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The light environment and growth of C_3 and C_4 tree species in the understory of a Hawaiian forest

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Summary. The light environment in the understory of a Hawaiian forest containing a C_4 tree species, *Euphorbia forbesii,* was characterized using photosynthetic photon flux density sensors connected to portable data acquisition systems and a strip chart recorder, and hemispherical "fisheye" photographs of the canopy. During July 1980, 86 μmol cm^{-2} day^{-1} was received in the understory of which approximately 40% was contributed by sunflecks. The understory received 2.4% of the light reaching the top of the canopy. Nearly all sunflecks had peak photon flux densities greater than 250 μmol m^{-2} s^{-1}, but two-thirds were less than 0.5 min in length. The number of minutes of sunflecks received per day at any site was highly variable, depending on cloudiness and the overstory canopy structure. On a relatively clear day a 10-fold difference in the number of minutes of sunflecks was observed between sample sites. Estimates obtained from hemispherical photographs were used to calculate the annual mean potential number of minutes of sunflecks per day received by saplings of *Euphorbia* and a C_3 tree species, *Claoxylon sandwicense.* The growth of saplings of both species was highly correlated with the estimates of the minutes of sunflecks and was similar for both species. Although C_4 photosynthesis is usually found in plants native to high-light environments, it does not appear to confer any disadvantage in terms of growth to *Euphorbia forbesii* in the low-light conditions of the forest understory.

Introduction

The forests in the Waianae Mountains of Oahu, Hawaii contain the only known C_4 tree species, *Euphorbia forbesii,* occurring in essentially closed-canopy, mesic forests (Pearcy and Troughton 1975). This species probably evolved from other Hawaiian *Euphorbia* species native to arid, high-light environments (Croizat and Degener 1936) and provides a unique system for investigating the adaptive response of a C_4 species to a shaded forest environment. Field investigations of water relations and the general characteristics of the environment, including the light regime (Robichaux and Pearcy 1980a), suggest that light is the primary limiting environmental factor for carbon gain and growth for seedlings and saplings in the understory. Laboratory studies have revealed that *E. forbesii* possesses many of the photosynthetic characteristics typical of C_3 shade plants (Robichaux and Pearcy 1980b).

Although several studies have determined the fractional transmission of light through the canopy of tropical forests and the temporal and spatial patterns of sunflecks (Evans 1956, Evans et al. 1960), these have provided only relative estimates of canopy transmission and were based on techniques that do not allow for determination of the photosynthetically active radiation. The only study in which the photon flux density (PFD) available to plants in the understory of a tropical forest was measured (Björkman and Ludlow 1972) showed that sunflecks were a major fraction of the available PFD and were responsible for a sizable portion of the daily CO_2 uptake by understory plants. The research reported here more fully characterizes the light environment of an evergreen subtropical forest understory, especially the dynamics and contribution of sunflecks, and assesses its significance to the growth of *E. forbesii* and a co-occurring C_3 tree species, *Claoxylon sandwicense.*

Materials and methods

Field site. All measurements were made at Pahole Gulch in the Waianae Mountains of Oahu. This site was previously used for studies of the general environment and water relations of *E. forbesii* and *C. sandwicense* (Robichaux and Pearcy 1980b; Pearcy and Robichaux 1982). The site covers about 2 ha in a north-facing ravine. Several small spur ridges and gulleys bisect the site, rendering the topography quite complex. Precipitation is estimated at 1,200 to 1,800 mm/yr with 75% falling between October and April (Robichaux and Pearcy 1980a). The vegetation is evergreen with the overstory canopy reaching a height of 10 to 20 m with occasional emergents to 30 m. The tree flora consists of a mixture of species native to the wet forests occurring at higher elevations than Pahole Gulch and others found in the lower dry forests (Carlquist 1970). Common canopy species include *Pisonia sandwicensis, Metrosiderous polymorpha, Osmanthus sandwicensis, Psidium guayava* and *Antidesma pulvinatum.* Both *Euphorbia forbesii* and *Claoxylon sandwicense* are common at this site, mostly occurring in the understory but occasionally reaching the canopy.

Light measurements. Most light measurements were made with homemade light sensors connected to 3 Campbell Scientific CR21 micrologger data acquisition systems. The light sensors were similar in principle to commercially available quantum sensors (Licor Inst. Inc., Model 190S) and were a modification of the design of Biggs et al. (1971). The principle modifications of the design were a deeper housing and a single 6.3 mm hole rather than seven smaller holes to control the angle of light incidence on the 400 to 700 nm bandpass filter. These homemade sensors were carefully calibrated against a Licor 190S quantum sensor under a xenon-arc lamp, and were compared to the quantum sensor under a variety of canopy and sky conditions; the agreement was within ±5%.

Six light sensors, mounted on the top of 0.5 m tall stakes and carefully leveled, were connected to each data acquisition system to give a total of 18 sensors at the site. The microloggers were placed in representative locations and the sensors were located within a 3 m radius of each at random azimuths and distances. The microloggers sampled the output from the sensors every 10 seconds and stored the data in the form of histograms with 10 classes that were either 30 or 50 μmol m^{-2} s^{-1} wide. The highest classes also included all samples that exceeded 300 or 500 μmol m^{-2} s^{-1}. These classes were chosen to allow adequate sampling over the photon flux range limiting to photosynthesis, yet also allowed sampling of fluxes that were saturating (see Robichaux and Pearcy 1980b). Programs in the micrologger computed the percentage of readings falling within each class over a 12 h period. Other programs in the micrologger accumulated the 10 sec readings for 3 sensors connected to each micrologger to give an estimate of the daily PFD reaching the understory. The data were recorded on magnetic tape cassettes for later computer processing.

For comparative purposes, daily PFD in the open was measured with a quantum sensor attached to an electronic integrator (Delta T Instruments, Model MV1) and placed in a clearing about 0.7 km from the Pahole Gulch site.

A quantum sensor connected to a portable strip-chart recorder (Linear Instruments, Model 440) was used to determine sunfleck intensities, sunfleck durations, and the time intervals between sunflecks. At a 10 cm h^{-1} chart speed, a resolution of about 0.3 min was possible with an engineers' scale. Occasional recordings at 10 cm min^{-1} were also made.

Canopy photographs. Hemispherical "fisheye" photographs (Anderson 1964a, 1971) were used to further characterize the canopy and light environment. A Telesar fisheye lens was mounted on the front of the 50 mm lens of a Nikkormat 35 mm camera, giving an effective focal length of 7.5 mm and a hemispherical field of view of 176°. The resulting image was nearly equiangular except for a slight deviation near the horizon. A small bubble level on a platform mounted around the lens was used to carefully level the camera on a tripod with the lens facing upward. A post with a small battery-powered light-emitting diode (LED) at the top extended up from the platform and into the field of view so that after alignment with a compass the LED image would be visible at North on the film. Pictures were taken on overcast days with black and white film (Kodak Inc., TRI X) and a red filter, or with color film (Kodak, high speed Ektachrome). Direct and diffuse site factors (Anderson 1971), which provide estimates of the potential minutes of sunflecks per day and diffuse light transmission, respectively, were determined for each photograph as follows: The negative images were projected onto a rear projection screen. A circular image with solar tracks computed for 21°N latitude, or a "spider web" grid, was drawn on the screen. The images corresponding to canopy gaps were measured along the tracks or within the grid to determine the direct and diffuse site factors, respectively.

Growth. During July, 1980, 7 individuals of *Euphorbia* and 8 individuals of *Claoxylon* were selected for growth measurements. They were selected as being apparently healthy individuals between 0.5 and 2 M tall, but otherwise without regard to location or the nature of the overstory canopy. Primary and secondary branches were assigned numbers according to the node of origin for *Euphorbia,* as indicated by the easily visible bud scars, or the distance along the mainstem or branch for *Claoxylon.* This system allowed remeasurement of the branch diameters at the same positions a year later and identification of any new branches produced. Branch diameters to the nearest 0.1 mm and lengths to the nearest 5 mm were recorded. Leaf widths and lengths to the nearest 5 mm and distance to or node of the oldest leaf on the branch were recorded. The measurements were repeated again in August, 1981 on the 6 surviving saplings of each species.

In order to estimate weights from these linear measurements, branches from other similar plants were harvested. In addition, a treefall had recently knocked over several plants so the main stems could be obtained from these individuals. All stems and branches were cut into sections 10 cm long and the diameter of each section was measured. The oven-dry weights were obtained and polynomial regression equations relating weight of a 10 cm section to diameter were determined for both species. Regression equations relating leaf dry weight to length and width were also determined. These equations were used to estimate the increase in above-ground weights of the in situ plants between July 1980 and July 1981.

Results

As shown in Fig. 1, the canopy at Pahole Gulch is nearly closed and the gaps are generally small. As a result, the measured PFD in the shade was quite low, ranging from 10 to 30 μmol m^{-2} s^{-1}, but short-duration sunflecks were relatively frequent (Fig. 2). The windy conditions prevalent at this site added to the complexity of the light environment, since canopy movement caused very rapid fluctuations in PFD so that often many short (1 to 10 sec) sunflecks were clustered together. The timing of sunflecks was dependent on topographic position, but in general they were most frequent between 1,000 and 1,500 h. Cloudiness also greatly influenced the light environment since all days were at least partly cloudy and many were mostly cloudy, especially in 1980. In addition to the normal cumulus clouds, a cloudbank typically forms over Mt. Kaala, 5 km to the east, and fragments of this are carried over Pahole Gulch by the strong easterly tradewinds. Thus, long sunfleck-free periods were often due to clouds rather than to lack of gaps in the canopy.

Analysis of the strip-chart recordings show that two-thirds of the sunflecks are 0.5 min or less in duration, while relatively few last longer than 5 min (Fig. 3). Because of the complex kinetics, it is difficult to determine the quantity of photons received during sunflecks of different lengths, but longer sunflecks certainly contribute a substantial fraction of the total. Sunflecks tended to be clustered so the time between them was usually quite short (Fig. 4). The

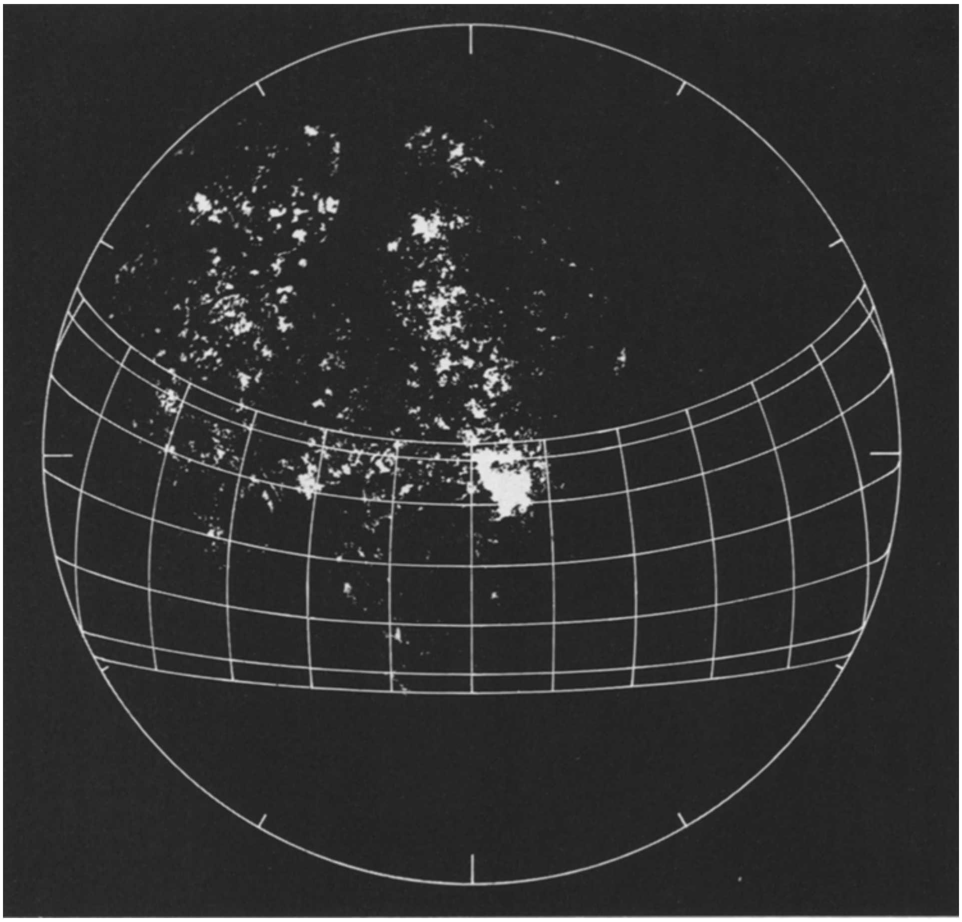

Fig. 1. Hemispherical "fisheye" photograph showing the canopy in Pahole Gulch. The solar tracks for day 21 of each month are superimposed on the photograph

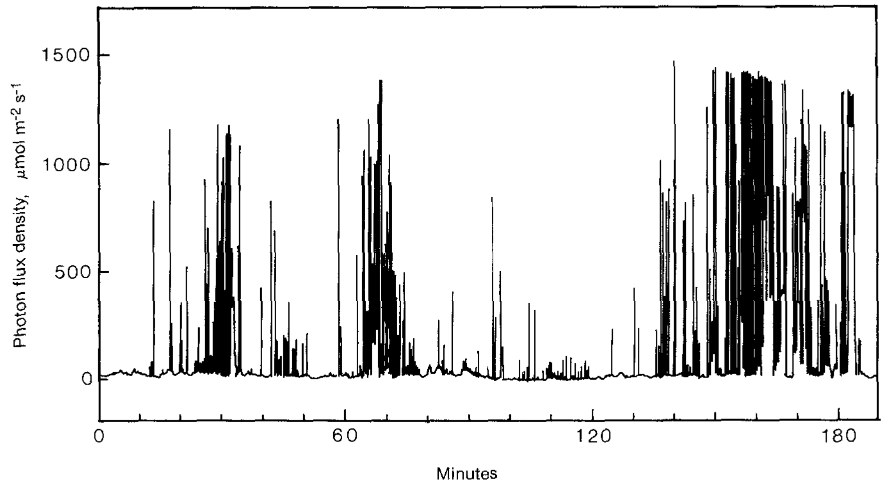

Fig. 2. Chart record showing the rapid changes in PFD in the understory due to sunflecks. Records for complete days are given in Pearcy and Calkin, 1982

peak PFD of the modal sunfleck was 250 µmol m^{-2} s^{-1}, while the average was 410 µmol m^{-2} s^{-1} (Fig. 5). Thus, essentially all sunflecks had peak PFDs higher than the 150 to 200 µmol m^{-2} s^{-1} required to saturate CO_2 uptake under constant light in *Euphorbia* and *Claoxylon* (Pearcy and Calkin 1983). Only a small proportion of the sunflecks approached PFDs expected under full sunlight above the canopy. Sunfleck length and PFD were only weakly correlated ($r = 0.30$).

The microloggers and light sensors performed well in Pahole Gulch. A major problem in characterizing understory light environments is the large number of sensors required (Anderson 1964b, Reifsnyder et al. 1971). The 3 data loggers and 18 sensors provided a reasonable solution to this problem. Moreover, the capacity for some internal data reduction greatly facilitated the acquisition and analysis of a large number of PFD measurements. For the 10 second sampling interval, 2.7×10^6 and 1.3×10^6 light measurements were made for the histogram and daily total PFD determinations, respectively, in 1980 alone. Daily total photon fluxes measured at 9 understory sites over 35 days in June, July and August, 1980 ranged from 55 to 138 µmol cm^{-2}, with a mean for all sites of 86 µmol cm^{-2}. Day-to-day variation was also quite high, depending on the amount

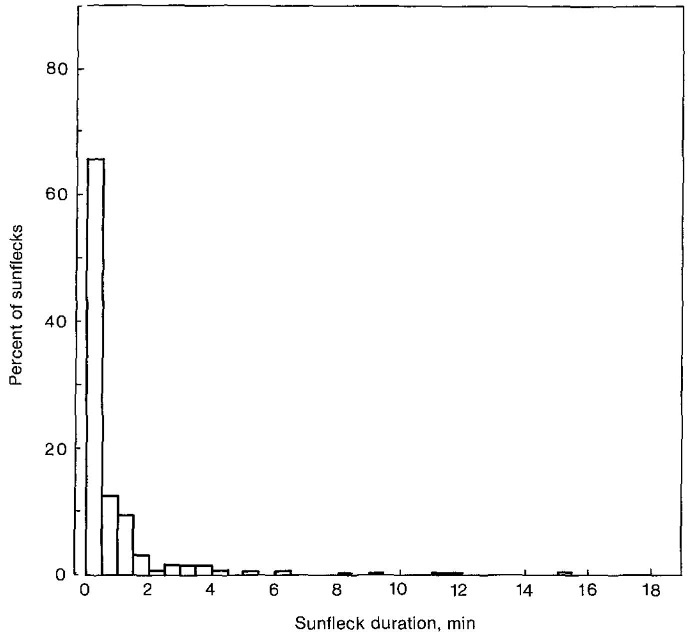

Fig. 3. Frequency histogram for sunfleck duration in Pahole Gulch during the summer of 1980

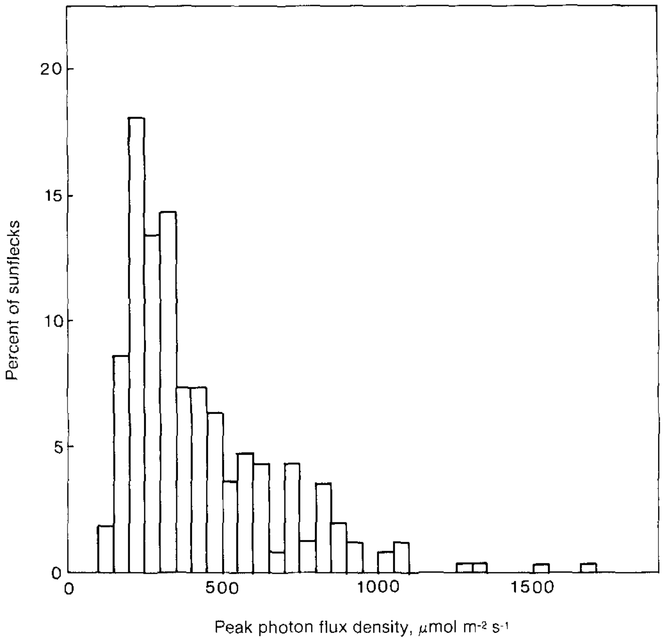

Fig. 5. Frequency histogram of the maximum PFD of sunflecks in Pahole Gulch during the summer of 1980

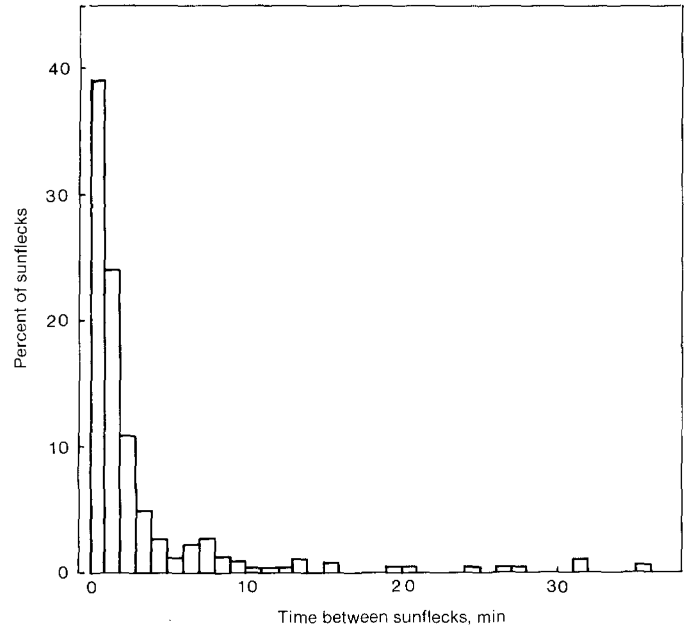

Fig. 4. Frequency histogram for the times between sunflecks in Pahole Gulch during the summer of 1980

and timing of cloudiness, with totals ranging from as low as 30 to 50 μmol cm^{-2} on cloudy days to as high as 150 to 250 μmol cm^{-2} on clearer days. In contrast, the mean daily photon flux measured in the open was 3,538 μmol cm^{-2}. Only $2.4 \pm 0.8\%$ of the light at the top of the canopy was transmitted to the forest floor. The transmissions for individuals sites ranged from 1.5 to 3.8%. Subtraction of the estimated diffuse light contribution suggested that about 40% of the total photon flux in the understory over the 5 week measurement period in 1980 was due to sunflecks. On relatively clear days, the contribution of sunflecks may be as great as 80%.

The histogram programs within the CR21 data loggers provide a convenient method for determining sunflecking at a relatively large number of locations within the forest. If fluxes above 150 μmol m^{-2} s^{-1} are arbitrarily defined to be sunflecks, then on the average there were about 10.6 min of sunflecks per day in 1980 (Fig. 6a), and 21 min per day in 1981 when conditions were less cloudy (Fig. 6b). The mean values for all sensors for individual days ranged from no sunflecks on cloudy days to nearly 40 min on the clearest days in both 1980 and 1981. Even the clearest days had some cloudiness, to these are not the maxima possible. Even so, the means for all days were only 21 and 46% of the clearest day values for 1980 and 1981, respectively, illustrating the large influence of cloudiness on sunflecks in the understory.

Coupled with this day-to-day variation is a large site-to-site variation in the minutes of sunflecks received. This is illustrated in Fig. 6c for July 23, 1981, a relatively clear day with a mean number of minutes of sunflecks of 37 min for all sites. Values at the individual sites on this day, however, ranged from a low of only 7 min to a high of 78 min, a 11-fold variation. Other clear days gave comparable results. However, a site that had the highest value on one day did not necessarily have the highest on another. This was because the occurrence of a sunfleck depended on the alignment of the sun and the canopy gap, and on the absence of a cloud in the path. Over periods of many days the effect of cloudiness would average out so that in the long-term, the canopy structure is the major determinant of the variation from site to site in the number of minutes of sunflecks received per day.

The occurence of sunflecks is also strongly dependent on the seasonal variation of solar angle. While detailed measurements were not made during the winter, the fisheye photographs provide a relative estimate of the seasonal changes. As shown in Table 1, the frequency of gaps along the solar track is highest in the summer and quite low at the lower solar angles in the winter. This, coupled with the greater cloudiness characteristic of the Hawaiian Islands

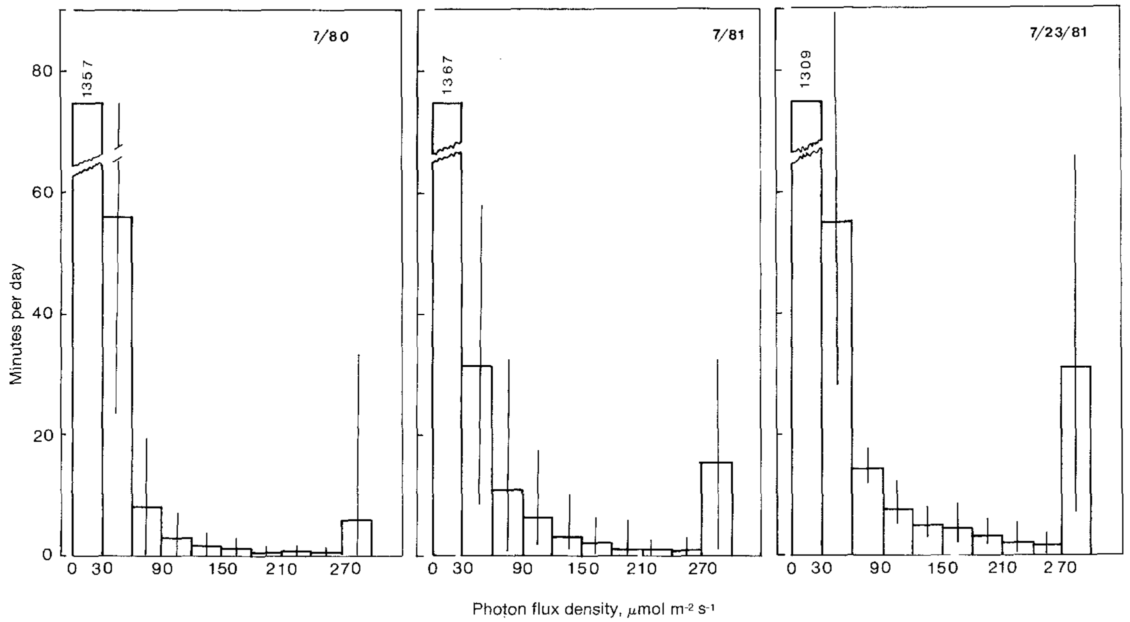

Fig. 6. Histograms showing the number of minutes per day that different PFDs are received on the forest floor in Pahole Gulch. The highest PFD (>270 μmol m^{-1} s^{-1}) includes all measurements exceeding this value. The means for all sample locations on all days in July, 1980 (left) and July 1981 (center), and for all locations on a single mostly clear day (right) are shown. The vertical lines through each bar give the range of variation

Table 1. Direct site factors and the potential number of minutes of sunflecks as estimated from hemispherical photographs taken in Pahole Gulch, Oahu

Month	Direct site factor, percent transmission	Potential sunfleck minutes per day
May/July	7.8 ± 4.1[a]	60.8 ± 31.7[a]
	(2.1–17.1)	(16.8–132)
March/September	4.3 ± 2.4	31.0 ± 17.4
	(0.1–8.6)	(3–63)
January/November	0.7 ± 1.1	4.9 ± 7.6
	(0–5.3)	(0–36)

[a] Mean and ±1 SD for 24 photographs. The numbers in parentheses are the range of values found

in the winter, suggests that the measured values probably correspond to the time of the yearly maximum. As can be seen from the solar track in July, the potential number of minutes of sunflecks per day in considerably greater than that actually measured, at least partly because cloudiness is not taken into account in estimates derived from the fisheye photographs. The range of variation from site to site is, however, comparable for the photographically estimated and measured values. This suggests that if cloudiness is taken into account, the photographic technique provides a good estimate of the relative spatial variation in minutes of sunflecks received. It also seems likely that if the photographically estimated values could be adjusted to account for cloudiness they would agree fairly well with the measured mean and range.

For logistical reasons, it is generally not possible to directly measure the amount of light available to a plant in a forest over periods much longer than a few days. However, in an evergreen forest such as found in Pahole Gulch, determination of diffuse and direct site factors from hemispherical canopy photographs provides a good alternative approach. This method, in conjunction with the growth measurements, made it possible to determine how growth varied as a function of the estimated fractional transmission of light through the canopy.

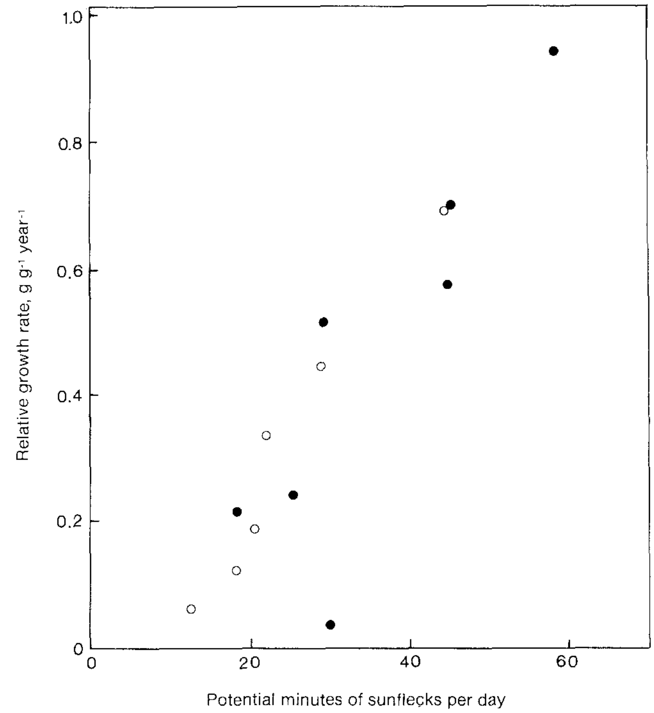

Fig. 7. Relative growth rates of *Euphorbia forbesii* (●) and *Claoxylon sandwicense* (○) plants as a function of potential minutes of sunflecks received as estimated from hemispherical photographs of the overstory canopy over each plant

Multiple regression analyses with the diffuse and direct site factors as the independent variables and relative growth rates (RGR) calculated from the plant weights as the dependent variable indicated that the diffuse site factor did not correlate significantly with growth, while the direct site factor, which gives the potential number of minutes of sunflecks, did. Thus, simple correlations were determined for potential sunflecking and growth, which were significant for both species ($P > 0.05$ for *Euphorbia*; $P > 0.01$ for *Claoxylon*). The RGRs of both species in the understory were very low, as would be expected in a strongly light-limited environment, but they varied greatly from plant to plant. The close relationship between RGR and the potential minutes of sunflecks received by the plants is apparent in Fig. 7. There is little difference in either the estimated RGR of the two species or in their relationship to the estimates of the minutes of sunflecks received.

Discussion

The forest understory in Pahole Gulch is clearly a low-light environment similar to other low-light forest understories, but brief periods of high light or sunflecks, although present at any location for only a small fraction of the day, contribute a large fraction of the daily photon flux. Their importance is further demonstrated by the close correlations between the spatial variations in gap frequency in the overstory, the major determinant of spatial variation in sunflecking, and tree sapling growth.

There are relatively few detailed measurements of photon fluxes in forest understories available for comparison to my results, and those reported have generally been made at a small number of sites or in less detail. In tropical forests, the most detailed measurements are those of Björkman and Ludlow (1972) in Queensland, Australia. Light levels there are apparently considerably lower than in Pahole Gulch, since only 21.0 μmol cm^{-2} day^{-1}, or 0.48% of the PFD above the canopy, reached the forest floor. It is not known if the measurement site is representative. On a clear day fewer sunflecks were received than in Pahole Gulch, although they contributed 62% of the daily total PFD, a figure comparable to values reported here. Measurements in a Costa Rican rainforest also gave daily fluxes comparable to those measured here (Strain, personal communication). Thus, the forest floor at Pahole Gulch may have light levels similar to some tropical forests, but may be less shady than others. It is comparable to at least some temperate deciduous forests (Hutchison and Matt 1977, Pitelka et al. 1980), but is much shadier and has shorter sunflecks than a subalpine coniferous forest where sunfleck responses and dynamics have been investigated (Young and Smith 1979). Measurements with different types of sensors and techniques are difficult to compare because of the spectral selectivity of the canopy. However, the occurrence of sunflecks appears comparable to values obtained with area survey techniques in S.E. Asian and Nigerian rain forests (Evans 1956, Evans et al. 1960) and with silicon cells in a Puerto Rican rain forest (Odum et al. 1970).

The timing and intensity distributions of sunflecks are probably important determinants of the ability of the photosynthetic apparatus to efficiently utilize them. Sunflecks occurring at a frequency of 1 to 10 seconds may be utilized quite efficiently since the photosynthetic apparatus may effectively integrate the light, resulting in higher photosynthetic rates than those predicted from the mean of steady-state rates measured at high and low light levels (Pollard, 1970; Gross 1982; Pearcy and Calkin, in preparation). However, more widely spaced sunflecks or single, short sunflecks occurring in isolation from others may not be utilized as efficiently because of an activation requirement of the photosynthetic apparatus (Gross and Chabot 1979) or stomatal limitations (Woods and Turner 1971). The short duration between sunflecks in Pahole Gulch may result in efficient utilization of the majority of them. Overstory canopy movement may be of considerable importance, since it causes rapid light changes but probably lengthens total exposure time and may increase total CO_2 uptake, relative to single, more slowly changing sunflecks expected under still conditions.

The large variation in understory light environments is well documented (Anderson 1966, Reifsnyder et al. 1971) but little is understood about the significance of this variation to plants. The seedlings and saplings of many tree species exhibit rapid acceleration in growth after tree falls create gaps that allow more light into the understory. However, if the gaps are large, water stress may impose new limitations. On the other hand, root competition or competition from herbaceous plants has been shown to be important in determining tree seedling growth in understories (Jarvis 1963). In Pahole Gulch, the small canopy gaps and short sunflecks probably do not impose water stress and there is little herbaceous understory growth in the areas where sapling growth was measured. It is unlikely that root competition effects would closely parallel variation in the direct site factor in the canopy. The strong relationship between growth and potential sunfleck occurrence is in agreement with the important role than sunflecks play in the leaf carbon balance of *Euphorbia* and *Claoxylon* (Pearcy and Calkin 1983). The results show that studies of the ecology of understory plants will require careful consideration of the spatial heterogeneity of the light environment, even where there are no obvious large gaps in the canopy, such as those created by tree falls.

Plants with C_4 photosynthesis are usually found in open, high-light environments and possess high photosynthetic capacities that make efficient use of the high photon flux densities. As a consequence, the general opinion is that C_4 plants should not be successful in a shaded habitat, except possibly where temperatures are high (Ehleringer and Björkman 1977, Ehleringer 1978). However, in the Pahole Gulch forest, the C_4 species, *Euphorbia,* had neither an advantage nor a disadvantage in terms of growth relative to the C_3 species, *Claoxylon.* Neither the growth measurements reported here nor the photosynthetic responses measured in the field (Pearcy and Calkin 1983) provide any evidence of a disadvantage associated with C_4 photosynthesis in this shaded forest environment. Indeed, the contrasting photosynthetic pathways would appear to be adaptively neutral in this environment.

Differences in gas exchange characteristics between the two species suggest that *Euphorbia* should have higher photosynthetic rates during sunflecks, whereas *Claoxylon* should maintain higher assimilation in diffuse light (Robichaux and Pearcy 1980b). However, responses at the leaf level do not appear to translate directly into whole plant growth differences. This may be because the diffuse and direct site factors covaried at the *Claoxylon* sites but not at the *Euphorbia* sites. However, many other factors are probably also involved. For example, the whorled leaf arrangement on the vertical stems of *Claoxylon* results in more self-shading than in the more open *Euphorbia* consisting of opposite leaves on horizontal branches. Moreover, I observed more herbivory of *Claoxylon* than of *Euphorbia*. Differences in allocation to the root systems could also be important, but are unknown.

While the responses of *Euphorbia* and *Claoxylon* to light in the understory are quite similar, observational and experimental evidence suggests that these two species utilize the light environment differently when the entire life cycle is considered. Understory individuals of *Claoxylon* usually flower and set seed, while *Euphorbia* plants in the understory almost never do. Nearly all of the seed produced by *Euphorbia* is from large individuals reaching at least into the bottom layers of the canopy with part of the crown exposed. The only exception I have observed was in several small individuals that were non-flowering in 1978 and 1979, but flowered in 1980 and 1981 after a large limb in the canopy broke off, alowing much more light into the understory at that location. Greenhouse *Euphorbia* plants have only flowered when grown at high light, never at low light. Thus, *Euphorbia* may be more of a "gap" species, depending more on high light for seed production, than is *Claoxylon*. Species requiring gaps for regeneration are common, even in many apparently mature tropical forests (Hartshorn 1978). Moreover, *Euphorbia* has a much larger capacity for photosynthetic acclimation to light than *Claoxylon* (Pearcy et al., in preparation), a suggested characteristic of gap species (Bazzaz and Pickett 1980). Since *E. forbesii* probably evolved from a high photosynthetic capacity species native to the high-light habitats more typical for C_4 plants, it is not surprising that this species can be characterized as having some specialization for situations in which high light is at least temporally available. Except for the highly unusual presence of C_4 photosynthesis and its associated characteristics, *Euphorbia forbesii* appears otherwise physiologically and ecologically similar to many other tropical and subtropical forest trees.

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