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Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: dynamic photosynthetic responses

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Abstract Hawaiian lobeliads have radiated into habitats from open alpine bogs to densely shaded rainforest interiors, and show corresponding adaptations in steady-state photosynthetic light responses and associated leaf traits. Shaded environments are not uniformly dark, however, but punctuated by sunflecks that carry most of the photosynthetically active light that strikes plants. We asked whether lobeliads have diversified in their dynamic photosynthetic light responses and how dynamic responses influence daily leaf carbon gain. We quantified gas exchange and dynamic light regimes under field conditions for ten species representing each major Hawaiian sublineage. Species in shadier habitats experienced shorter and less numerous sunflecks: average sunfleck length varied from 1.4 ± 1.7 min for *Cyanea floribunda* in shaded forest understories to 31.2 ± 2.1 min for *Trematolobelia kauaiensis* on open ridges. As expected, the rate of photosynthetic induction increased significantly toward shadier sites, with assimilation after 60 s rising from ca. 30% of fully induced rates in species from open environments to 60% in those from densely shaded habitats. Uninduced light use efficiency—actual photosynthesis versus that expected under steady-state conditions—increased from 10 to 70% across the same gradient. In silico transplants—modeling daily carbon gain using one species' photosynthetic light response in its own and other species' dynamic light regimes—demonstrated the potential adaptive nature of species differences: understory *Cyanea pilosa* in its light regimes outperformed gap-dwelling *Clermontia parviflora*, while *Clermontia* in its light regimes outperformed *Cyanea*. The apparent cross-over in daily photosynthesis occurred at about the same photon flux density where dominance shifts from *Cyanea* to *Clermontia* in the field. Our results further support our hypothesis that the lobeliads have diversified physiologically across light environments in Hawaiian ecosystems and that those shifts appear to maximize the carbon gain of each species in its own environment.

Keywords Sunflecks · Dynamic response of photosynthesis · Light heterogeneity · Induction · Light use efficiency

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Introduction

The native Hawaiian lobeliads (six genera, ca. 125 species) have undergone striking adaptive radiations in habitat, leaf form, and floral morphology (Carlquist 1970; Givnish et al. 1995, 2004; Givnish 1998). Given that they have invaded nearly the entire spectrum of light environments on moist sites at mid to high elevations—from open alpine bogs and sea cliffs to densely shaded rainforest understories—the Hawaiian lobeliads provide a model system with which to study the evolution of photosynthetic adaptations to different light regimes (Givnish et al. 2004). Previous research on 11 species representing each of the major Hawaiian sublineages showed that they occupy habitats that receive

2.1–30.0 mol m^{-2} day^{-1} photon flux density (PFD), and that species show coordinated responses in several components of their steady-state photosynthetic light responses to this light gradient (Givnish et al. 2004). As expected from economic theory, maximum photosynthetic rates (A_{max}), half saturation, dark respiration, maximum carboxylation rate, carboxylation efficiency, electron transport capacity, leaf nitrogen content, and leaf mass per unit area measured in the field all increase with native PFD. Furthermore, area-based photosynthetic rates show adaptive crossover, with species native to higher PFD having higher assimilation at higher PFD than species native to lower PFD, and lower assimilation at lower PFD than species native to lower PFD. These results strongly suggest that differences in steady-state photosynthetic light responses are adaptive. Instantaneous leaf compensation points lay far below the actual minimum PFD levels inhabited by each species, but whole-plant compensation points—which incorporate the costs of leaf and non-leaf construction—corresponded much better to minimum PFD levels (Givnish et al. 2004).

Shaded environments are not uniformly dark, but punctuated by sunflecks, short bursts of bright light, that carry up to 90% of the photosynthetically active light that strikes plants (Pearcy 1990; Poorter and Oberbauer 1993; Naumburg et al. 2001). Sunflecks a few seconds or minutes long can account for up to 65% of total carbon gain in forest understories (Chazdon 1988; Pfitsch and Pearcy 1989). The ability of a leaf to use sunflecks depends on: (1) the rate of photosynthetic induction once a leaf is strongly illuminated, (2) the rate of loss of induction between sunflecks, and (3) the ability to continue fixing carbon at high rates after a sunfleck (post-illumination carbon fixation). The relative contribution of photosynthesis during sunflecks to daily carbon gain also depends on: (4) the "resting" photosynthetic rate in dim light, (5) the maximum photosynthetic rate achievable, and (6) the lengths of sunflecks and interfleck periods. Photosynthetic induction and loss of induction are dependent on three processes operating at different time-scales. RuBP regeneration activates rapidly in sunflecks and deactivates rapidly in shade; Rubisco activation in sunflecks and slower deactivation in shade is a slower process, typically operating over a few minutes; and stomatal opening in sunflecks and slower closing in shade proceeds slower yet, and is usually the only cause of shifts in assimilation after 10 min at saturating PFD (Pearcy 1990; Sassenrath-Cole and Pearcy 1994).

To maximize use of dynamic light, understory plants should undergo physiological induction and open their stomata rapidly in response to sunflecks, and slowly lose induction and close stomata afterwards, while sun-adapted species should undergo induction more slowly and lose it more rapidly. Such patterns have been observed in several studies (e.g., Chazdon and Pearcy 1986a, b; Poorter and

Oberbauer 1993; Tinoco-Ojanguren and Pearcy 1995; Valladares et al. 1997; Cai et al. 2005). In some cases, the rate of induction was influenced by vapor pressure deficit (VPD) and its effect on the rate of stomatal opening and closure (e.g., Tinoco-Ojanguren and Pearcy 1993). In almost every study to date, however, comparisons have only been made between two or three species, or two or three categories of species based on their relative distributions along a light gradient. Never has a quantitative relationship been drawn between measures of the light regimes inhabited by several species and the dynamic photosynthetic responses of those species.

Here we document variation in the dynamic light regimes and dynamic photosynthetic light responses of 11 species of Hawaiian lobeliads that span a 13-fold difference in daily PFD. We ask whether species in habitats characterized by infrequent, short sunflecks are capable of rapid photosynthetic induction and efficient light use in sunflecks and how dynamic responses influence daily carbon gain. For two common species that inhabit rainforest understories (*Cyanea pilosa* subsp. *longipedunculata*) and gaps (*Clermontia parviflora*) on windward Hawai'i, we quantify rates of stomatal opening, closure, and physiological gains and loss of induction in response to dynamic light environments. We use these measurements to parameterize a model for carbon uptake, and then relate the differential distribution of these species along the light gradient to the conditions under which each has a carbon gain advantage, using in silico transplants to the dynamic light regimes experienced by both species in the field.

Materials and methods

Study sites and species

We studied 11 species that together represent each major clade of Hawaiian lobeliads and span a gradient in daily PFD from 2.3 to 30.0 mol m^{-2} day^{-1} (Tables 1, 2; Givnish et al. 2004). We selected species native to a narrow elevation range (1,000–1,250 m) with moderate to heavy rainfall (>1,500 mm year^{-1}). *Brighamia* does not meet these criteria, but is adapted to cooler, effectively moister conditions than expected based on its elevation, given the strong onshore breezes and trade winds in its natural sea-cliff habitat. Whenever possible, we measured light availability, photosynthetic physiology, and leaf traits in three populations growing under natural conditions. It proved impossible to access the rare natural populations of two federally endangered species, *Brighamia insignis* and *Delissea rhytidosperma*. These species were instead studied at outplantings established from wild seed sources by the National Tropical Botanic Garden at Limahuli on Kaua'i.

Table 1 Habitat distributions, elevational range and number of study populations of the 11 species of Hawaiian lobeliads investigated[a]

Species	Habitat[b,c]	Elevational range[b] (m)	n
Cyanea floribunda	Wet forest understories	460–1,520	3
Cyanea pilosa subsp. *longipedunculata*	Wet forest understories	610–1,520	3
Cyanea hirtella	Wet forest understories	1,030–1,400	1
Cyanea leptostegia	Diverse mesic forest	1,000–1,300	3
Clermontia parviflora	In gaps and as epiphytes, wet forest	120–1,460	3
Lobelia yuccoides	Ridges and openings, diverse mesic forest	750–1,200	2
Delissea rhytidosperma	Diverse mesic forest	300–1,000	1
Clermontia fauriei	Openings, diverse mesic to wet forest	365–1,400	3
Trematolobelia kauaiensis	Openings, wet forest	650–1,575	2
Lobelia villosa	Summit bogs on windswept ridges	1,200–1,580	2
Brighamia insignis	Sea cliffs	0–400	1

[a] For population localities see Givnish et al. (2004)

[b] Habitat and elevation data from Lammers (1999) and R. A. Montgomery and T. J. Givnish (personal observations)

[c] Habitat terminology follows Wagner et al. (1990)

Table 2 Daily sunfleck activity experienced by field populations of 11 species of Hawaiian lobeliads. Means which differ significantly from each other are indicated by *different letters*. *PFD* Photon flux density

Species	Daily PFD (mol m^{-2})			Sunfleck length (min)				Daily minutes of sunflecks		
	Mean	SE	Sensors (n)	Mean	SE	Maximum	SE	Mean	SE	Sensors (n)
Cyanea floribunda	2.3 a	0.2	49	1.4 e	1.7	21.4 g	19.6	31 f	21	48
Cyanea pilosa	3.2 a	0.4	52	1.5 e	2.3	30.3 fg	27.2	67 ef	29	25
Cyanea hirtella	6.2 ab	0.9	11	2.9 de	3.5	117.5 efg	41.0	191 cde	43	11
Cyanea leptostegia	7.0 b	0.6	29	6.0 de	2.2	140.6 ef	25.3	195 d	27	29
Clermontia parviflora	8.3 b	0.8	52	8.8 cde	1.6	215.7 de	18.2	243 d	19	56
Lobelia yuccoides	15.1 c	2.4	25	1.9 e	2.1	28.3 fg	24.4	384 b	26	31
Delissea rhytidosperma	15.3 c	2.1	13	19.7 abc	3.7	392.5 bc	60.5	384	51	14
Clermontia fauriei	15.8 c	1.3	59	13.2 bcd	1.9	291.5 cd	21.5	340 bc	23	40
Trematolobelia kauaiensis	21.1 d	2.1	31	31.2 a	2.1	505.3 ab	24.8	517 a	26	30
Lobelia villosa	28.4 e	1.1	23	25.0 abc	4.8	640.6 a	55.5	533 ab	59	6
Brighamia insignis	30.0 e	3.0	12	24.9 ab	3.4	220.3 de	39.3	226 cde	42	12

Light regimes

We measured daily courses of PFD (μmol photosynthetically active photons m^{-2} s^{-1}) over five to 12 individuals in each study population using GaAsP photodiodes (G1118; Hammamatsu, New Jersey) connected to dataloggers (Campbell Scientific, Utah). We mounted photodiodes on plastic poles directly above the crowns of ten to 15 individuals of each species in each of three populations (total of 30–45 sensors per species). Sensor height varied among individuals and species due to height difference of individuals and is expected to represent the variation in light arriving at the crowns of adults of our study species. PFD levels were logged at 10-s intervals during daylight hours. For detailed description of calibration of sensors and measurements, see Givnish et al. (2004). We defined a sunfleck as any period during which PFD continuously exceeded 150 μmol m^{-2} s^{-1}. We based this threshold on our contemporaneous measurements of steady-state photosynthetic light responses on the same individual plants: average light saturation point across species was 147 ± 10 μmol m^{-2} s^{-1} under steady-state conditions. Based on 168–785 sensor-days per species, we calculated the mean $\pm$ SE of minutes of sunflecks per day, sunfleck length, and maximum sunfleck length per day, and constructed histograms of sunfleck length for each species.

Gas exchange measurements

We measured dynamic photosynthetic light responses by quantifying rates of photosynthetic induction during continuous periods of strong illumination (induction curves) and

during a series of simulated sunflecks (Valladares et al. 1997). Gas exchange was measured in the field on attached, fully expanded leaves from five individuals whose light regimes and static photosynthetic light responses had been quantified (Givnish et al. 2004). We used a LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Neb.) equipped with a red/blue LED light source and a CO_2 mixing system. All measurements were made under ambient relative humidity (ca. 75%), leaf temperature (20–25°C) and CO_2 concentration (360–380 p.p.m.). For induction curves, leaves were shaded in early morning with black cloth and covered with white paper to reflect heat; leaves were not shaded the day before due to the constant possibility of torrential rain at remote field sites. Measurements were started after leaves had been darkened for at least 60 min. Leaves were clamped into the measurement cuvette and allowed to equilibrate at low light (10 μmol m^{-2} s^{-1}), after which they were exposed to saturating light (1,000 μmol m^{-2} s^{-1}). Gas exchange was then logged every second until the photosynthetic rate stabilized (ca. 30–60 min). Induction state (% of fully induced photosynthetic rate) was calculated as a function of time since illumination; induction state at 60 s was tabulated to facilitate comparisons with other studies (Chazdon 1988). Photosynthetic responses to simulated sunflecks were measured on both uninduced leaves (shaded for at least 60 min) and induced leaves (exposed to saturating irradiance prior to study). Uninduced leaves were treated as for the induction curves. Induced leaves were exposed to saturating irradiance until gas exchange stabilized. In each case, leaves were then given a series of sunflecks of duration 2, 5, 10, 20, 40, 60 and 80 s. Sunflecks were 1,000 μmol m^{-2} s^{-1} in intensity, and leaves were returned to 10 μmol m^{-2} s^{-1} for 60 s between sunflecks; sunflecks were always given in the same order (see Valladares et al. 1997).

Modeling the effects of dynamic responses

We modeled daily carbon gain in response to dynamic light regimes for individuals of *Cyanea pilosa* var. *longipedunculata* and *Clermontia parviflora*. These species co-occur in wet montane forests on windward Hawai'i, with *Cyanea* occurring in shaded understories while *Clermontia* inhabits forest gaps and edges (Givnish et al. 2004). For both species, we quantified: (1) the rate of physiological induction after the start of illumination (see above), (2) the rate of stomatal opening after the start of illumination, (3) the rate of loss of physiological induction after entry into shaded conditions (10 μmol m^{-2} s^{-1}), and (4) the rate of stomatal closure after entry into the same shaded conditions. These measurements and associated variables (Givnish et al. 2004) were used to parameterize the model of Naumburg et al. (2001) for the response of carbon uptake to

a dynamic light regime under conditions in which moisture is not limiting (S1).

We conducted in silico transplants to evaluate daily carbon uptake for each species in its own dynamic light regime and in that of the other species. Models for each species were run using light-sensor data collected simultaneously over individuals of each species for a total of 8 days spread evenly over the year. Daily PFD ranged from 0.3 to 9.4 mol m^{-2} day^{-1} in *Cyanea*'s understory microhabitat, and 1.9–35.8 mol m^{-2} day^{-1} in *Clermontia*'s gap microhabitat. Daily carbon uptake was plotted against total daily PFD for each model run and fit to a Michaelis–Menten equation following Givnish et al. (2004); the resulting responses were used to evaluate the point at which mean carbon uptake for *Clermontia* exceeds that of *Cyanea*, and to quantify the effective compensation point for each species under a dynamic light regime. In addition, we compared the expected photosynthetic performance during sunflecks using the dynamic model against the expectation using steady-state photosynthetic rates, in order to evaluate photosynthetic limitation during sunflecks due to dynamic responses for each species as a function of light conditions. In silico "transplants" differ from true transplants in that they do not incorporate acclimation of species to the growth environment (including light and other factors), but they precisely capture what the photosynthetic properties of a species in its native habitat would imply, if unchanged, for carbon uptake in other habitats. We note that we have conducted common studies on this group and find strong evidence for genetically based changes among species in their steady-state photosynthetic responses (unpublished data).

To examine the mechanisms responsible for differences in model results for *Clermontia* and *Cyanea*, we assessed the relative roles of biochemical versus stomatal limitations during induction, initial stomatal conductance, and photosynthetic rates during intervals between sunflecks following Allen and Pearcy (2000). We recalculated assimilation rate (A) throughout induction to a constant c_i equal to that at A_{max}. At any moment during induction, the relative difference between this recalculated assimilation rate (A^*) and A_{max}—that is, $(A_{max} - A^*)/A_{max}$—reflects the limitation imposed by incomplete biochemical activation. Conversely, the limitation due to stomatal conductance is $(A^* - A)/A_{max}$; the total limitation relative to steady-state responses is $(A_{max} - A)/A_{max}$. From the time courses of these limitations, we calculated the time required for biochemical limitation to relax to 50% (L_m50) and maximum stomatal limitation ($L_s$max) at any point during induction.

Statistical analysis

Data were analyzed using general linear models that compared photosynthetic responses based on species (categorical

variables) and light regime (continuous variables). We examined bivariate relationships using standardized major axis regression calculated using (S)MATR (version 2.0; Falster et al. 2006), given that there were errors in the estimation of the mean values of all parameters (Sokal and Rohlf 1995). Phylogenetically structured analyses (e.g., Felsenstein 1985; Pagel 1999) were not employed because we believe they are inappropriate for the kind of data reported here, which reflect both genetic differences among related species *and* differences among those species in light habitat. Given that photosynthetic light responses are highly plastic in response to conditioning light levels and that different species/lineages of Hawaiian lobeliads occur in substantially different light environments, using a phylogenetically structured analysis on field data would conflate the effects of phylogeny and ecology (see Givnish et al. 2004).

Results

Light environments

Sunfleck length and frequency were significantly related to estimates of total daily PFD across species (Table 2). In general, species in habitats with low daily PFD experienced short and numerous sunflecks, while those in sunnier habitats experienced much longer and less numerous sunflecks. Average sunfleck length increased significantly with daily PFD (Fig. 1; $r = 0.829$, $P < 0.005$), and varied from
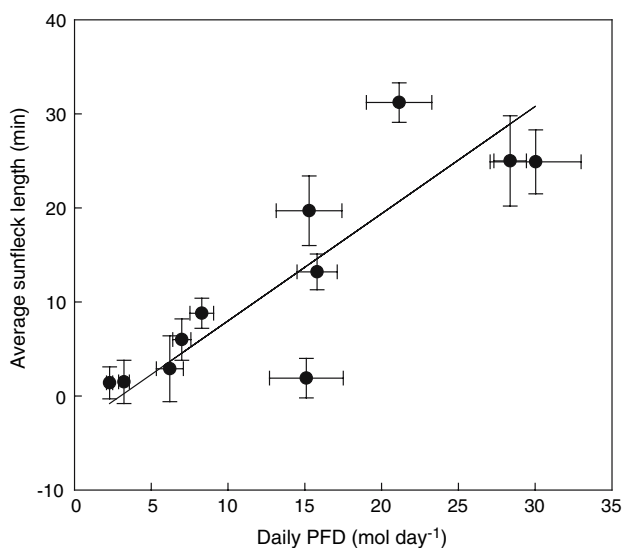
Fig. 1 Average fleck length (min) as a function of average daily photon flux density (PFD) for ten representative species of Hawaiian lobeliads. *Data points* and *error bars* represent the mean ± SE of light data from all datalogged individuals of each species. The *line* represents the reduced major-axis regression. *Lobelia yuccoides* is the outlier lying below the left end of the regression line

1.4 ± 1.7 min for *Cyanea floribunda* in shaded forest understories to 31.2 ± 2.1 min for *Trematolobelia kauaiensis* on open ridges (Table 2). Total minutes of sunflecks varied from 31 ± 21 min day^{-1} for *C. floribunda* to 533 ± 59 min day^{-1} in *Lobelia villosa* in open alpine bog sites (Table 3), and also increased significantly with daily PFD across species ($r = 0.649$, $P < 0.05$). Average sunfleck length, maximum sunfleck length, and total minutes of sunflecks all increased significantly with each other ($r = 0.723$–0.874, $P < 0.02$–0.001), but maximum sunfleck length was not significantly correlated to daily PFD ($P > 0.08$). Despite strong differences in average length and total minutes of sunflecks, it appears that all species can experience quite long sunflecks (Table 2). Even the most shaded species, *C. floribunda*, occasionally experienced sunflecks as long as 21 min.

The distribution of sunfleck lengths varied substantially among species (three representative species shown in Fig. 2). For example, 26% of sunflecks in the shaded understories where *C. pilosa* occurs were <20 s in duration. In contrast, only 9% of sunflecks were <20 s long on the open ridges where *T. kauaiensis* grows. The gap-inhabiting species *Clermontia parviflora* (Fig. 2) had a distribution of sunfleck lengths intermediate between those of shade-dwelling *Cyanea pilosa* (Fig. 2) and ridge-dwelling *T. kauaiensis* (Fig. 2).

Dynamic photosynthetic responses

Across species, instantaneous photosynthetic rates increased with the amount of time previously uninduced leaves spent in bright light. After 60 s of illumination, average induction states across species ranged from 30 to 59% of fully induced photosynthetic rates. Species differed significantly in induction state after 60 s ($F_{1,9} = 2.78$, $P < 0.015$): species from low-light habitats were more induced after 60 s of high light than species from high-light habitats (Fig. 3). There was a tighter decline in percentage induction after 60 s with average sunfleck length when *L. yuccoides* was excluded (Fig. 3). *L. yuccoides* showed unusually low induction after 60 s, but its light regime also had unusually short sunflecks for its moderate total daily PFD (Fig. 1).

Average uninduced light use efficiency (LUE) ranged from 10 to 75% across species, with both extremes of the range occurring in very short, 2-s simulated sunflecks (Fig. 2). As fleck length increased, uninduced LUE initially declined for species from shadier microsites (e.g., *C. pilosa*) and increased for species from sunnier microsites (e.g., *Trematolobelia*); the general tendency for uninduced LUE to increase in longer flecks across species (Fig. 2) reflects induction within those flecks and during preceding, shorter flecks to which leaves were exposed during the

Table 3 Trait values and model parameters related to differences in estimated daily carbon gain[a] for *Cyanea pilosa* subsp. *longipedunculata*[b] and *Clermontia parviflora*[b] in the Olaʻa Tract, Hawaiʻi Volcanoes National Park

| Symbol	Description	*Clermontia parviflora*	*Cyanea pilosa*
		Trait or parameter value (±1 SE)	
τ_{gi}	Time constant for biochemical opening signal for stomata (s)	400[c]	5.5
τ_{gd}	Time constant for biochemical closing signal for stomata (s)	1,000	550
τ_{Rd}	Time constant for Rubisco deactivation and loss of induction (s)	578	1,318
$L_m 50$	Time to 50% relaxation of biochemical limitation (s)	93 ± 20	150 ± 83
$L_s max$	Maximum stomatal limitation during induction (%)	13 ± 2.3	9 ± 1.9
$g_s ini$	Stomatal conductance prior to induction (μmol m^{-2} s^{-1})	0.19 ± 0.01	0.23 ± 0.04
$A_{interfleck}$	Assimilation rate in low light periods between flecks (μmol m^{-2} s^{-1})	**0.22 ± 0.04**[d]	**0.35 ± 0.02**
R_d	Dark respiration rate (μmol m^{-2} s^{-1})	**1.09 ± 0.10**	**0.47 ± 0.08**

[a] A full list of parameters used in the photosynthesis model are found in S1

[b] *Cyanea* occurs in shaded forest understories that average 3.2 mol photons m^{-2} day^{-1}. In contrast, *Clermontia* occurs in gaps and along forest edges that average 8.3 mol photons m^{-2} day^{-1}

[c] Values without SE represent parameters used in the model that were fit to composite responses of each species

[d] For values ± SE, those in *bold* indicate significant difference between species at the $P < 0.01$ level in a *t*-test


Fig. 2 Histograms of sunfleck lengths (*upper panels*) and light use efficiency (LUE) in simulated lightflecks (*lower panels*) for three species of Hawaiian lobeliads that represent low-, moderate- and high-light environments occupied by species in the lineage. *Data points* and *error bars* represent the mean ± SE of photosynthetic data for five individuals of each species. Histograms are from PFD measurements for all data-logged individuals of each species. LUE was calculated as the percent of CO_2 assimilated in a lightfleck compared to the amount that would have been assimilated with an instantaneous response to PFD change. *Closed circles* Induced leaves, *open circles* uninduced leaves
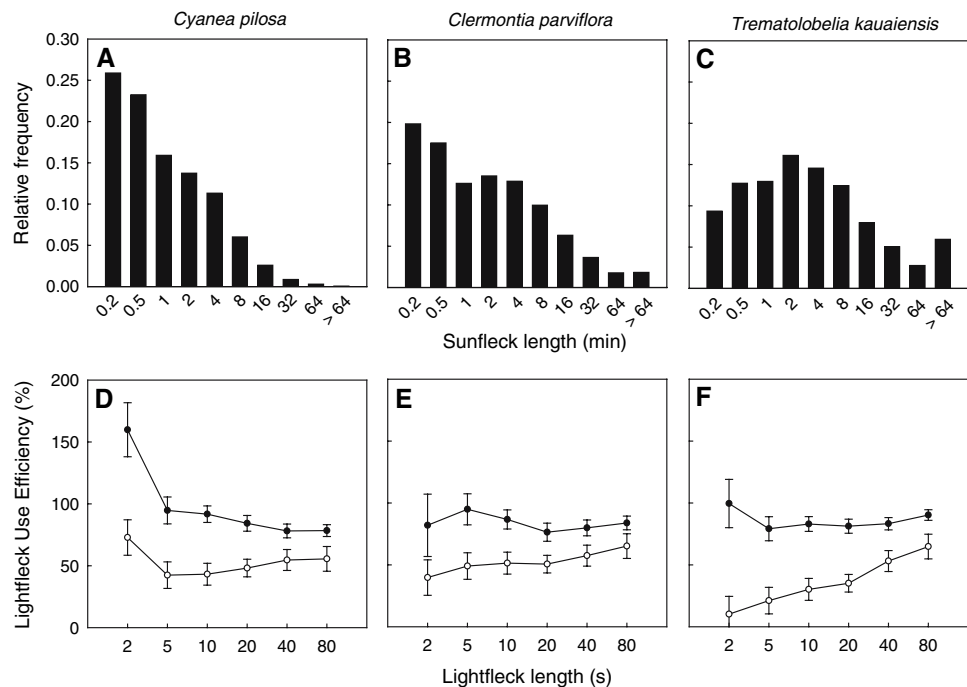
experimental protocol. The opposing trends in uninduced LUE between sun and shade species resulted in a significant species × lightfleck length interaction ($F_{40,165} = 1.96$, $P < 0.01$).

Average induced LUE ranged from 36 to 160% across species, with the extremes in *L. yuccoides* and *C. pilosa*, respectively; induced LUE was always was higher than uninduced LUE (Fig. 2). Both extremes of induced LUE again occurred in 2-s flecks. In general, induced LUE decreased with fleck length in all species, although these

trends were much stronger in shaded species and strongest among the shortest flecks across all species (Fig. 2). There was again a significant species × lightfleck length interaction ($F_{40,150} = 3.18$, $P < 0.0001$), largely due to differences during short flecks among species. Across species, there was no significant correlation of induced LUE in 2-s flecks to any measure of the light environment across species. In contrast, uninduced LUE in 2-s flecks declined significantly with total minutes of sunflecks (Fig. 4; $r = 0.678$, $P < 0.045$ across species).
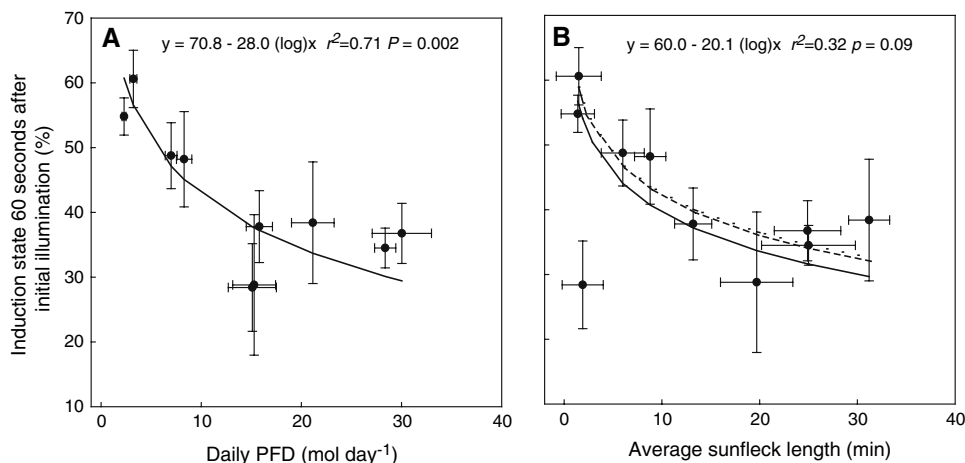
Fig. 3 Leaf induction state as a function of average daily PFD (*left-hand panel*) and average sunfleck length (*right-hand panel*) for ten representative species of Hawaiian lobeliads. *Data points* and *error bars* represent the mean $\pm$ SE of photosynthetic data from five individuals of each species, and the mean $\pm$ SE of PFD measurements for all datalogged individuals of each species. Leaf induction state was calculated as the percent of maximum photosynthesis rates achieved after 60 s of illumination following a long period in low light. *Curves* represent best fit reduced major axis regression lines; in the *right-hand panel* the *dashed line* excludes the outlier *L. yuccoides* ($y = 62.3 - 19.9$ ln x; $r^2 = 0.83$, $P = 0.006$ for 7 *df*)
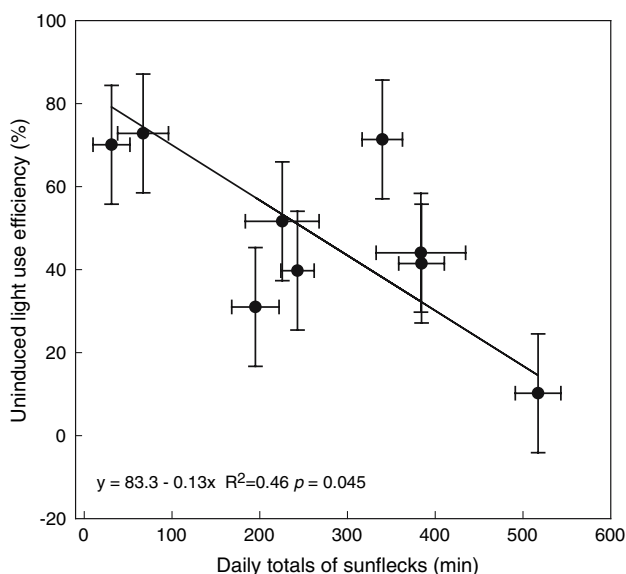
Fig. 4 LUE in a 2-s lightfleck by uninduced leaves as a function of daily minutes of sunflecks for ten representative species of Hawaiian lobeliads. *Data points* and *error bars* represent the mean $\pm$ SE of photosynthetic data from five individuals of each species, and the mean $\pm$ SE of PFD measurements for all datalogged individuals of each species. LUE was calculated as the percent of CO_2 assimilated in the lightfleck compared to the amount that would have been assimilated with an instantaneous response to PFD change. The *line* represents the best fit reduced major axis regression line. For abbreviations, see Figs. 1 and 2

Simulation models

In silico "transplants" of *Cyanea pilosa* and *Clermontia parviflora* in each other's dynamic light regime showed adaptive crossover in the area-based daily photosynthetic rates of these species, with *Cyanea* outperforming *Clermontia* below a daily PFD of roughly 3.5 mol m^{-2} day^{-1}, and *Clermontia* outperforming *Cyanea* in more sunlit microsites (Fig. 5). The distributions of both species along the daily PFD gradient exhibit similar crossover, with *Cyanea* being relatively more common (69% of all sampled individuals) below 3.5 mol m^{-2} day^{-1} and *Clermontia* being relatively more common (70% of all individuals) above that level (Fig. 5). Mass-based rates of photosynthesis for *Cyanea* and *Clermontia* also exhibit crossover, but at substantially higher total PFDs (ca. 7.5 mol m^{-2} day^{-1}) than did the area-based rates (data not shown).

On average, *Cyanea* gained 6.1 mmol CO_2 m^{-2} day^{-1} more than *Clermontia* across the range of light environments occupied by *Cyanea*. Similarly, *Clermontia* gained 24.3 mmol CO_2 m^{-2} day^{-1} more than *Cyanea* in light environments *Clermontia* inhabited. Although the absolute advantage in carbon gain per unit area was greater at high PFD, the proportional differences were much higher at low light levels. *Cyanea* gained an average of 14% less carbon than *Clermontia* in *Clermontia* light environments, while *Clermontia* gained an average of 183% less carbon than *Cyanea* in *Cyanea* light environments. In fact, in many of the microsites occupied by *Cyanea*, *Clermontia* showed negative daily assimilation, even without taking into account nighttime respiration or the amortized costs of leaf and non-leaf tissue construction.

We fit a simple Michaelis–Menten function to our simulation results for each species and calculated daytime leaf compensation points of 1.77 mol m^{-2} day^{-1} for *Clermontia* and 0.92 mol m^{-2} day^{-1} for *Cyanea*. These values compare with instantaneous leaf compensation points of 10.4 and
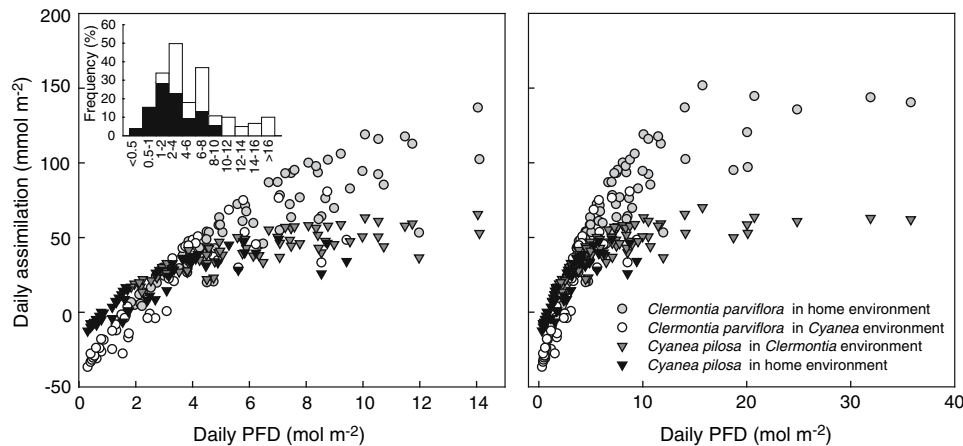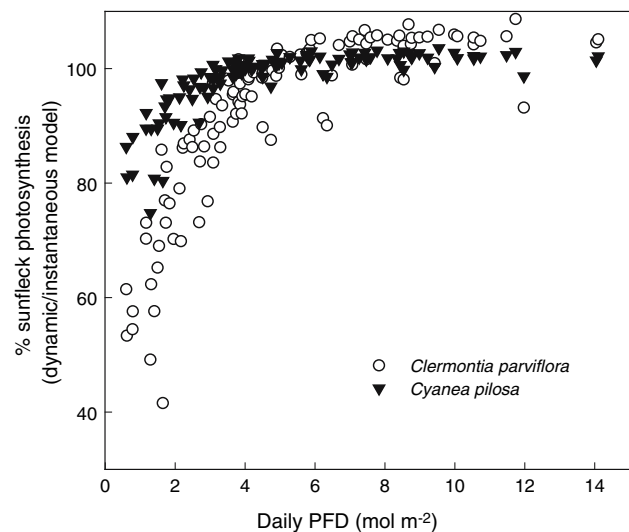
Fig. 5 Total daily photosynthesis (mmol CO_2 m^{-2} day^{-1}) as a function of daily PFD for *Cyanea pilosa* subsp. *longipedunculata* and *Clermontia parviflora* in the Olaʻa Tract, Hawaiʻi Volcanoes National Park. The graph on the *left* is an enlargement of the responses at low PFD. The stacked histogram *inset* on the left represents the distribution of average daily PFD for each species: *Cyanea* (*solid bars*) and *Clermontia* (*hollow bars*). Each *data point* represents simulated of photosynthesis from a single daily PFD trace from a single sensor. *Circles* represent simulations using average physiological data of five individuals of *Clermontia* and daily PFD data from *Clermontia*'s habitat (*open circles*) or from *Cyanea*'s habitat (*light gray circles*). *Inverted triangles* represent simulations using average physiological data of five individuals of *Cyanea* and daily PFD data from *Cyanea*'s habitat (*black triangles*) or from *Clermontia*'s habitat (*dark gray triangles*)

2.8 μmol m^{-2} s^{-1}, respectively—or roughly 0.45 and 0.12 mol m^{-2} day^{-1}—based on steady-state light responses for these species. Steady-state rates thus understate compensation points by a factor of 3.9–7.7 for *Clermontia* and *Cyanea*, respectively. On 19% of the individual-days modeled, *Cyanea pilosa* received daily PFD less than or equal to its apparent compensation point; no individual of *Clermontia parviflora* received less than its apparent compensation point (Fig. 5).

A comparison of dynamic and steady-state light responses shows that both species operate well below the steady-state expectations at low daily PFD totals (<ca. 4 mol m^{-2} day^{-1}), with *Cyanea* showing a deficit of up to 25% and *Clermontia* showing much larger deficits, up to 60% (Fig. 6). Dynamic limitations to sunfleck photosynthesis declined as daily PFD rose, and average sunfleck length increased, with such limitations essentially disappearing above ca. 5 mol m^{-2} day^{-1} in *Cyanea*, and above ca. 8 mol day^{-1} in *Clermontia* (Fig. 6). As expected, understory *Cyanea* shows faster stomatal responses to the beginning and end of sunflecks than gap-dwelling *Clermontia* (Table 3). However, both species show nearly the same stomatal conductance under shady conditions (0.23 vs. 0.19 μmol m^{-2} s^{-1}) and almost the same degree of maximum stomatal limitation (13 vs. 9%). A major reason for the divergent behavior of these species instead appears to be the much lower initial biochemical limitation (i.e., higher low-light rates of photosynthesis) of shaded leaves in *Cyanea* versus *Clermontia*. Higher respiration rates in *Clermontia* (1.09 vs. 0.46 μmol CO_2 m^{-2} s^{-1}) also appear to be important and lead to substantial carbon loss between sunflecks. In microsites receiving less than 3.5 mol PFD m^{-2} day^{-1}, *Clermontia* lost an average of 6.1 mmol C m^{-2}

Fig. 6 Photosynthesis in sunflecks predicted by the dynamic model as a percentage of that predicted from steady-state photosynthetic light responses for *Cyanea pilosa* subsp. *longipedunculata* and *Clermontia parviflora* in the Olaʻa Tract, Hawaiʻi Volcanoes National Park. Each *data point* represents the results of a simulation model based on a single daily PFD trace. For both species, there are data points that exceed 100%. These correspond to models where average stomatal conductance was lower in the steady-state models than in the dynamic models

day^{-1}, whereas *Cyanea* gained an average of 8.3 mmol C m^{-2} day^{-1}.

Discussion

Adaptive radiation—the rise of a diversity of ecological roles and attendant adaptations—is a fundamental process

linking ecology and evolution (Givnish 1997). While there have been tremendous advances in our knowledge of the origin and phylogeny of Hawaiian plant and animal radiations (e.g., see Baldwin et al. 1991; Givnish et al. 1995; Piano et al. 1997; Lindqvist et al. 2003; Gillespie 2004; Price and Wagner 2004; Rundell et al. 2004; Sakai et al. 2006), for many of these radiations we lack the functional data necessary to understand the ecological significance of phenotypic divergences seen within them.

A body of work has developed on functional trait variation in Hawaiian plant radiations, notably on *Euphorbia* and *Scaevola* (Robichaux and Pearcy 1980, 1984; Pearcy et al. 1982), the silversword alliance (Robichaux 1984; Robichaux and Canfield 1985; Robichaux et al. 1990), and *Schiedea* (Sakai et al. 2006). Our research on the Hawaiian lobeliads adds to this body of literature and contributes to our understanding of the extent of habitat divergence and accompanying functional diversification in the most species-rich Hawaiian flowering plant lineage. Previously, we demonstrated that the lobeliads occupy a broad range of light habitats and have diversified in steady-state photosynthetic physiology in an apparently adaptive fashion (Givnish et al. 2004). Here we have shown that the lobeliads have also diversified in their dynamic photosynthetic responses to their light regimes, that these shifts appear to maximize carbon gain of each species in their own light environment, and thus appear to be adaptive.

Light regimes and dynamic photosynthetic responses

This study is the first to report a statistically significant increase across species in the rapidity of photosynthetic induction with decreasing daily PFD (Fig. 3), which is itself closely correlated with sunfleck length (Fig. 1). As expected, species from habitats with shorter sunflecks show more rapid rates of induction. Similarly, uninduced LUE in short flecks declined significantly with total minutes of sunflecks across species (Fig. 4). That is, in the absence of induction, species from habitats with shorter sunflecks and less total sunfleck time were able to achieve a higher fraction of potential photosynthesis during short sunflecks. Previous studies have compared the dynamic responses of only two or three species—or two or three categories of species—that differ in light regime (e.g., Chazdon and Pearcy 1986a, b; Valladares et al. 1997; Cai et al. 2005). Thus, while such studies have generally found that plants from shadier habitats show faster induction, the agreement with theory in each individual study has necessarily been qualitative. Our analysis substantially extends this prior research by demonstrating a strong quantitative relationship between dynamic photosynthetic traits and dynamic light environments across a large group of closely related species (Figs. 2, 3, 4, 5). These results parallel our findings for

steady-state photosynthetic light responses (Givnish et al. 2004) and provide additional evidence for the adaptive diversification of photosynthetic physiology in the Hawaiian lobeliads.

We found that sunfleck length was positively correlated with total daily PFD across sites and species, consistent with results from a number of other studies (e.g., Chazdon et al. 1988; Chazdon and Pearcy 1991; Leakey et al. 2005). However, Hawaiian forests appear to be brighter than other tropical forests (Givnish et al. 2004) and have correspondingly longer sunflecks (see Chazdon et al. 1988; Lee 1989; Pearcy and Chazdon 1990; Valladares et al. 1997). Indeed, species from the lowest PFD regimes in this study can experience flecks as long as 20 min; such long sunflecks are known to cause photoinhibition in other Hawaiian plants (e.g., *Cibotium* tree ferns; Durand and Goldstein 2001). Because total daily PFD and sunfleck length are generally strongly correlated, it is difficult to determine which is a stronger driver of the observed dynamic responses. Increased average sunfleck length accounts more powerfully for the drop in induction after 60 s seen in brighter environments if *L. yuccoides* is excluded, but *L. yuccoides* experiences unusually short sunflecks for its light regime, and total daily PFD is more explanatory when all species are included. Taken together, these findings suggest that both sunfleck length and total daily PFD help shape dynamic photosynthetic light responses.

Despite the significant relationships of dynamic photosynthetic responses to dynamic light regimes across species, our data showed substantial dynamic limitation of photosynthesis during sunflecks, especially in microsites or on days with low daily PFD (see Figs. 2, 6). Uninduced leaves showed only 10–75% LUE across species, with uninduced LUE generally higher in longer (and later) sunflecks, and in species receiving lower daily PFDs in nature. In shady microsites, it is likely that leaf induction state is often below 100%, as our model for daily photosynthesis by *Cyanea pilosa* and *Clermontia parviflora* demonstrated (Figs. 5, 6). As expected, induced LUE was generally about 100% across species for sunflecks >5 s in duration (Fig. 2). LUE exceeded 100% only in induced leaves during short, 2-s sunflecks (Fig. 2), reflecting post-illumination carbon fixation (Sharkey et al. 1986; Kirschbaum et al. 1998).

Based on our analyses, understory *Cyanea* and most especially gap-dwelling *Clermontia* appear to be limited by dynamic photosynthetic responses at low daily PFDs (Fig. 6). Our results are thus similar to those of Naumburg et al. (2001) and Naumburg and Ellsworth (2002) for temperate tree species, in that differences in dynamic light responses are most important in densely shaded microsites, and are least important in species with faster rates of induction and slower rates of loss of induction. Our data suggest that the most important differences between *Cyanea* and

Clermontia are the latter's much greater biochemical limitation of photosynthesis in uninduced leaves, and much greater rate of dark respiration. In low-PFD environments, *Clermontia* thus loses substantial amounts of carbon between sunflecks, and never gets fully induced during short to moderately long sunflecks. Our data clearly indicate the importance of moving beyond steady-state photosynthetic light responses, and the need to incorporate dynamic responses in analyses of adaptation to different light regimes.

Adaptive nature of responses

Our previous work showed that the steady-state light response curves of *Cyanea pilosa* and *Clermontia parviflora* exhibit adaptive crossover, with *Clermontia* having higher instantaneous, mass-based assimilation rates than *Cyanea* at light levels >ca. 300 µmol m^{-2} s^{-1} and *Cyanea* having higher assimilation rates than *Clermontia* at lower light levels (Givnish et al. 2004). Here we provide similar evidence of adaptive crossover in our estimates of daily, area-based assimilation using in silico transplants that take dynamic photosynthetic responses into account (Fig. 5). For daily PFDs less than 3.5 mol m^{-2} day^{-1}, *Cyanea* had higher rates of daily carbon gain; above 3.5 mol m^{-2} day^{-1}, *Clermontia* had an advantage. Furthermore, the crossover PFD observed corresponds roughly to the crossover in the relative abundance of *Cyanea* versus *Clermontia* (Fig. 5). *Clermontia* had an large absolute (24.3 mmol CO$_2$ m^{-2} day^{-1}) but relatively small (14%) photosynthetic advantage over *Cyanea* in the microsites occupied by *Clermontia*. *Cyanea* had an small absolute (6.1 mmol CO$_2$ m^{-2} day^{-1}) but relatively huge (183%) advantage over *Clermontia* in the microsites occupied by *Cyanea*.

In silico "transplants" permit analyses that focus on the effects of differences among sites in one or more specific environmental factors (e.g., daily trajectories of PFD) on performance by plants as a function of one or more specific physiological parameters. This approach is, we believe, a powerful means of quantifying the potential advantages of particular traits in various environments. However, it must be recognized that in silico transplants differ from true transplants in two important respects; they do not include: (1) the effects of environmental differences other than those (i.e., PFD trajectories) specifically incorporated in the model, and (2) the effects of plasticity in creating additional differences in physiological responses in plants that develop under different conditions.

Strong inputs of radiant energy during sunflecks not only increase PFD, but also leaf temperature, vapor pressure deficit (VPD), leaf water potential, and the extent of photoinhibition as well (Young and Smith 1979; Robichaux and Pearcy 1980; Chazdon 1988; Le Gouallec et al. 1990;

Watling et al. 1997; Valladares and Pearcy 2002). Thus, photosynthesis in a dynamically varying light environment may respond not only to PFD but also to temperature, VPD, and plant water supply. Leakey et al. (2005) recently showed that shifts in leaf temperature during sunflecks in *Shorea leprosula* growing in rainforest in lowland Sabah substantially reduced carbon uptake during sunflecks, given that leaf temperatures could rise by up to 10°C and reach 38°C during sunflecks, and given that steady-state photosynthesis was 40% lower at 38°C than at its optimum at 29°C. Low VPD in lowland rainforest understories, high air temperatures, intense PFD during sunflecks, and low stomatal conductance in uninduced leaves, should all work to elevate leaf temperatures substantially during sunflecks. Given that our study species mostly occur in cool, mid-elevation cloud forests, it seems unlikely that excursions in leaf temperature have a substantial effect on lobeliad photosynthesis during sunflecks. However, we do believe that shifts in leaf water potential and/or plant water content during sunflecks and over the course of the day could have a substantial impact on photosynthesis. During the course of this and other studies in Hawai'i, we observed drop-offs in photosynthetic rate after mid-day—similar to those seen in many other venues—that seem most easily explained in terms of shifts in plant water status. To explore this issue, we have now begun research on the interaction of light and moisture supply in determining photosynthetic rate.

It is widely recognized that the light environment in which a plant develops affects its photosynthetic morphology and physiology (e.g., Ellsworth and Reich 1992; Kitajima 1994; Valladares et al. 2005). It is almost surely the case, therefore, that had we actually transplanted individuals of *Cyanea pilosa* and *Clermontia parvifolia* into microsites differing in daily PFD, plastic responses to light regime would have influenced the response of daily carbon uptake to daily PFD. However, given the rate at which rats and other introduced herbivores attack lobeliads, and the legally protected status of most areas that continue to support these often rare plants, it was impossible for us to conduct physical transplants for the species involved. Nevertheless, we believe that the in silico transplants have great value because they show how photosynthetic responses would provide an advantage under certain conditions and not under others, and confirm that the photosynthetic characteristics shown by two different species appear to fit them to the different ranges of dynamic light regimes that each species inhabits.

Including dynamic photosynthetic light responses raised compensation points compared with those calculated from steady-state photosynthetic responses (see Results). These results parallel those of Timm et al. (2002), and reflect the slower rise of photosynthesis during sunflecks when dynamic constraints are included, balanced against a fixed

rate of dark respiration. These calculated increases in apparent compensation point are independent of those that would result from including the costs of constructing leaf and non-leaf tissue, and which can substantially increase the whole-plant compensation point (Givnish 1988; Givnish et al. 2004). The increase in compensation point due to incorporating dynamic responses does, however, raise an important question: does the rate of respiration actually remain constant in induced and uninduced leaves? Some of the published traces of net carbon uptake in induced vs. uninduced leaves (e.g., see Chazdon and Pearcy 1991) suggest that respiration may be elevated somewhat in induced leaves. If this were to be shown to be the case generally, it would cast considerable light on the most nagging question regarding photosynthetic induction: what is the disadvantage of rapid induction, such that many sun-adapted species lack it?

Finally, our model for daily carbon uptake by *Cyanea pilosa* and *Clermontia parviflora* provides yet another example of adaptive crossover, a reversal in the rank of species by growth or photosynthetic rate along an environmental gradient. This concept, though unnamed until recently, entered the modern physiological literature with Horn's (1971) analysis of optimal leaf arrangement in tree crowns as a function of light availability in early versus late succession, and has been implicit or explicit in dozens of optimality models since then (e.g., Cowan and Farquhar 1977; King 1981; Givnish 1986, 2002; Tilman 1988). In each of these studies, the "optimal" strategy—which maximizes growth relative to that resulting from other strategies—varied with environmental conditions, creating qualitative or quantitative predictions regarding the expected distribution of species with different strategies. Such models have played an important role in plant ecophysiology, allowing us to move from studies of functional differences associated with different morphologies or physiologies to rigorous predictions regarding the expected distributions of different kinds of plants, and ultimately should shed light on the structure of different kinds of plant communities and their relationship to variation in specific environmental factors. The notion of crossover and rank reversal in empirical plant studies began with comparisons by Björkman et al. (1972) of photosynthetic rates among leaves of *Atriplex triangularis* grown at different light levels, and has proceeded to the present in similar studies by Givnish (1988), Sack and Grubb (2001), Montgomery and Chazdon (2002), Givnish et al. (2004), Sack (2004), Poorter and Bongers (2006), and Seiwa (2007). Studies such as these should—especially when combined with both common garden experiments and field studies—continue to provide new, tightly reasoned insights into the foundation for differences in the distributions of individual plant species and the composition and structure of plant communities.

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