The Importance of Sunflecks for Forest Understory Plants

Photosynthetic machinery appears adapted to brief, unpredictable periods of radiation

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In many forests with closed canopies, only a small fraction (0.5–5%) of the solar radiation incident above the canopy reaches the understory. Understory plants of these forests experience a highly dynamic light environment, with brief, often unpredictable periods of direct solar irradiance (sunflecks) punctuating the dim, diffuse background irradiance.

The contribution of sunflecks to the daily and seasonal light environment of forest understory plants has long been appreciated (Evans 1956, Lundegarth 1921), but only within the last ten years have detailed studies focused on the extent to which photosynthesis and growth of understory plants are influenced by sunfleck activity (Chazdon 1986, Chazdon and Pearcy 1986a,b, Pearcy 1983, 1987, Pearcy et al. 1985, Pfitsch and Pearcy 1989a,b). These studies have revealed that sunflecks are a vital resource for light-limited understory plants (Chazdon 1988, Pearcy 1988, 1990).

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Photon flux density can increase a hundredfold in seconds

In this article, we describe patterns of sunfleck activity in temperate and tropical forests and discuss the significance of sunflecks for photosynthesis, growth, germination, and reproduction of plants living in shaded forest understory habitats.

What is a sunfleck?

All habitats are characterized by some degree of diurnal fluctuation in irradiance, ranging from sunflecks lasting only a few seconds or less in heavily shaded sites to cloud-induced fluctuations ("shadeflecks") lasting up to an hour or longer in open sites (Knapp and Smith 1987). The nature of sunflecks—their size and shape, duration, and peak photon flux density—depends on the height and precise arrangement of vegetation within the forest canopy as well as the position of the sun in the sky, a function of solar declination and solar time.

The occurrence of a sunfleck at a particular location and time in the forest understory depends on different, often interacting factors: the coincidence of the solar path with a canopy opening; the movement of clouds that obscure or reveal the sun; and the wind-induced movement of foliage and branches (in the canopy or in the understory plants them-

selves). These factors interact to yield a highly dynamic light environment in which the photon flux density reaching leaves can increase or decrease over two orders of magnitude in a matter of seconds.

Depending on the size of canopy openings and the depth of the forest canopy, these changes can be extremely localized, sometimes illuminating only a small surface area on a single leaf (Figure 1; Chazdon et al. 1988, Pearcy 1987). When canopy openings are fairly large, as in the case of open, xeric forests, or branch- and tree-fall gaps of mesic forests, rather large patches (up to tens of square meters) of understory vegetation may be illuminated by a single sunfleck, or, in the terminology of Smith et al. (1989), a "sunpatch."

Just as there is no clear boundary between the understory and the forest edge, the distinction between a sunfleck and a sunpatch is rather arbitrary. In relatively open coniferous forests, for example, sunpatches may last up to an hour or more, and peak photon flux density frequently reaches full-sun irradiance (Reifsnyder et al. 1971, Smith et al. 1989, Young and Smith 1979). In contrast, most sunflecks in closed-canopy understory sites within tropical evergreen forests are less than two minutes long, with maximal photon flux density only rarely reaching full-sun irradiance (Björkman and Ludlow 1972, Chazdon 1986, Pearcy 1983, 1987).

Within a given forest type, sunflecks can be distinguished as brief pulses of predominantly direct radiation in contrast to the relatively con-
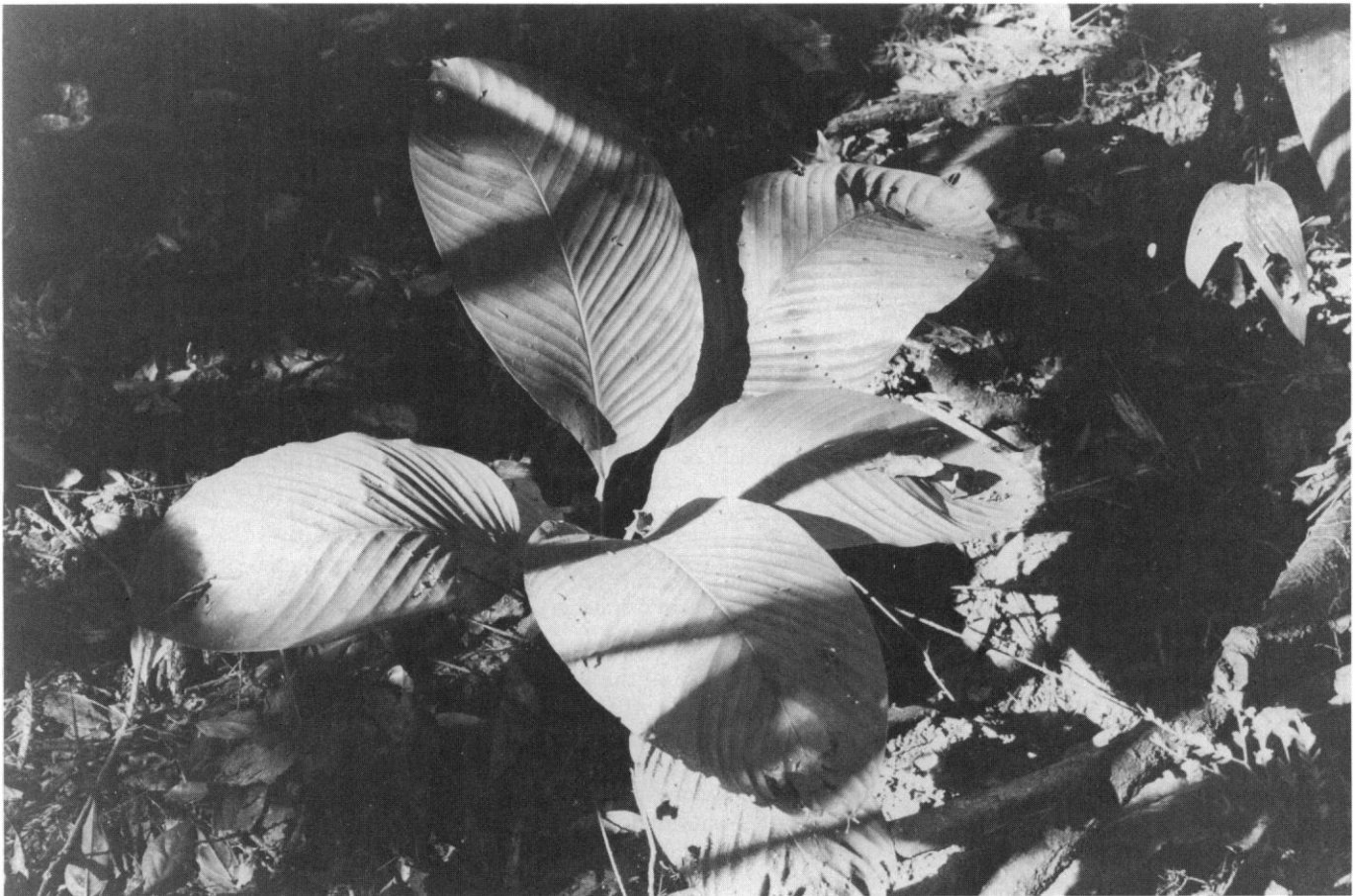
Figure 1. Sunflecks in the understory of a tropical rainforest.

stant levels of background diffuse radiation (Figure 2). Transmitted diffuse radiation has a low red:far-red ratio (0.13–0.70) compared to sunflecks (0.37–1.3), which are enriched in direct sunlight (Chazdon and Fetcher 1984b, Lee 1987).

Because levels of diffuse radiation vary widely within, as well as among, forest types, a universal criterion for describing sunfleck activity cannot be applied. For mesic forest understories, diffuse background radiation generally falls between 5–50 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} (Figure 2; Chazdon and Fetcher 1984a, Chazdon et al. 1988, Pfitsch and Pearcy 1989a, Weber et al. 1985). In xeric forests and beneath crop canopies, diffuse radiation can exceed 100–200 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} on clear days, and more than 350 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} on cloudy days (Pearcy et al. 1990, Young and Smith 1979, 1983).

Appropriate spatial and temporal sampling protocols for measurement of sunfleck activity vary according to sunfleck dynamics and weather con-

ditions within particular forests (Chazdon 1988). A further difficulty in defining sunfleck periods, particularly in tall forests with dense canopies, is the high frequency of sunflecks generated by penumbral effects (Miller and Norman 1971, Smith et al. 1989). To transmit full-sun irradiance, a canopy gap must exceed an angular size of 0.5 degrees, the apparent diameter of the solar disk as viewed from Earth's surface. Penumbral sunflecks contain a relatively high proportion of diffuse radiation, and may therefore reach maximal photon flux density only slightly higher than background diffuse irradiance (Figure 2). Nevertheless, the overall importance of these abundant, weak sunflecks for daily carbon gain may equal or exceed that of relatively infrequent bright sunflecks.

How much light, and how does it vary?

In characterizing sunfleck activity within a particular forest type, several

considerations apply. What is the relative contribution of sunflecks to daily, seasonal, or yearly photon flux density? What is the temporal and spatial distribution of sunflecks? What is the maximal photon flux density reached during sunflecks? Duration, frequency, and peak irradiance are all important determinants of carbon gain during sunflecks (Chazdon and Pearcy 1986b, Pearcy et al. 1985). Furthermore, descriptions of the spatial distribution of sunflecks relative to leaf size and canopy structure of individual understory plants are necessary to evaluate whole-plant patterns of light interception and carbon gain (Chazdon et al. 1988). With these considerations in mind, we summarize here what is known about sunfleck activity in temperate and tropical forest understory habitats.

Sunfleck activity varies greatly within and among forest types. Generally, sunfleck duration and peak irradiance decrease as tree height and leaf-area index increase. On clear
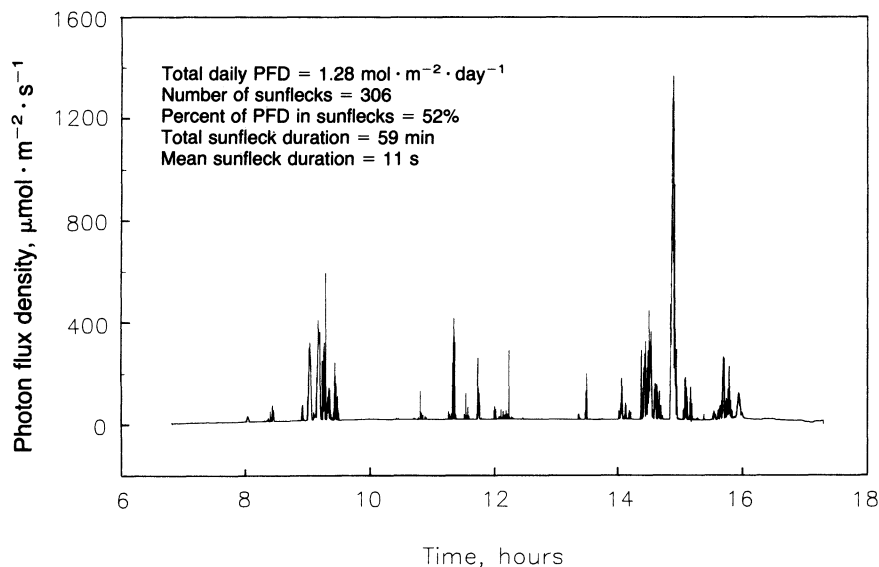
Figure 2. The daily course of photon flux density in the understory of a lowland rainforest in Mexico, showing periods of sunfleck activity throughout the day.

Figure 2 inset text:
Total daily PFD = 1.28 mol · m^{-2} · day^{-1}
Number of sunflecks = 306
Percent of PFD in sunflecks = 52%
Total sunfleck duration = 59 min
Mean sunfleck duration = 11 s

days, from 10 to 85% of daily photon flux density may be contributed by sunflecks, defined as readings exceeding 50 μmol · m^{-2} · s^{-1} (Chazdon 1986, Pearcy 1983, Pfitsch and Pearcy 1989a).

Despite tremendous variation, long-term estimates of the percentage of total photon flux density contributed by sunflecks are remarkably similar between temperate deciduous forests during summer and tropical wet forests. Estimates of 45–55% for a temperate deciduous forest during the summer (Weber et al. 1985) and 40% for a five-week period in a Hawaiian subtropical forest (Pearcy 1983) were consistent with the range of variation measured in studies of five different tropical evergreen and deciduous forests (Björkman and Ludlow 1972, Chazdon 1986, Chazdon et al. 1988, Lee 1989, Pearcy 1988).

Within a single day, the fraction of daily photon flux density contributed by sunflecks can vary more than threefold, even among sites within a one-meter radius (Chazdon 1988, Pearcy 1988). In densely shaded forest understories, most sunflecks are extremely brief. More than 60% of the sunflecks received during the summer in a Hawaiian rain forest understory were less than 30 seconds long (Pearcy 1983), whereas sunflecks in a redwood forest understory had a median duration of 2 seconds (Pfitsch and Pearcy 1989a). Sunflecks tend to be clustered temporally (Figure 2), a

likely consequence of the vertical and horizontal clumping of foliage in forest canopies.

Consistent with their brief exposures, sunflecks are often restricted spatially. Measurements of sunfleck activity along a 2.1-meter line transect in a Mexican rainforest showed that minutes of sunflecks per day ranged from 7 to 33 minutes among 16 sensors spaced 15 cm apart. More than 90% of these sunflecks hit only one sensor (Chazdon et al. 1988). Daily photon flux density varied among sensors by a factor of five. Sunfleck activity was so localized that daily patterns of irradiance among sensors at distances greater than 0.6 m were not significantly correlated (Chazdon et al. 1988).
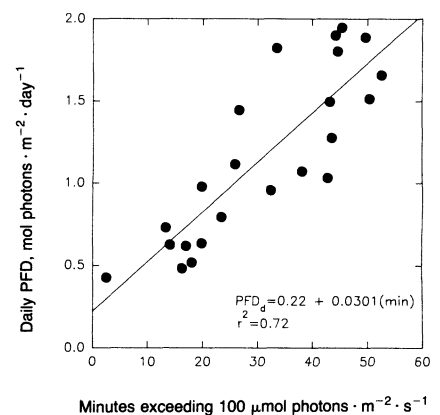
Because of the high frequency of penumbra in tall temperate and tropical forests, the maximal photon flux density reached during sunflecks rarely exceeds 500 μmol · m^{-2} · s^{-1}. During most sunflecks, peak photon flux density is below 100 μmol · m^{-2} · s^{-1} (Figure 2; Chazdon et al. 1988, Pearcy 1983, Pfitsch and Pearcy 1989a).

Variation in daily photon flux density among microsites beneath a relatively closed canopy can be largely attributed to small-scale differences in sunfleck incidence (Figure 3). In forest understory and gap-edge microsites in a Costa Rican rainforest, daily photon flux density was highly correlated with the total duration of sunflecks

(readings higher than 100 μmol · m^{-2} · s^{-1}) on a single day (Figure 3; R^2 = 0.721; $p < 0.001$). A regression line can be used to estimate daily photon flux density in the absence of sunflecks: 0.22 mol · m^{-2} · day^{-1}, in this case. Because light strongly limits production in forest understory plants, spatial and temporal variations in sunfleck incidence are likely to have a significant influence on patterns of growth, survival, and reproduction within understory plant populations.

Importance for carbon gain, growth, and reproduction

Several field studies have documented the importance of sunflecks for daily carbon gain in understory plants. Daily variation in carbon gain by the redwood forest understory herb *Adenocaulon bicolor* was strongly related to daily variation in total sunfleck photon flux density (Figure 4; Pfitsch and Pearcy 1989a). During the summer, an estimated 35% of the daily carbon gain occurred during sunflecks for seedlings of *Acer saccharum* in the understory of a mixed hardwood forest in Michigan (Weber et al. 1985). Such long-term estimates are unavailable for most understory species examined, however. Based on single-day measurements in temperate and tropical forests, the percent of daily carbon gain occurring during

Figure 3 inset:
$PFD_d = 0.22 + 0.0301(\text{min})$
$r^2 = 0.72$

Minutes exceeding 100 μmol photons · m^{-2} · s^{-1}

Figure 3. The relationship between total minutes of sunflecks per day and daily total quantum flux (photon flux density [PFD]) in understory and gap-edge habitats in a Costa Rican rainforest, based on readings taken at five-second intervals. Sunflecks were defined as periods when PFD exceeded 100 μmol · m^{-2} · s^{-1}.
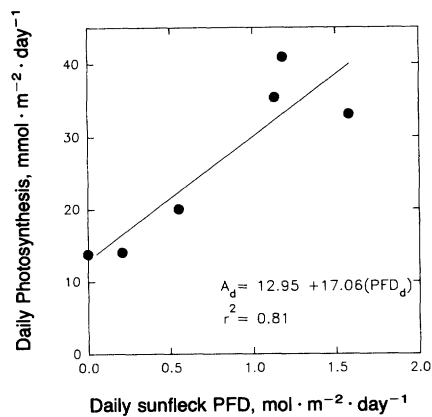
Figure 4. Total daily carbon gain of *Adenocaulon bicolor* as a function of daily photon flux contributed by sunflecks on different days within a redwood forest. (Data from Pfitsch and Pearcy 1989a.)

sunflecks (periods of photon flux density exceeding 50 μmol $\cdot$ m^{-2} $\cdot$ s^{-1}) ranged from 32 to 65% (Björkman et al. 1972, Pearcy 1987, Pearcy and Calkin 1983, Pfitsch and Pearcy 1989a).

Recent studies show that carbon isotope ratios of leaf tissue may reveal long-term patterns of photosynthetic use of sunflecks in understory species (Pearcy and Pfitsch in press). During a sunfleck, the ratio of intracellular to ambient carbon dioxide pressure generally drops because of increased rates of carbon assimilation, accompanied by relatively slow stomatal opening. Because the discrimination by ribulose-1,5-bisphosphate carboxylase/oxygenase against ^{13}C relative to ^{12}C is sensitive to this ratio (Farquhar et al. 1982), the isotopic fractionation from the ambient air to fixed carbon should reflect the overall proportion of carbon fixed during sunflecks (Pearcy and Pfitsch 1991).

Carbon isotope ratios (δ^{13}C) of *A. bicolor* plants in redwood forest understory sites increased significantly as the cumulative daily exposure to sunflecks increased (Pearcy and Pfitsch in press). Based on measured ratios of intracellular to ambient carbon-dioxide pressures during sunfleck and shade periods, Pearcy and Pfitsch estimated that 46% of the carbon gain that went to biomass production was attributed to sunflecks in the brightest *Adenocaulon* sites. In microsites with relatively little direct photon flux density, this percentage

decreased to 9.1%. Although carbon isotope ratios offer a promising technique for an integrative measure of the overall contribution of sunflecks to biomass production, rapid changes in photosynthetic capacity and stomatal conductance, as well as temporal and spatial variation in plant water relations, may reduce the accuracy of these estimates (Knapp and Smith 1987, 1990).

Sunflecks also have been shown to influence the establishment and growth of tree saplings, shrubs, and herbs in forest understories. In a Mexican rainforest, sunfleck activity affected seed germination in the pioneer species *Piper auritum* and *Piper umbellatum* (Orozco-Segovia 1986). Among seeds placed in three understory microsites, percentage germination was significantly higher in the microsite that received longer sunflecks with enhanced red:far-red ratios. The vast majority of shade-tolerant understory species can germinate under diffuse light conditions (Angevine and Chabot 1979).

Evidence is mounting that growth rates and reproductive effort of a variety of herbaceous and woody species are significantly enhanced in understory microsites receiving more total sunfleck irradiance, and therefore greater daily total photon flux density. Seedlings of *Euphorbia forbesii* and *Claoxylon sandwicense* in a Hawaiian evergreen forest understory showed a linear relationship between relative growth rate and the potential minutes of sunflecks per day, as estimated from hemispherical photographs (Figure 5; Pearcy 1983). Height growth of saplings of the shade-tolerant tree *Lecythis ampla* in a Costa Rican rainforest was significantly correlated with the proportion of daily photon flux density contributed by sunflecks (Oberbauer et al. 1988). Long-term studies of *Aster acuminatus* in eastern deciduous forests of the United States show that light levels in understory microsites were significantly correlated with average plant size and sexual reproductive effort among patches (Pitelka et al. 1980). Sexual and vegetative reproductive allocation in ramets of *Arnica cordifolia* were significantly greater in sunpatches than in intermediate and shaded understory microsites (Young 1983).
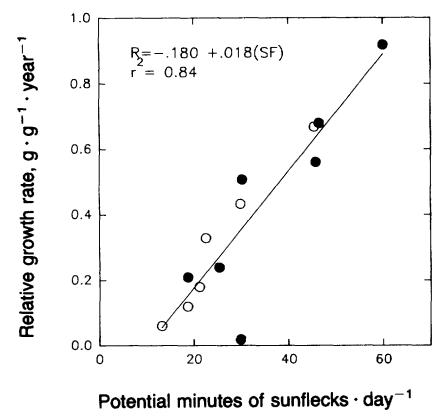

Figure 5. Relative growth rate of *Euphorbia forbesii* (filled circles) and *Claoxylon sandwicense* (open circles) in a Hawaiian forest understory as a function of average duration of potential sunflecks per day (in minutes), estimated from hemispherical photographs. (Data from Pearcy 1983.)

Physiological determinants of sunfleck use

Although understory plants appear capable of maintaining a positive carbon balance in the absence of sunflecks, light remains the major environmental factor limiting growth and reproduction in deeply shaded understory environments. Therefore, shade-adapted understory plants are expected to exhibit well-developed physiological mechanisms for the efficient use of sunflecks. These mechanisms become apparent through investigations of dynamic responses of photosynthesis to rapid fluctuations in irradiance (Chazdon 1988, Pearcy 1988). Analyses of steady-state photosynthetic light responses offer limited insight into patterns of sunfleck use.

Photosynthetic responses to brief sunflecks typical of mesic forest understory habitats are strongly affected by whether or not leaves have been previously exposed to saturating or near-saturating irradiance (Figure 6). In leaves exposed to 10 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} for at least several hours, from 20 to 60 minutes of saturating irradiance are needed to reach steady-state rates of photosynthesis (Chazdon and Pearcy 1986a, Pearcy et al. 1985, Pfitsch and Pearcy 1989b). This induction requirement for maximal photosynthetic rates is an intrinsic feature of photosynthesis in all plants, although the time period for photo-
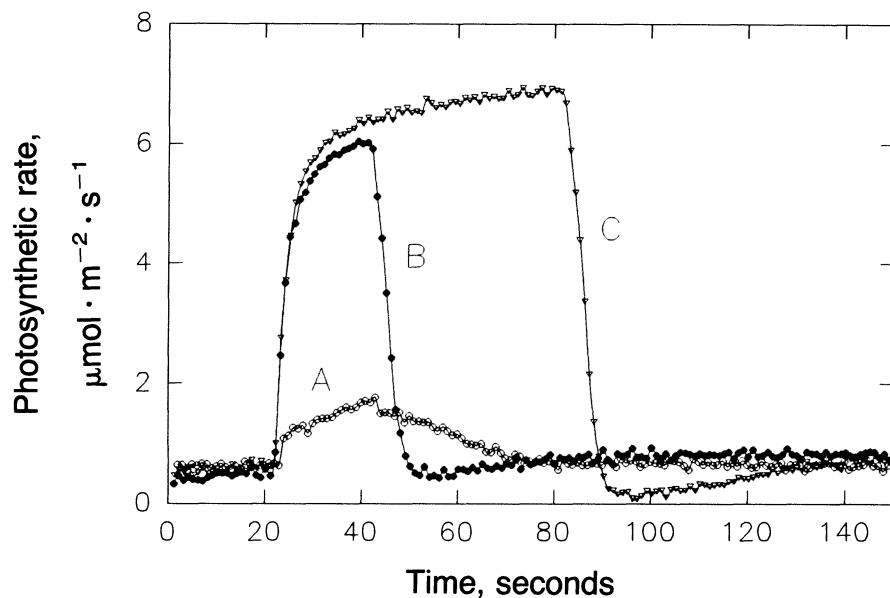
Figure 6. Dynamic photosynthetic responses of the understory species *Alocasia macrorrhiza* to artificial sunflecks of different duration and for leaves at different states of induction. Response A is to a 20-second sunfleck for a leaf that has previously been exposed to low-light conditions for more than 2 hours and is therefore not induced. Response B is also to a 20-second sunfleck but for a fully induced leaf. Response C is to a 60-second sunfleck for a fully induced leaf. Note the development of a post-illumination carbon dioxide burst after the 60-second sunfleck but not after the 20-second sunfleck.

synthetic induction may vary among species and environmental conditions (Walker 1981).

Field and laboratory studies have demonstrated, however, that constant irradiance is not required to effect induction (Chazdon and Pearcy 1986a, Pearcy et al. 1985, Pfitsch and Pearcy 1989b). For the Australian understory species *Alocasia macrorrhiza*, the rate of induction during a sequence of artificial sunflecks 60 seconds long and 120 seconds apart was not substantially different from the rate observed during constant illumination at the same high-light level (Chazdon and Pearcy 1986a). During the initial phases of induction in *Alocasia*, enzymatically based biochemical limitations on photosynthesis appear to be more important than limitations involving carbon dioxide diffusion through partially closed stomata (Seeman et al. 1988), although stomatal limitations increase when initial stomatal conductances are low (Kirschbaum and Pearcy 1988b).

Once *Alocasia* leaves have undergone induction and are again exposed to low irradiance, induction loss follows a negative exponential function, with a half-time of approximately 25 minutes (Chazdon and Pearcy 1986a). For this species, the rate of induction loss was considerably slower than the rate of induction. Other species, such as *Adenocaulon bicolor*, exhibit faster rates of induction loss (Pfitsch and Pearcy 1989b).

Mechanisms underlying differential rates of induction loss among species are as yet unclear. For many understory microsites, sunfleck periods are not sufficiently long to effect complete induction. Leaves of forest understory plants, such as *Adenocaulon*, may therefore remain at intermediate stages of photosynthetic induction during much of the day (Pfitsch and Pearcy 1989b). Because exposure to individual sunflecks enhances the photosynthetic use of subsequent sunflecks, daily carbon gain may be more dependent on the precise temporal sequence of sunflecks than on daily integrated total photon flux density.

The efficiency of sunfleck use can be calculated by comparing observed carbon gain with predicted carbon gain based on an instantaneous change in steady-state rates of photosynthesis at the same high and low photon flux densities. This measure of efficiency increases during leaf induc-

tion, as observed photosynthetic rates gradually approach maximal steady-state rates (Chazdon and Pearcy 1986a,b). Regardless of leaf induction status, however, the efficiency of sunfleck utilization decreases as sunfleck duration increases (Chazdon and Pearcy 1989b, Pearcy et al. 1985). For fully induced leaves of shade plants, carbon gain during five-second sunflecks exceeds predictions based on instantaneous, steady-state rates by 30–80% (Chazdon and Pearcy 1986b, Pearcy et al. 1985). This enhanced carbon gain is due to postillumination carbon-dioxide fixation, a consequence of the transient disequilibrium between the light and dark reactions of photosynthesis.

Studies by Sharkey et al. (1986) indicate that the observed build-up of pools of triose phosphates during artificial five-second sunflecks after induction in *Alocasia* is sufficient to account for the enhancement of carbon gain due to post-illumination carbon-dioxide fixation. This build-up of reduced photosynthetic intermediates requires that the rate of electron transport exceed the potential rate of carboxylation (Kirschbaum and Pearcy 1988a).

As sunfleck duration increases to 40 seconds or more, observed carbon gain is equal to or less than steady-state predictions (Chazdon and Pearcy 1986b, Pearcy et al. 1985, Pfitsch and Pearcy 1989a). Responses to these longer sunflecks are often characterized by a distinctive post-illumination carbon-dioxide burst, resulting from metabolism of a residual pool of photorespiratory metabolites (Vines et al. 1982; Figure 6c). No postillumination carbon dioxide burst is evident during artificial sunflecks less than 20 seconds long (Chazdon and Pearcy 1986b; Figure 6b). Although few species have been examined in detail, efficiency of sunfleck use has been shown to vary among species as well as with light conditions during growth within a species (Chazdon and Pearcy 1986b, Chazdon 1988, Pearcy et al. 1987). Further research is needed to clarify the underlying bases for these important physiological differences.

Photosynthesis during sunflecks may be further restricted by high leaf temperatures and transpiration rates, leading to permanent heat damage

(Rackham 1975), stomatal closure (Woodward 1981), or wilting (Young and Smith 1979). Transpiration rates of understory plants are typically two to five times higher in sunflecks than in shade (Elias 1983, Smith 1981). Among seven subalpine understory species, decreases in xylem water potential during sunpatches led to midday wilting for four species (Smith 1981).

Increased water loss in the subalpine forest herbs *Arnica cordifolia* and *Arnica latifolia* may indirectly reduce photosynthesis during prolonged sunpatches through a decrease in xylem pressure potential followed by decreased stomatal conductance (Knapp et al. 1989, Young and Smith 1979). Daily carbon gain of these species increased during periods of frequent, intermittent cloud cover (Knapp et al. 1989, Young and Smith 1983).

In the Mexican understory shrub *Piper hispidum*, stomatal responses to humidity were strong, whereas stomatal responses to photon flux density were weak (Mooney et al. 1983). When relative humidity decreased from 95% to 85%, stomatal conductance decreased by more than 50%. This response serves to reduce water loss when evaporative demand is high and to maximize photosynthesis when evaporative demand is low. More field data are needed to examine the extent to which ambient humidity, soil water status, and leaf temperature influence sunfleck use in a wide range of natural habitats.

Shade-adapted understory species may exhibit photoinhibition during sunflecks lasting 10 minutes or longer (Le Gouallec et al. 1990, Powles and Björkman 1981). Studies by Le Gouallec et al. (1990) on the southeast Asian rainforest understory species *Elatostema repens* showed that induction occurred during the beginning of a series of artificial sunflecks (30-minute exposures at 700 μmol $\cdot$ m^{-2} $\cdot$ s^{-1}), whereas photoinhibition occurred later during the same sequence. The redwood forest understory herb *Oxalis oregana* exhibits protective leaflet movements in response to 20–50 minute sunflecks exceeding 300–400 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} (Powles and Björkman 1981). In this species, changes in leaflet orientation serve to prevent photoinhibitory inac-

tivation of the photosystem II reaction centers (Powles and Björkman 1981).

Conclusions

By focusing attention on the dynamic nature of understory light regimes, we have become aware of the importance of sunflecks for carbon gain and growth of forest species. In many ways, the photosynthetic machinery of shade-adapted plants appears to be adapted to respond quickly and efficiently to brief, unpredictable periods of enhanced direct radiation. These adaptations include a relatively low rate of induction loss, a high electron-transport capacity relative to carboxylation capacity, and stomatal opening at low photon flux density.

Yet all plants experience fluctuations in light conditions, even in the absence of a forest canopy. Cloud-induced light fluctuations strongly influence carbon gain and water-use efficiency of subalpine plants (Knapp and Smith 1987, 1990). Rapid light fluctuations also occur within crop canopies (Desjardins et al. 1973, Pearcy et al. 1990) and grassland canopies (Tang et al. 1988).

In view of the prevalence of fluctuating light conditions, a reevaluation of the ecophysiological significance of steady-state photosynthetic properties of leaves is now appropriate. Similar arguments can also be made for evaluating the importance of dynamic responses to changes in nutrient and water supply.

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