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Photosynthetic Responses of C_3 and C_4 Species from Cool Shaded Habitats in Hawaii

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Summary. The C_4 species, *Euphorbia forbesii,* and the C_3 species, *Claoxylon sandwicense,* occupy cool, shaded habitats in Hawaii. Both of these species exhibit the photosynthetic characteristics of typical shade plants: low light-saturated photosynthetic rates, low dark respiration rates, low light levels for saturation of photosynthesis, and low light compensation points. In addition, the quantum yields of the two species are similar at leaf temperatures near 22° C, reflecting a significant increase in the quantum yield of *E. forbesii* over that of C_4 species from open habitats. *C. sandwicense* has a lower dark respiration rate than *E. forbesii.* Hence, since the quantum yields of the two species are similar at cool temperatures, *C. sandwicense* has a higher photosynthetic rate than *E. forbesii* at low incident photon flux densities. As a consequence, *C. sandwicense* should have a greater carbon gain than *E. forbesii* under the diffuse radiation conditions of their native habitat. However, since *E. forbesii* has a higher light-saturated photosynthetic rate than *C. sandwicense, E. forbesii* may have a greater carbon gain than *C. sandwicense* during sunflecks.

Introduction

It has been suggested that the selective advantages of C_4 photosynthesis over C_3 photosynthesis are maximal under conditions of high leaf temperatures, high light intensities, and limited water supplies (Björkman 1973). This is supported by the fact that C_4 species occur predominately in hot, open, and arid habitats (Ehleringer 1978; Doliner and Jolliffe 1979; Teeri 1979; Tieszen et al. 1979). In these habitats, C_4 species usually exhibit high photosynthetic temperature optima, high light-saturated photosynthetic rates, and high mesophyll conductances to CO_2 relative to C_3 species (Björkman 1976).

It has also been suggested that C_4 photosynthesis confers a selective disadvantage relative to C_3 photosynthesis under cool, shaded conditions (Ehleringer 1978). This follows from the observation of Ehleringer and Björkman (1977) that C_4 species have lower quantum yields than C_3 species at temperatures below 30° C. Quantum yields of C_3 species, which exhibit an oxygen inhibition of photosynthesis, decline as leaf temperatures increase, falling from 0.069 mol CO_2 per mol absorbed photons at 14° C to 0.042 mol CO_2 per mol absorbed photons at 38° C (Ehleringer and Björkman 1977). In contrast, quantum yields of C_4 species, which lack an oxygen inhibition of photosynthesis under normal atmospheric conditions, remain constant with leaf temperature at 0.053 mol CO_2 per mol absorbed photons (Ehleringer and Björkman 1977). The crossover temperature, where the C_3 and C_4 species have identical quantum yields, is between 29° and 30° C. As a consequence, C_4 species have a lower potential for carbon gain than C_3 species in shaded habitats with cool to moderate temperatures (Ehleringer 1978).

We have discovered, however, that certain C_4 Hawaiian *Euphorbia* species occupy cool, shaded habitats and exhibit the photosynthetic responses of typical shade plants, suggesting that C_4 photosynthesis may not be inherently disadvantageous under these conditions (Robichaux and Pearcy 1980). In the present study, therefore, we compare the photosynthetic characteristics of the C_4 species, *Euphorbia forbesii,* and the C_3 species, *Claoxylon sandwicense,* to determine their relative photosynthetic performances under the cool, shaded conditions of their native habitat.

Materials and Methods

Seedlings of *Euphorbia forbesii* and *Claoxylon sandwicense* were collected in a cool, shaded, and mesic ravine in Pahole Gulch in the northern Waianae Mountains of Oahu, Hawaii (158°12′W longitude; 21°33′ latitude; 600 m elevation). Both species are common understory trees in the mesic forest community at this site and both are members of the Euphorbiaceae. Seeds of *Euphorbia celastroides* were collected on an open, arid hillside at Kaena Point, Oahu (158°17′ longitude; 21°35′ latitude; 15 m elevation). This species served as an open habitat, C_4 "control" for the photosynthetic light response measurements. Typical midday diffuse photon flux densities (400–700 nm) at the Pahole Gulch site are only 1–2% of those at the Kaena Point site, while typical midday leaf temperatures at the Pahole Gulch site are 8–12° C below those at the Kaena Point site (Robichaux and Pearcy 1980).

For the photosynthetic measurements, the plants were grown in a Percival model PGW 132 chamber under a temperature regime of 26° C day/20° C night and a daylength 12 h. The incident photon flux densities at canopy height in the chamber were 0.10 ± 0.02 mmol m^{-2} s^{-1} for *E. forbesii* and *C. sandwicense* and 0.55 ± 0.05 mmol m^{-2} s^{-1} for *E. celastroides.*

Photosynthetic rates were determined for attached single leaves with an open system gas exchange apparatus incorporating a Horiba Instruments model VIA-500R IR CO_2 analyzer. Detailed descriptions of this apparatus and the general measurement procedures are provided in Robichaux and Pearcy (1980). For the measurements at low O_2, appropriate CO_2 partial pressures were obtained by mixing pure N_2 with N_2 containing 0.1% CO_2 and approximately 2% O_2. Light absorptance values (400–700 nm) for the leaves used in the photosynthetic measurements were determined with an integrating sphere (Rabideau et al. 1946) and

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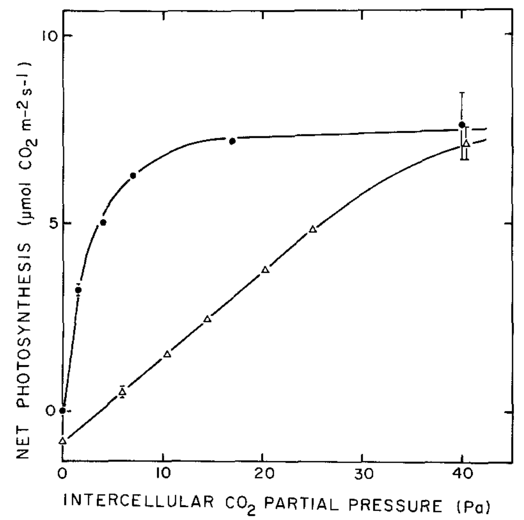


Fig. 1. CO_2 dependence of photosynthesis in *E. forbesii* (C_4; closed circles) and *C. sandwicense* (C_3; open triangles). Vertical bars indicate the range of variation for triplicates at low and high intercellular CO_2 partial pressures. Leaf temperature is 22° C

Table 1. Oxygen dependence of photosynthesis in *E. forbesii* (C_4) and *C. sandwicense* (C_3). Variation is the same as in Fig. 1. Leaf temperature is 22° C

Characteristic	Euphorbia forbesii	Claoxylon sandwicense
Net photosynthesis[a] (μmol CO_2 m^{-2} s^{-1})		
21% O_2	8.5	5.7
1% O_2	8.7	8.1
Mesophyll conductance (mm s^{-1})		
21% O_2	2.1	0.7
1% O_2	2.1	1.1

[a] Light-saturated rate

a Lambda Instruments model LI-190S quantum sensor. The light source for the photosynthetic and absorptance measurement was a Christie Electric Corporation model UF30 2.5 kW short arc xenon lamp

Results and Discussion

As shown in the photosynthetic CO_2 response curves of Fig. 1, *E. forbesii* has a higher efficiency of CO_2 utilization than *C. sandwicense* at low intercellular CO_2 partial pressures. The mesophyll conductances to CO_2 calculated from the initial slopes of these curves are 2.1 and 0.7 mm s^{-1} for *E. forbesii* and *C. sandwicense*, respectively. *E. forbesii* also has a lower CO_2 compensation point than *C. sandwicense;* the CO_2 compensation point is O Pa in *E. forbesii* and 4 Pa in *C. sandwicense* (Fig. 1). In addition, as indicated in Table 1, lowering the O_2 partial pressure results in a subtantial increase in both the light-saturated photosynthetic rate and the mesophyll conductance of *C. sandwicense*, while there is little or no effect for *E. forbesii*. Hence, *C. sandwicense* and *E. forbesii* exhibit the distinguishing physiological features of C_3 and C_4 photosynthesis, respectively, as postulated by Bjorkman (1976).

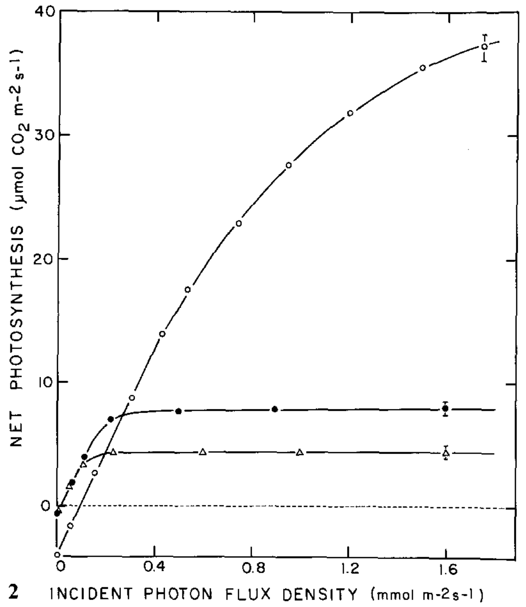
The photosynthetic light response curves of *E. celastroides, E. forbesii,* and *C. sandwicense* are shown in Fig. 2. Maximal photosynthetic rates and dark respiration rates are much lower in *E. forbesii* and *C. sandwicense* than in *E. celastroides.* In addition, the light levels for saturation of photosynthesis and the light compensation points of *E. forbesii* and *C. sandwicense* are low compared to those of *E. celastroides.* Relative to *E. celastroides,* therefore, both *E. forbesii* and *C. sandwicense* exhibit the photosynthetic responses of typical shade plants (Boardman 1977).

When the initial portion of Fig. 2 is enlarged, it is apparent that the initial slopes of the photosynthetic light response curves of *E. forbesii* and *C. sandwicense* are similar (Fig. 3). When these slopes are divided by the light absorptance values of the respective leaves, the quantum yield obtained for both species is approximately 0.062 mol CO_2 per mol absorbed photons.

This similarity of the quantum yields of *E. forbesii* and *C. sandwicense* at 22° C contrasts with the results of Ehleringer and Bjorkman (1977), and reflects a significant increase in the quantum yield of *E. forbesii* over that of other C_4 species. This is apparent in Fig. 4, where the temperature response curves of quantum yield are shown for *E. forbesii* and *C. sandwicense.* The quantum yield of *C. sandwicense* declines markedly as leaf temperatures increase, falling from 0.064 mol CO_2 per mol absorbed photons at 16° C to 0.042 mol CO_2 per mol absorbed photons at 34° C. In contrast, the quantum yield of *E. forbesii* remains constant with leaf temperature at a value of 0.062 mol CO_2 per mol absorbed photons. Thus, while the quantum yield of *C. sandwicense* is similar to that of other C_3 species, the quantum yield of *E. forbesii* is significantly higher than that of other C_4 species as reported by Ehleringer and Björkman (1977). The resulting crossover temperature, where *E. forbesii* and *C. sandwicense* have identical quantum yields, is 22 to 23° C (Fig. 4); this contrasts markedly with the 30° C crossover temperature reported by Ehleringer and Björkman (1977). The mean midday leaf temperature for *E. forbesii* and *C. sandwicense* at the Pahole Gulch site during a five day measurement period in the summer of 1978 was 21.9° C ± 1.2° C. At this leaf temperature, the quantum yields of these two species are virtually identical (Fig. 4). Midday leaf temperatures during the winter were approximately 3° C cooler (Robichaux and Pearcy 1980).

While the underlying mechanism responsible for the higher quantum yield of *E. forbesii* is unknown, its ecological implications are clear. It overcomes the inherent disadvantage of C_4 photosynthesis in cool, shaded habitats as postulated by Ehleringer (1978). The only difference in the photosynthetic characteristics of *E. forbesii* and *C. sandwicense* that may represent a disadvantage for the C_4 species is the difference in dark respiration rate. As shown in Fig. 5, *E. forbesii* exhibits a significantly higher dark respiration rate than *C. sandwicense* over a wide range of leaf temperatures. Since the quantum yields of the two species are similar under cool conditions, this difference in dark respiration rate translates into a difference in net photosynthetic rate at low light levels. For example, at a leaf temperature of 22° C and an incident photon flux density of 0.03 mmol m^{-2} s^{-1}, which corresponds to the midday diffuse radiation level measured at the Pahole Gulch site (Robichaux and Pearcy 1980), the photosynthetic rates of *C. sandwicense* and *E. forbesii* are 1.1 and 1.0 μmol CO_2 m^{-2} s^{-1}, respectively (see Fig. 3). Integrated over a full day, this difference in photosynthetic rate under diffuse radiation conditions should result in a significant difference in the net carbon gain of these two species.

On clear days at the Pahole Gulch site, however, a significant proportion of the total daily photon flux can be contributed by



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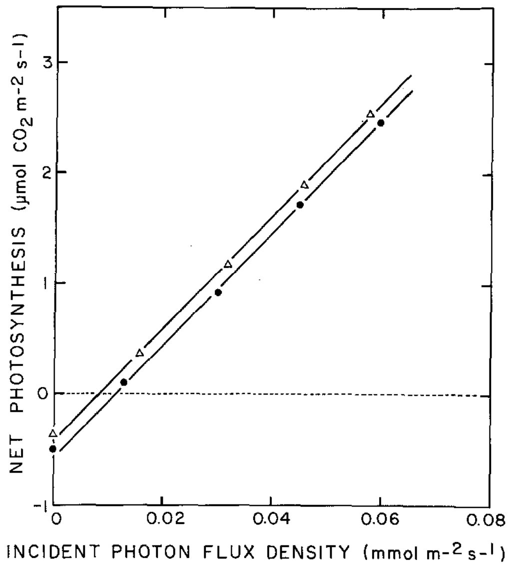

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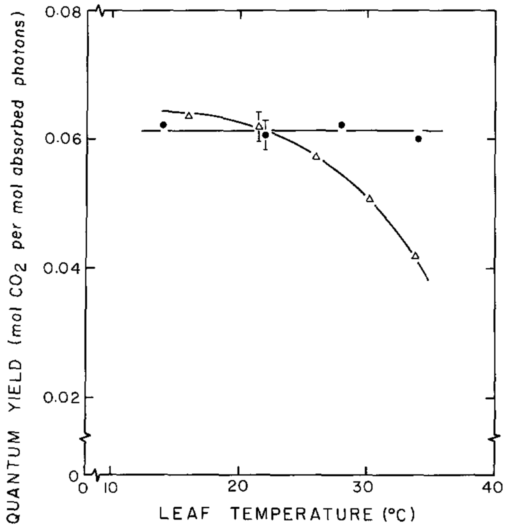
Fig. 2. Light dependence of photosynthesis in *E. celastroides* (C_4; open circles), *E. forbesii* (C_4; closed circles), and *C. sandwicense* (C_3; open triangles). Vertical bars indicate the range of variation for triplicates. Variation is much lower at low photon flux densities. Leaf temperatures are 32° C for *E. celastroides* and 22° C for *E. forbesii* and *C. sandwicense*. These temperatures correspond to those in the native habitats of these species during the growing season

Fig. 3. Light dependence of photosynthesis at low photon flux densities in *E. forbesii* (C_4) and *C. sandwicense* (C_3). Symbols are the same as in Fig. 1. Leaf temperature is 22° C



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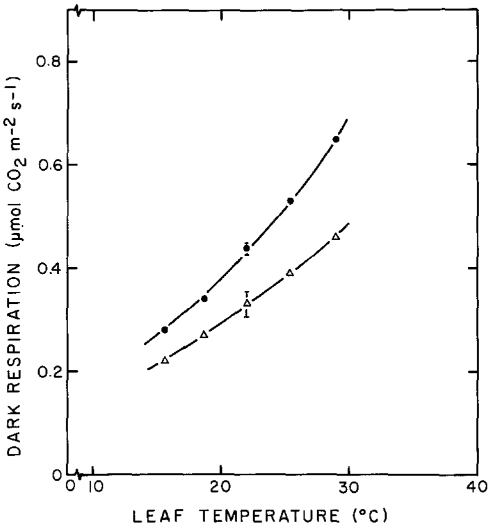

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Fig. 4. Temperature dependence of absorbed quantum yield in *E. forbesii* (C_4) and *C. sandwicense* (C_3). Symbols are the same as in Fig. 1. Vertical bars indicate the range of variation for triplicates. Mean light absorptance values are 0.87 and 0.86 for *E. forbesii* and *C. sandwicense*, respectively

Fig. 5. Temperature dependence of dark respiration in *E. forbesii* (C_4) and *C. sandwicense* (C_3). Symbols are the same as in Fig. 1. Vertical bars indicate the range of variation for triplicates

sunflecks (Fig. 6). Incident photon flux densities during these brief periods of direct solar radiation frequently reach 0.25 to 0.30 mmol m^{-2} s^{-1} and may reach 1.60 to 1.80 mmol m^{-2} s^{-1}, levels that are sufficient for saturation of photosynthesis in both *E. forbesii* and *C. sandwicense* at 22° C (see Fig. 2). Under these light-saturated conditions, the photosynthetic rate of *E. forbesii* is 50 to 60% higher than that of *C. sandwicense*. In addition, we have measured increases in leaf temperature of 5° C during the first 50 s of typical sunflecks, and have recorded leaf temperatures as high as 30° C during prolonged sunflecks. As shown in Fig. 7, these increases

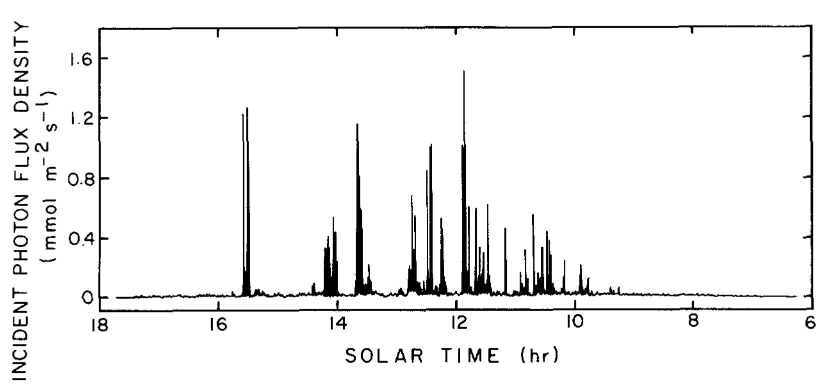

Fig. 6. Incident photon flux densities at the Pahole Gulch site on a clear summer day. The recorder output reads from right to left

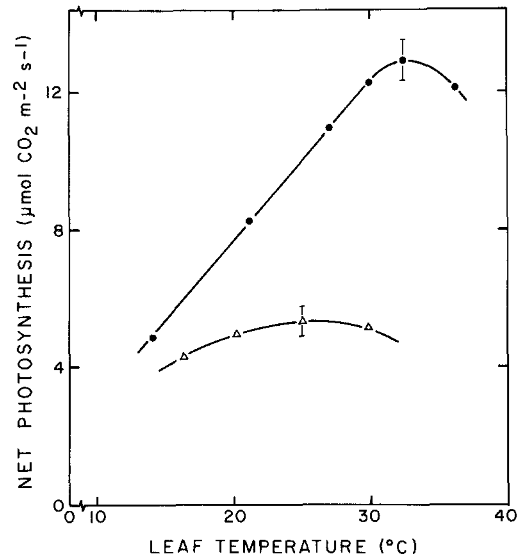

Fig. 7. Temperature dependence of photosynthesis in *E. forbesii* (C_4) and *C. sandwicense* (C_3). Symbols are the same as in Fig. 1. Vertical bars indicate the range of variation for triplicates

in leaf temperature may result in a substantial increase in the light-saturated photosynthetic rate of *E. forbesii* relative to that of *C. sandwicense*. With respect to net daily carbon gain, this higher photosynthetic rate of *E. forbesii* during sunflecks may compensate to a large extent for its lower photosynthetic rate during diffuse radiation conditions.

The actual number of sunflecks required for *E. forbesii* to have the same net daily carbon gain as *C. sandwicense* depends on several factors, such as the time courses of the photosynthetic response to sunflecks in these two species. Gross and Chabot (1979) found that maximal photosynthetic response to sunflecks required about 60 s in their C_3 shade species. Since the sunflecks at the Pahole Gulch site are frequently longer than 60 s in duration, they may be sufficient for maximal photosynthetic responses in *E. forbesii* and *C. sandwicense*. However, more detailed field measurements will be necessary before we can be certain about the role of sunflecks in the daily carbon balance of these two species.

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