensively about the dynamics in intensity and duration that involve the specific forms of variable irradiance found in natural environments, including understories and plant canopies (Figure 1). As a result, associations between these different types of variable sunlight and corresponding physiological responses are rare, even though there is a growing number of studies on intermittent sun exposure in understory species (often labeled loosely as sunflecks; see below), but substantially fewer canopy studies that also employ empirical measurements (Way and Pearcy 2012).

Actual measurements of sunlight within dark understory environments show that the most frequent sunflecks, by far, are significantly >100 μmol m^{-2} s^{-1} of photosynthetically active radiation (photon flux density (PFD), 0.4 – 0.7 microns; <5% of full sunlight) above ambient levels, and last for only seconds at a given location (Smith et al. 1989, Pearcy 1990). Although this intensity is greater than the combined diffuse and penumbral background (ambient) sunlight in dark understories (often below a PFD of 10 μmol m^{-2} s^{-1}), they certainly cannot be considered 'intense' when compared with typical sun episodes of greater intensity and longer duration that occur frequently in a much greater array of understory habitats and leaf canopies. For example, most sun/shade transitions for horizontal leaves at the canopy periphery occur with minimum durations ranging from minutes to tens of minutes, and can experience up to 100% of full sunlight (although leaves at the very top of canopies often have more inclined orientations, reducing the sunlight incidence according to the cosine law). For one quantitative example, a ratio of the opening size to the distance to the incident surface of ~0.006 (e.g., 0.6 m opening and an incident

distance of 100 m) would generate a maximum exposure of nearly 33% of full sunlight that would last for <2 min (see Figures 2 and 3 in Smith et al. 1989). In contrast, a 0.1 m opening in a leaf canopy and an incident leaf 0.5 m distant (i.e., upper canopy) would result in full sunlight (numbra) exposure for ~1 h. For the same opening size (0.1 m) at the top of a tall tree, no full sunlight from this opening would be possible in the understory, only penumbral sunlight (plus ambient shade light) for brief periods lasting only seconds. For any canopy opening to generate full sun (numbra), a minimum duration of ~8 min would have to occur, and would be generated by a ratio of opening size to incident distance of at least 0.015, i.e., a 1.5 m opening ~100 m away, or a 0.15 m opening ~10 m away from an incident leaf (Smith et al. 1989). Thus, full sun intensity is only possible with a large enough and, thus, long-lasting enough sunpatch, challenging the idea that sunflecks can be brief periods of high-intensity sunlight. Sunpatches that generate numbra must also be large enough to last at least 8 min (e.g., as they move across the forest understory), a combination of intensity and duration that can result in significant physiological effects on both plant carbon and water exchange processes (Young and Smith 1979; Knapp and Smith 1987).

Other sources of variable sunlight

In addition to diffuse sunlight generated by non-secular reflection from the surroundings, another common source of variable sunlight incidence is cloudiness. A wide variety of cloud types and temporal patterns can generate a similar range of intensities and durations that is independent of, but superimposed on, the influence of vegetation architecture (Figure 1). Similarly, the dynamics of sun exposure generated by cloud cover is usually not on time scales of seconds (sunflecks), but minutes or even hours (similar to the durations of sunpatches, gaps and clearings) depending on cloud type (e.g., cirrostratus, nimbocumulus, etc.), winds aloft and the ground speed of cloud formation, dissipation and movement. Thus, cloud effects on the sun/shade intensity and duration pattern are added to those created by vegetation structure. In fact, direct-beam sunlight coming through openings in thicker cumulus clouds can be amplified due to reflectance from cloud edges (Figure 2, W.K. Smith, unpublished data). Two previous reports of similarly high values of photosynthetic photon flux density have come from lower-altitude sites (Gu et al. 2001, Dye et al. 2009). Clear skies also generate a diffuse radiation of ~10–15% of total solar irradiance, while clouds can generate a much greater sky component of diffuse irradiance (up to ~1/3 of full sunlight values).

Although ambient diffuse and penumbral direct-beam sunlight can have important effects on sunlight absorption and processing in an understory or plant canopy (e.g., Stenberg 1990), very little is known about their spatial and temporal characteristics and differences (Figure 1). This is despite the universal presence of both for virtually all plants. Notably, the more omnidirectional nature of cloud-generated, diffuse light can be important, especially in enhancing the effective penetration of sunlight into plant crowns and canopies, stimulating canopy carbon gain (Farquhar and Roderick 2003, Gu et al. 2003). At the individual leaf level, an impact on the absorption and processing of diffuse versus direct-beam photons for photosynthesis has also been reported (Brodersen and Vogelmann 2007). Changes in future cloud characteristics are one of the most challenging ingredients in predicting accurately future global-warming impacts.

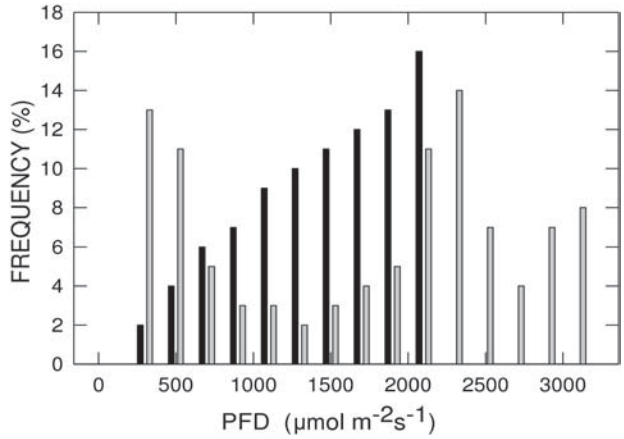

Figure 2. Frequency distribution of PFD values (200 μmol m^{-2} s^{-1} intervals) during a typical clear (black bars) and cloudy (grey bars) day measured on 26 July and 17 August 2009, respectively, on Medicine Bow Peak (3654 m elevation), Snowy Range, Medicine Bow Mountains, SE Wyoming. Specifically, high PFD values correspond to sunlight passing through openings between thick, nimbocumulus clouds typical of afternoon periods. Similarly high PFD values also associated with cloud openings have been reported in two previous studies (Gu et al. 2001, Dye et al. 2009).

A final consideration of the nature of environmental diffuse sunlight regimes is cloud immersion. This relatively common feature of coastal mountains, in particular, can have a significant impact on both understory and canopy sunlight regimes. Cloud immersion can come in varying degrees temporally because of the effects of potentially rapid cloud movements and the accompanying variation of thickness and sunlight penetration. However, little is known about the effects of intensity, duration and wavelength on incident sunlight in the understory and within plant canopies (Reinhardt et al. 2010; Berry and Smith 2012).

Ecophysiological impacts

As opposed to such low-intensity, short-lived sun exposures (i.e., sunflecks), longer durations and correspondingly greater intensities can cause elevated leaf temperatures, especially in

low-wind habitats such as the understory or within dense leaf canopies. In this regard, the often more inclined leaves on the canopy periphery enable sunlight penetration deeper in the canopy, but not wind. It is noteworthy that, because the numbra is surrounded by the penumbral ring, understory or canopy leaves can often experience only penumbra (at the edge of the sunpatch), or both, as the sun moves across the sky and canopy opening. Also, because the typically shorter distance between the periphery and interior leaves of crowns and canopies is less than the distance to the understory, within-canopy sun exposures tend inherently to be of longer duration and, thus, greater intensity (e.g., sunpatches versus sunflecks) than those of the understory beneath. Also, plant species shorter than trees (e.g., shrubs, grasses and herbs) would create more intense, longer sun episodes for the same opening size in the canopy.

It is now well documented that plants in dark understories, or leaves lower in dense leaf canopies, experience numerous sunfleck episodes where the time-dependent process of photosynthetic induction and post-illumination CO_2 fixation may play particularly important roles in dictating carbon gain, growth and survival (Pearcy and Way 2012, Way and Pearcy 2012). However, for the occurrence of sun/shade intervals of minutes or longer, induction effects may become secondary to other potential limitations such as elevated leaf temperatures, water stress and photosynthetic photoinhibition (e.g., Niinemets 2012, Way and Pearcy 2012), especially in plants of short stature and those growing below more sun-exposed, understory habitats. Thus, the physiology of photosynthetic induction and post-illumination photosynthesis should be most important in situations with shorter exposure durations and lower intensities (e.g., smaller canopy openings or taller vegetation). Moreover, the two most apparent situations important for responding physiologically to sunflecks are dark understories or dense leaf canopies. Many other types of habitats and leaf canopies experience several other forms of sunlight exposure such as sunpatches, gaps and clearings (Figure 1). An important perspective to consider is the prevalence in the plant kingdom of dark understories or canopies with a significant number of heavily shaded leaves. Unfortunately, and as pointed out (Pearcy and Way 2012, Porcar-Castell and Palmroth 2012, Way and Pearcy 2012), empirical documentation and quantification of variable sunlight occurrence within different canopies, and the physiological response of different leaves, is rare in the literature (but see the modeling approaches in Thornley 2002 and Posada et al. 2012).

Diffuse sunlight and penumbral sunlight, which vary in intensity and occurrence, are probably the most common sources of variable sunlight in natural environments, both of which have, to our knowledge, not been evaluated comprehensively so far. Given that these are constant and ubiquitous components of the radiation environment of all plants, evidence suggesting that particular species may photosynthesize better under diffuse or penumbral sunlight rather than direct-beam sunlight (Young and Smith 1983, Farquhar and Roderick 2003, Brodersen and Vogelmann 2007) may be particularly relevant. It is also worth noting that penumbra is a less intense form of direct sunlight that is not diffuse in directional nature. However, physiological responses aimed directly at the specific effects of penumbral sunlight, or combinations of diffuse and penumbral PFD, have, to our knowledge, not been reported so far.

Conclusions

As proposed here, the commonly applied term 'sunfleck', as well as other terms describing sun exposure such as 'sunpatch', can be more precisely defined based on intensity and duration. This includes many other specific forms of variable sunlight that can elicit substantial physiological responses in virtually all habitats. A better quantitative understanding and the corresponding nomenclature that distinguishes sunflecks from longer-lasting, more intense sunlight exposures such as sunpatches (as defined here) and sungaps could have important applications in addressing future questions concerning important ecosystem processes such as changing cloud patterns in a global-change future.

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