Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points[1]

Thomas J. Givnish,[2] Rebecca A. Montgomery,[2,4] and
Guillermo Goldstein[3]

[2]Department of Botany, University of Wisconsin, Madison, Wisconsin 53706 USA; and [3]Department of Biology, University of
Miami, P.O. Box 249118, Coral Gables, Florida 33124 USA

Six endemic genera/sections of lobeliads (Campanulaceae) occupy nearly the full range of light regimes on moist sites in the Hawaiian Islands, from open alpine bogs and seacliffs to densely shaded rainforest interiors. To determine whether this clade has undergone a corresponding adaptive radiation in photosynthetic adaptations, we studied the natural light habitats and physiological characteristics of 11 species representing each sublineage. Across species in the field, average photon flux density (PFD) varies from 2.3 to 30.0 mol · m^{-2} · d^{-1}, and maximum assimilation rate (A_{max}) ranges from 0.17 to 0.35 µmol CO_2 · g^{-1} · s^{-1}. Across species, A_{max}, dark respiration rate (R), Michaelis-Menten constant (k), light compensation point, specific leaf area (SLA), maximum carboxylation rate (V_{cmax}), maximum rate of electron transport (J_{max}), photosynthesis at saturating CO_2 (A_{satCO_2}), and carboxylation efficiency (α) all increase significantly and in tightly coupled fashion with PFD, in accord with classical economic theory. Area-based rates have a higher degree of physiological integration with each other and tighter coupling to PFD than the corresponding mass-based rates, despite the energetic importance of the latter. Area-based rates frequently show adaptive cross-over: high-light species outperform low-light species at high PFD and vice versa at low PFD. A_{max}-mass has little relationship to leaf mass per unit area (LMA), leaf N content, or leaf lifespan individually, but a multiple regression explains 96% of the variance in A_{max}-mass across species in terms of SLA, leaf N content, and average PFD. Instantaneous leaf compensation points range from 0.1 to 1.2% full sunlight, far lower than the ecological (whole-plant) compensation points (ECPs) of 1.1 to 29.0% sunlight calculated based on photosynthetic parameters, leaf longevity, and allocation to leaf vs. nonleaf tissue. The ECPs are much closer to the lower limits of PFD actually experienced by lobeliads, suggesting they may play an important role in restricting species distributions. Taken together, these data provide evidence for an adaptive radiation in photosynthetic traits that is strongly correlated with—and indeed may help determine—the light regime that each species inhabits.

Key words: adaptive cross-over; adaptive radiation; *Brighamia*; *Clermontia*; *Cyanea*; *Delissea*; *Lobelia*; photosynthetic light response; *Trematolobelia*.

The Hawaiian lobeliads (Campanulaceae: Lobelioideae) consist of five genera and two sections of *Lobelia*, all endemic to the Hawaiian archipelago. This group is one of the most spectacular examples of adaptive radiation in flowering plants and has undergone striking diversifications in habitat, growth form, leaf shape, flower morphology, and mode of seed dispersal (Rock, 1919; Carlquist, 1965, 1970; Lammers, 1990; Givnish et al., 1994, 1995). With ca. 110 species, they comprise one-ninth of the Hawaiian flora (Wagner et al., 1990) and include alpine bog rosettes, seacliff succulents, and trees, treelets, and shrubs of mesic and wet forest edges and interiors. A few species are epiphytes and vines. A cpDNA phylogeny indicates that this remarkably divergent group arose from a single colonization (Givnish, 1998; T. J. Givnish et al., unpublished manuscript).

Surprisingly, nothing is known about the lobeliads' diversification in photosynthetic adaptations, even though they have invaded nearly the entire range of light environments in moist to wet habitats in Hawaii. Such habitats include (a) open alpine bogs and gaps in subalpine forest for *Lobelia* sect. *Galeatella* and *Trematolobelia*; (b) partly shaded seacliffs, interior rock faces, dry forests, and mesic- and wet-forest edges for *Brighamia*, *Lobelia* sect. *Revolutella*, *Delissea*, *Clermontia*, and purple-fruited *Cyanea*; and (c) densely shaded wet-forest interiors for orange-fruited *Cyanea* (Givnish, 1998).

Photosynthetic adaptations to contrasting light environments have long been a core concern of physiological ecologists (e.g., Björkman et al., 1972; Björkman, 1981; Chazdon and Pearcy, 1986a, b; Chazdon, 1988, 1992; Givnish, 1988, 1995; Pearcy, 1988, 1990; Mulkey et al., 1993, 1996; Kitajima, 1994; Sims and Pearcy, 1994; Chazdon et al., 1996; Walters and Reich, 1996, 2000; Feild et al., 2001; Valladares et al., 2002). Despite this, such adaptations have only rarely been studied in large numbers of closely related taxa (*Euphorbia* and *Scaevola*, Robichaux and Pearcy 1980, 1984; *Acer*, Lei

TABLE 1.   Natural distributions of the 11 species of Hawaiian lobeliads investigated and location and number of study populations. Elevation and habitat data from Lammers (1990) and T. J. Givnish and R. A. Montgomery, personal observations; habitat terminology follows Wagner et al. (1990).

Species	Habitat	Elevational range (m)	Localities (island)	Elevation (m)	N
Cyanea floribunda	Wet forest understories	460–1520	Pu'u Maka'ala Natural Area Reserve (Hawai'i)	1300	3
Cyanea pilosa subsp. *longipeduculata*	Wet forest understories	610–1520	Ola'a forest, Hawaii Volcanoes National Park (Hawai'i)	1250	3
Cyanea hirtella	Wet forest understories	1030–1400	Pihea Trail, Koke'e (Kaua'i)	1300	1
Cyanea leptostegia	Diverse mesic forest	1000–1300	Forest off Mohihi Road above YMCA camp, Canyon Trail, Koke'e (Kaua'i)	1200–1250	3
Clermontia parviflora	In gaps and as epiphytes, wet forest	120–1460	Ola'a forest, Hawaii Volcanoes National Park (Hawai'i)	1250–1300	3
Lobelia yuccoides	Ridges and openings, diverse mesic forest	750–1200	Kalalau Valley rim and forest near Hongwanji camp, Koke'e (Kaua'i)	1150–1300	2
Delissea rhytidosperma	Diverse mesic forest	300–1000	Limahuli Garden (Kaua'i)	50	1
Clermontia fauriei	Openings, diverse mesic to wet forest	365–1400	Pihea and Alakai Swamp Trails, Koke'e (Kaua'i)	1300	3
Trematolobelia kauaiensis	Openings, wet forest	650–1575	Pihea and Alakai Swamp trails, Koke'e (Kaua'i)	1300	2
Lobelia villosa	Summit bogs on wind-swept ridges	1200–1580	Alakai Swamp Trail, Koke'e (Kaua'i)	1300	2
Brighamia insignis	Seacliffs	0–400	Limahuli Garden (Kaua'i)	50	1

and Lechowicz 1997a, b, 1998; *Psychotria*, Valladares et al., 1997, 2000) and never for plants whose distributions along light gradients have been quantified and whose phylogenetic relationships to each other are known in detail.

The Hawaiian lobeliads are a model system with which to study the evolution of photosynthetic adaptations to light availability, given their diversity in leaf form, distribution from nearly full sun to dense shade, and existence of a DNA phylogeny with which to interpret the roles of ecology vs. phylogeny in shaping the characteristics of present-day species. We have therefore initiated a long-term investigation of the ecology and evolution of lobeliad photosynthetic adaptations to different light regimes, focusing on 11 species that represent each major Hawaiian lineage. This first report details the light regimes experienced by these species in the field and their in situ photosynthetic light responses, leaf longevities, specific leaf area, N content, and various measures of mesophyll photosynthetic capacity. We analyze relationships among photosynthetic parameters, leaf traits, and photon flux density across species to test whether these trends accord with theoretical predictions. We ask whether species show evidence of differential adaptation to light availability in the form of adaptive cross-over in photosynthetic light response—that is, do shade species outperform sun species at low light levels, with the reverse at high light levels? Finally, we test whether the lowest light level at which each species is found corresponds to its ecological compensation point, based on the balance of the instantaneous rate of photosynthesis against current leaf respiration, nighttime leaf respiration, leaf construction costs amortized on leaf lifetime, and allocation to nonleaf tissue (Givnish, 1995, 1998).

MATERIALS AND METHODS

Study sites and species—We studied 11 species representing each major clade of Hawaiian lobeliads (Table 1). A cpDNA restriction-site phylogeny places *Cyanea* sister to *Clermontia*, *Brighamia* sister to *Delissea*, and *Trematolobelia* sister to *Lobelia* sect. *Galeatella*; *Cyanea-Clermontia* is sister to *Brighamia-Delissea*, and short branches connect this clade to *Lobelia* sect. *Revolutella* and *Trematolobelia-Galeatella* (Givnish et al., 1995; Givnish,

1998). Within the large genus *Cyanea* (ca. 65 spp.), there is a basal split between the purple-fruited species (exemplified by *Cy. leptostegia*) that typically grow in more open forests, and the orange-fruited species (exemplified by *Cy. floribunda*, *Cy. hirtella*, and *Cy. pilosa* var. *longipedunculata*) that typically inhabit densely shaded understories (Givnish et al., 1995). In *Clermontia*, *Cl. fauriei* is sister to all other taxa (except one intergeneric hybrid), while *Cl. parviflora* is one of the most recently derived species based on more recent study using ISSR variation (Givnish et al., 2000).

To facilitate comparisons based primarily on differences in light availability, we chose species native to a narrow elevational range (1000–1250 m) in areas with moderate to heavy rainfall (>1500 mm/yr). *Brighamia* does not meet these criteria, but occupies cooler conditions than expected based on elevation, given its exposure to strong onshore breezes and trade winds in its seacliff habitat. So far as is known, the taxa sampled exhibit ecologies typical of congeners, especially in the five smallest groups: *Brighamia* (two spp.), *Delissea* (10 spp.), *Trematolobelia* (five spp.), *Lobelia* sect. *Galeatella* (four spp.), and *Lobelia* sect. *Revolutella* (nine spp.) (Rock, 1919; Carlquist, 1970, 1974). In *Cyanea* (65 spp.) and *Clermontia* (22 spp.), sampling was constrained by rarity (nearly half of *Cyanea* species are extinct or highly endangered), accessibility, and time. We included one pair of sister species in *Cyanea* (*Cy. floribunda*, *Cy. pilosa*) as well as members of two of the remaining five sublineages recognized by Givnish et al. (1995); *Cy. floribunda* was included partly because it occupied the shadiest microsites of any lobeliad we know. Wherever possible, we measured light availability, photosynthetic physiology, and related leaf traits in three natural populations growing under relatively undisturbed conditions (Table 1). It proved impossible to access natural populations of two federally endangered species (*Brighamia insignis* and *Delissea rhytidosperma*), which we instead studied at outplantings established by the National Tropical Botanical Garden on northern Kaua'i. Species were also grown and studied at four light levels at ca. 1200 m on Hawai'i; results from this common-garden investigation will be presented elsewhere.

Light regimes—We measured daily courses of photon flux density (PFD, in micromoles per square meter per second) immediately above 5–12 plants per population of each species, using GaAs photodiodes (Hamamatsu, New York, New York, USA) connected to CR-10X dataloggers equipped with multiplexers (Campbell Scientific, Logan, Utah, USA). Photodiodes were calibrated against a LI-COR 190S quantum sensor (LI-COR, Lincoln, Nebraska, USA). We logged 10-s average of 1-s measurements for 2 wk each in winter and summer in 28 study populations. Rarity and difficulty of access permitted study of only two populations of *Lobelia villosa*, *L. yuccoides*, and *Trema-*

tolobelia kauaiensis, and only one of *Cyanea hirtella*. Average values of instantaneous and total daily PFD were tabulated for each individual; means ± SE (N = number of individuals) were then calculated for each species. Within each species, we compiled similar statistics for the focal individuals whose photosynthetic performance was measured and tabulated the lowest average PFD for an individual plant within each species. Across species, the mean PFD for focal plants is strongly correlated with that for all conspecifics (y = $1.11x + 0.21$, r^2 = 0.84, $P < 0.0001$ for 9 df). Given the strength of the relationship between focal and global PFDs, and the much larger and more representative sample across all plants within a species, we related interspecific trends in photosynthetic parameters to global PFD rather than local PFD. This is a conservative approach: many of the trends reported are as strong, and often slightly stronger, when related to focal PFD instead.

Photosynthetic measurements—*Static light responses*—We measured steady-state (i.e., fully induced) photosynthetic light responses (assimilation rate [A] vs. PFD curves) of each species in the field, using attached, fully expanded leaves from five individuals whose light regimes had been quantified. Leaves were clamped into the cuvette of an LI-6400 portable photosynthesis system (LI-COR) equipped with a red/blue LED light source and a CO_2 mixing system. We measured photosynthesis at 10–15 PFD levels between 0 and 1000 (to 1500) μmol $\cdot$ m^{-2} $\cdot$ s^{-1}. At each PFD level, gas exchange values were recorded after stomatal conductance and CO_2 uptake stabilized, beginning at a PFD of 500 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} to photoactivate ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco) and open the stomata (Pearcy, 1990; Valladares et al., 1997). We maintained relative humidity, leaf temperature, and cuvette CO_2 concentration within narrow limits close to those experienced by most species (ca. 75% relative humidity, 20°–25°C, 360 μmol/mol CO_2). All measurements were made between 0600 and 1300 hours. There was little relationship between precipitation and season during the period of this study, so we did not stratify sampling between ''dry'' and ''wet'' seasons. Specific leaf area (SLA, in square centimeters per gram), its inverse leaf mass per unit area (LMA, in grams per square meter) and leaf N content (in milligrams per gram) were determined from leaf punches, excluding veins >1.5 mm diameter. Net photosynthetic rates per unit leaf mass and area were each fit to the Michaelis-Menten model

$$A(\text{PFD}) = A_{\max}\text{PFD}/(k + \text{PFD}) - R \qquad (1)$$

(where $A_{\max}$ = maximum assimilation rate, k = Michaelis-Menten constant, and R = dark respiration rate) (Fig. 1) using a third-order Newton-Rapheson algorithm. Data for individual leaves fit this model quite well, with values of r^2 generally exceeding 0.98. The slope of the linear portion of the light response curve (the first three or four points, depending on goodness of fit) was estimated using linear regression, and quantum yield (ϕ) was then calculated as that slope divided by absorptance.

Compensation points—Instantaneous leaf compensation points (ICPs) were calculated by setting $A(\text{PFD}) = 0$ and solving for PFD in the Michaelis-Menten equation. Ecological (i.e., whole-plant) compensation points (ECPs) were calculated following Givnish (1995), taking into account nighttime leaf respiration, leaf construction costs amortized over leaf lifetimes, and allocation to nonleaf tissue, assuming identical rates of turnover for leaf and nonleaf tissue. Leaf construction costs (in grams of CO_2 per gram) were based on the mean for species native to moist Hawaiian forests (Baruch and Goldstein, 2000). We estimated the amortized construction cost of nonleaf organs using 0.56 as the fractional allocation to nonleaf organs (based on greenhouse data for 9-mo-old *Clermontia fauriei*), assuming that nonleaf tissues had the same lifetimes as leaf tissue. The calculated ECPs are thus provisional and depend primarily on interspecific differences in photosynthetic light response and leaf longevity, not on differences in resource allocation. Calculated ECPs are likely to be somewhat higher than actual minimum light requirements because root and (especially) stem tissue turnover should be substantially less than that measured for leaves. Therefore, we also calculated the leaf compensation point (LCP) by taking into account only the respiration rate and amortized construction cost of leaf tissue. The LCPs should provide a lower bound on the actual ecological compensation point by setting the overhead associated
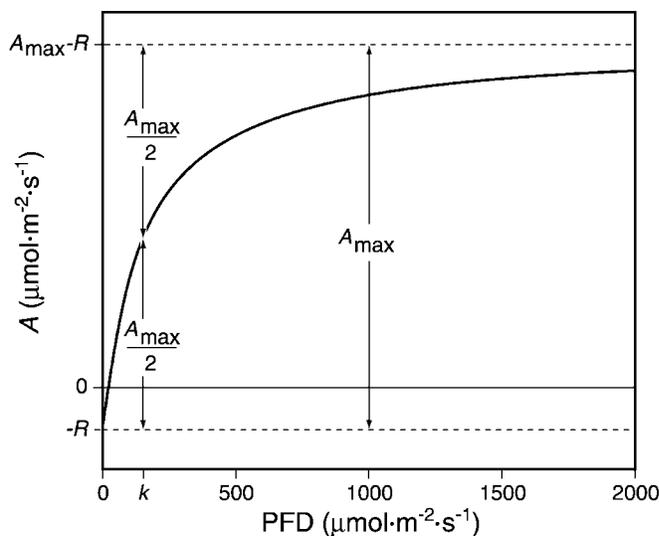

Fig. 1. Schematic diagram of Michaelis-Menten photosynthetic light response, showing asymptotic convergence of net carbon uptake on $A_{\max} - R$ at high PFD, rising from $-R$ (dark respiration) at zero PFD and traversing half the potential range in net uptake by a PFD of k (see Eq. 1). Note that $A_{\max}$ is substantially above the actual maximum net photosynthetic rate. The instantaneous compensation point (ICP) is achieved where A(PFD) = 0, that is, at the photon flux density at which the light-response curve crosses the x-axis.

with nonleaf organs equal to zero. The calculated ECPs provide an upper bound on actual ECPs. Taken together, LCPs and calculated ECPs should bracket a species' actual minimum light requirements.

Mesophyll photosynthetic capacity—We measured CO_2 response curves (A vs. c_i) on the same five, fully induced leaves of each species used for light response curves. We varied c_i from nearly 0 to 1000 (to 1500) μmol/mol in seven steps, all at saturating PFD, by varying cuvette (CO_2) with other conditions constant. We used these data to estimate carboxylation efficiency α (initial slope of A vs. c_i), maximum photosynthetic rate at saturating CO_2 (A_{satCO_2}), maximum rate of electron transport ($J_{\max}$), maximum carboxylation rate ($V_{\max}$), and CO_2 compensation point (Γ) using Photosyn Assistant (Dundee Scientific, Dundee, UK), based on the photosynthetic models of Farquhar et al. (1980), von Caemmerer and Farquhar (1981), Sharkey (1985), Harley and Sharkey (1991), and Harley et al. (1992).

In situ leaf characteristics—In addition to SLA and leaf N content, we measured the absorptance of each leaf studied for photosynthesis, using an appropriately filtered quantum sensor and an integrating sphere (LI-COR). Leaf longevity was estimated by marking the petioles of newly expanded leaves with a census-specific colored ink at bimonthly intervals and then monitoring the presence or absence of each marked leaf and fraction of surviving tissue at subsequent censuses. We followed all leaves produced on at least 10 twigs on different individuals of each species for at least 1 yr. The resulting data were analyzed using an equilibrium conveyor-belt model to obtain leaf longevity (LL) as

$$\text{LL} = NT/n, \qquad (2)$$

where N is the average total number of leaves held per twig, T is the average intercensus time interval, and n is the average number of new leaves per census. Estimates obtained using this approach were similar to those calculated by applying more complex demographic techniques to the dates of leaf births, partial losses, and deaths (results not shown).

Data analysis—The Fisher least significant difference (LSD) multiple comparison of means ANOVA was used to determine which species significantly differed in average daily PFD. Correlations and simple LMS regressions

TABLE 2. Photon flux density (PFD) experienced by field populations of 11 species of Hawaiian lobeliads. Total numbers of sensors and sensor days used in calculating means and standard errors are shown (see text). Superscripts indicate which means differ significantly from each other.

Species	Daily total PFD ($mol·m^{-2}·d^{-1}$)		Instantaneous PFD ($\mu mol·m^{-2}·s^{-1}$)		Sensors (N)	Sensor days (N)
	Mean	SE	Mean	SE		
Cyanea floribunda	2.3[a]	0.2	53.1	4.7	49	639
Cyanea pilosa	3.2[a]	0.4	74.6	8.0	52	785
Cyanea hirtella	6.2[ab]	0.9	143.8	20.3	11	89
Cyanea leptostegia	7.0[b]	0.6	161.7	13.6	29	360
Clermontia parviflora	8.3[b]	0.8	192.0	17.9	52	785
Lobelia yuccoides	15.1[c]	2.4	349.6	55.7	25	320
Delissea rhytidosperma	15.3[c]	2.1	353.8	49.6	13	182
Clermontia fauriei	15.8[c]	1.3	365.9	30.3	59	794
Trematolobelia kauaiensis	21.1[d]	2.1	505.1	48.4	31	364
Lobelia villosa	28.4[e]	1.1	656.8	24.6	23	305
Brighamia insignis	30.0[e]	3.0	695.2	68.5	12	168

among measured variables across species were calculated using standard techniques. Regressions involving PFD used light data expressed on a daily basis (in moles per square meter per day). Log transformation was used to linearize relationships where necessary. Phylogenetically structured analyses (e.g., Felsenstein, 1985; Harvey and Pagel, 1991; Pagel, 1994, 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 (Björkman, 1981) 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.

Backward-elimination multiple regressions were used to identify variables with significant effects on A_{max}. Potential predictors of A_{max} included raw and log-transformed values of PFD, leaf N content, SLA, LMA, stomatal conductance, and leaf longevity.

Given the large number (27) of morphological, physiological, and environmental parameters quantified for each species, and the strong likelihood of cross-correlations among them, we used principal components analysis (PCA) to identify the most important axes of covariation among parameters (PC-ORD; McCune, 2002). We conducted PCA on three sets of parameters, involving those based on leaf area (e.g., in grams of CO_2 per square meter), leaf mass (e.g., in grams of CO_2 per gram), or both, including in each case the four traits that depend on both area and mass or neither (SLA, Γ, and leaf lifespan), and excluding PFD and SLA's inverse LMA. We assessed the strength and pattern of covariation among parameters using joint plots of each parameter (including PFD) against the ordination axes. Joint plots portray the strength and direction of a parameter's association with the ordination axes by superimposing vectors whose components are the correlation coefficients (*r*) of that parameter with each axis (McCune, 2002).

We counted the number of species pairs that displayed adaptive cross-over, in which the light response curve of the species native to higher PFD starts lower than that of the low-light species, but ends higher. Björkman et al. (1972) and Givnish (1988, 1995) argue that low-light species should outperform others at low PFD, and high-light species should outperform others at high PFD, especially when performance is measured as photosynthesis per unit leaf mass or other energetic investment or as whole-plant carbon gain per unit investment in leaf and nonleaf tissue. To test this proposition, we first constructed a diagonal matrix tabulating adaptive cross-overs, nonadaptive cross-overs, and non-cross-overs for all 55 ordered species pairs, with the order of individual columns/rows reflecting the rank of each species by average daily PFD. We then randomly permuted the rows and columns of this matrix in tandem, effectively shuffling the PFDs associated with each species. This process was repeated 100 000 times. The resulting distribution of "adaptive" vs. "nonadaptive" cross-overs above the diagonal was used to calculate whether the actual number of adaptive cross-overs significantly exceeded the null expectation.

RESULTS

Light environments—Across species, average instantaneous PFD varies 13-fold in essentially continuous fashion, from 53 ± 5 $\mu mol · m^{-2} · s^{-1}$ for *Cyanea floribunda* in shaded wet-forest understories to 695 ± 69 $\mu mol · m^{-2} · s^{-1}$ for outplanted *Brighamia insignis* on an open hillside (Tables 1 and 2). The corresponding daily totals ranged from 2.3 ± 0.2 to 30.7 ± 3.0 $mol · m^{-2} · d^{-1}$. The minimum average PFD experienced by a species is strongly correlated with its average PFD ($y = 0.132x^{1.31}$; $r^2 = 0.90$, $P < 0.0001$ for 9 df); the minimum/mean ratio is 31 ± 16%, with the expected value rising from 12 to 40% with increasing PFD.

Based on significant differences in mean PFD, essentially five groups of species occupy significantly different portions of the light gradient (Table 2). Close relatives in some lineages (e.g., orange-fruited *Cyanea floribunda* and *Cy. pilosa* in the shadiest sites and species of *Trematolobelia* and *Lobelia* sect. *Galeatella* in some of the brightest sites) occupy similar portions of the PFD gradient, but in others (*Brighamia-Delissea*, *Clermontia*) they do not. Based on the data available, different groups of Hawaiian lobeliads often occupy significantly different light regimes, even when some close relatives are compared.

Photosynthetic light responses—Classical economic theory (Björkman et al., 1972; Björkman, 1981; Givnish, 1988, 1995) predicts that species adapted or acclimated to sunny habitats should display higher maximum rates of photosynthesis and higher rates of dark respiration and require more light to saturate photosynthesis and balance respiration than shade species. These predictions are nicely illustrated by the static light responses of *Clermontia parviflora* and *Cyanea pilosa*, which occur under gaps and dense canopies, respectively, in the same wet forests of windward Hawai'i (Fig. 2). As expected, photosynthesis per unit leaf mass in *Clermontia parviflora* reaches higher maximum levels, saturates at higher light levels, entails a higher rate of dark respiration, and requires more light to balance leaf respiration (i.e., has a higher leaf compensation point) than does *Cyanea floribunda* (Fig. 2). The static light response curves cross, with *Clermontia* having an advantage above 290 $\mu mol · m^{-2} · s^{-1}$ and *Cyanea* having an edge under darker conditions (see Discussion for further details). *Cyanea* has an instantaneous leaf light compensation point of 2.8 ±
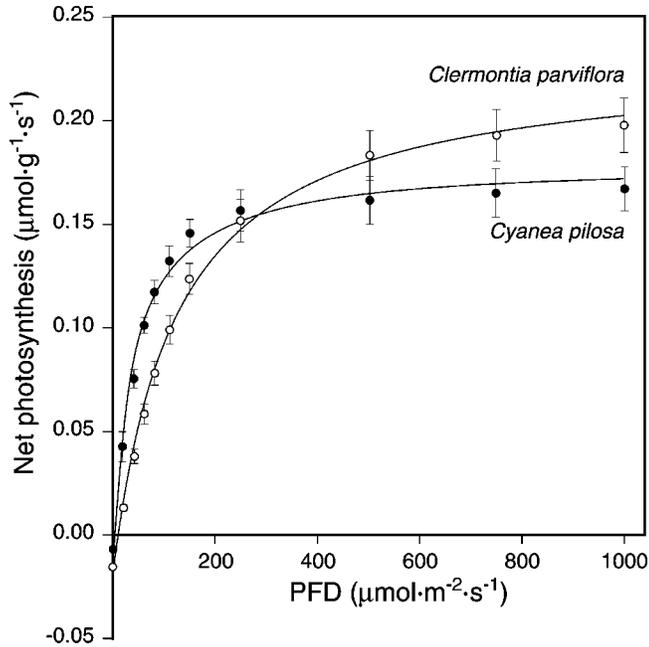
Fig. 2. Static photosynthetic light responses of *Cyanea pilosa* subsp. *longipedunculata* and *Clermontia parviflora* in the Ola'a Tract, Hawaii Volcanoes National Park. Dots and error bars represent the mean ± SE of measurements on five individuals of each species; curves are Michaelis-Menten functions based on the mean values of A_{max}, k, and R across individuals. Net CO_2 assimilation shows adaptive cross-over, with understory *Cyanea* having a higher rate of net photosynthesis below ca. 290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PFD and gap-dwelling *Clermontia* having a higher rate above that light level. Compared with *Cyanea*, *Clermontia* has a higher maximum rate of carbon uptake, needs more light to saturate photosynthesis, and possesses a higher respiration rate and instantaneous light compensation point.

0.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, while *Clermontia* requires 10.4 ± 1.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to achieve zero net photosynthesis.

Across species, maximum photosynthetic rate per unit leaf area (A_{max}) varies from 10.8 to 35.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, increasing with average PFD at an ever-decreasing rate (Fig. 3A: $y = 5.09x^{0.326}$, $r^2 = 0.64$, $P < 0.005$ for 9 df). Mass-based A_{max} does not increase with average PFD when all species were included (Fig. 3B). Four species deviate from the significant relationship seen in the other species, however. Three outliers (*Clermontia fauriei*, *Lobelia kauaensis*, *Trematolobelia kauaiensis*) grow in nutrient-poor bogs or boggy openings (Table 1), while two of these and *Brighamia insignis* have large amounts of achlorophyllous water-storage tissue in their leaves (T. J. Givnish and J. Redmer, unpublished data). When all four outliers—each with unusually low leaf N contents (in milligrams per gram) (Table 3)—are excluded, mass-based A_{max} increases significantly with average PFD (Fig. 3B: $y = 0.0146x + 0.114$; $r^2 = 0.75$, $P < 0.001$ for 5 df).

Dark respiration per unit area increases significantly with PFD (Fig. 4A: $y = 0.054x + 0.348$, $r^2 = 0.77$, $P < 0.0005$ for 9 df), but not per unit mass ($r = 0.17$, NS). The ratio of respiration to maximum photosynthetic rate (R/A_{max}) rises significantly with PFD, from ca. 0.06 to 0.13, as daily PFD increases roughly 13-fold (Fig. 4B: $y = 0.0027x + 0.056$, $r^2 = 0.65$, $P < 0.003$ for 9 df). That is, species in denser shade have respiration rates that are a lower fraction of their maximum photosynthetic rates. R and A_{max} are themselves closely correlated on both mass and area bases, with $R = 0.099A_{max}$
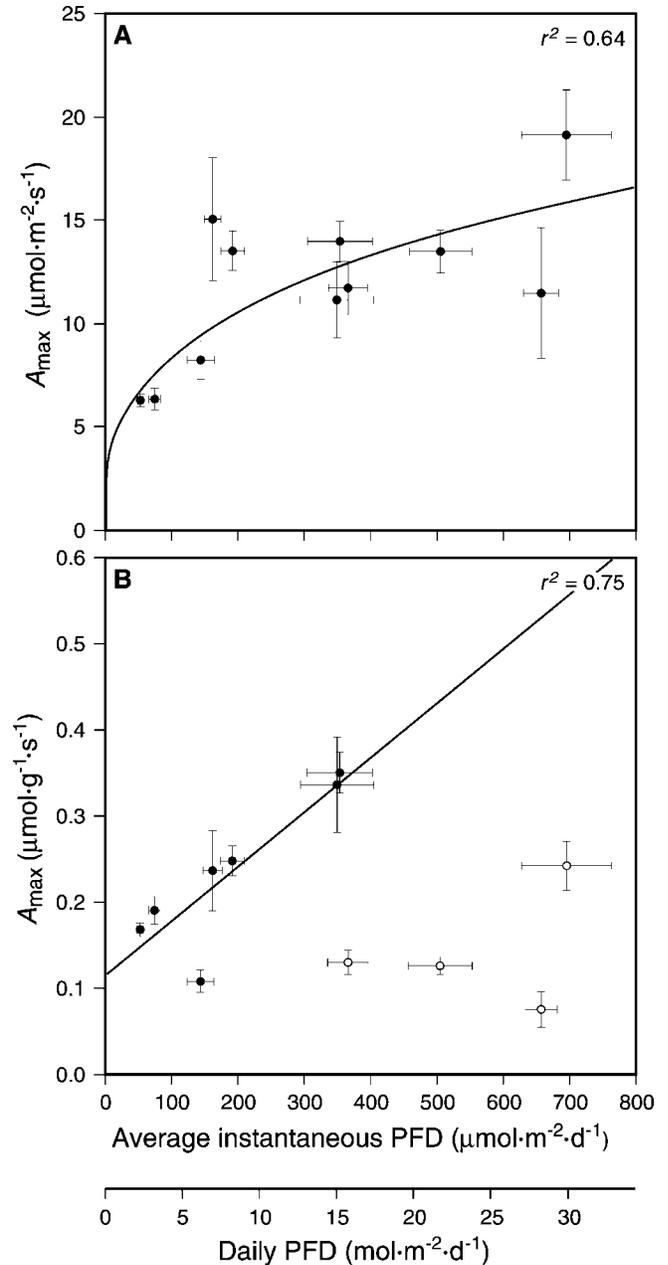
Fig. 3. Maximum photosynthetic rate (A_{max}) as a function of average photon flux density experienced by 11 representative species of Hawaiian lobeliads, expressed per unit (A) leaf area and (B) leaf mass. Dots and error bars represent the mean ± SE of photosynthetic data for five individuals of each species, and the mean ± SE of PFD measurements for all datalogged individuals of each species. From left to right, the species are *Cyanea floribunda*, *Cy. pilosa* var. *longipedunculata*, *Cy. hirtella*, *Cy. leptostegia*, *Clermontia parviflora*, *Lobelia yuccoides*, *Delissea rhytidosperma*, *Cl. fauriei*, *Trematolobelia kauaiensis*, *L. villosa*, and *Brighamia insignis*; the same sequence is used for all plots of photosynthetic data as a function of PFD (see Table 3). Curves represent LMS regressions: (A) $A_{max} = 5.09PFD^{0.326}$, $r^2 = 0.64$ for all species ($P < 0.005$ for 9 df); and (B) $A_{max} = 0.0146PFD + 0.114$, $r^2 = 0.75$ excluding four species of boggy sites or possessing substantial water storage tissue (hollow dots) ($P < 0.001$ for 5 df).
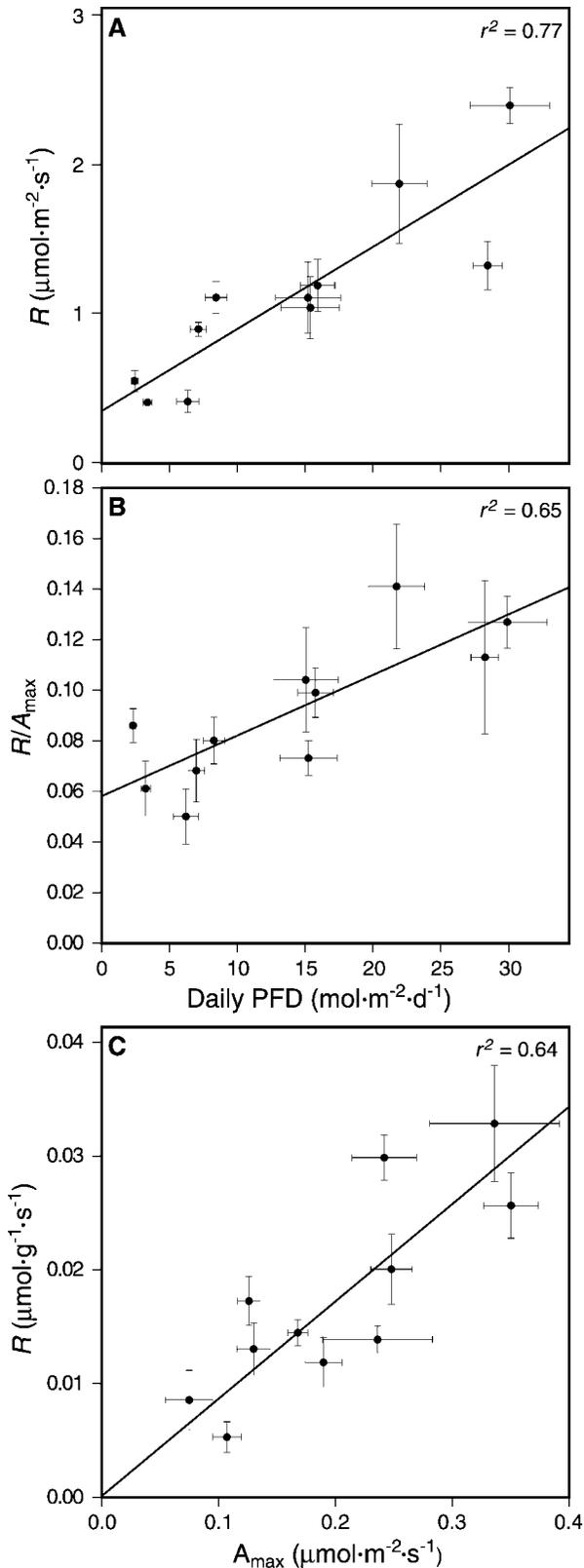
Fig. 4.   Respiration for 11 species of Hawaiian lobeliads, expressed (A) per unit leaf area as a function of average daily PFD ($R = 0.054$PFD $+ 0.348$, $r^2 = 0.77$, $P < 0.0005$ for 9 df); (B) as a fraction of A_{max} and function of PFD ($R/A_{max} = 0.0027$PFD $+ 0.056$, $r^2 = 0.65$, $P < 0.005$ for 9 df); and (C) as a function of A_{max} alone ($R = 0.099.A_{max}$, $r^2 = 0.64$, $P < 0.005$ for 9 df).

for a regression through the origin (Fig. 4C: $r^2 = 0.64$, $P < 0.005$ for 9 df).

The sign of the relationship between leaf nitrogen and light availability depends on the units of expression. N_{area} increases with average PFD while N_{mass} decreases, but neither relationship is significant (Table 4). The difference between the area- and mass-based trends in A_{max}, N, and R reflects the increase in leaf mass per unit area with average PFD (Fig. 5A: $y = 2.54x + 35.2$, $r^2 = 0.38$, $P < 0.05$ for 9 df). The shift in the mass allocated to a given surface area affects leaf diffusional properties and cell layering, ultimately affecting the measured patterns of gas exchange. As expected, the Michaelis-Menten parameter k (see Eq. 1) increases sharply with PFD (Fig. 5B), reflecting a highly significant rise in the amount of light needed to saturate photosynthesis in leaves with greater LMA and often greater thickness.

Light compensation points—Instantaneous compensation points (ICPs) range from 2.8 ± 1.4 µmol · m^{-2} · s^{-1} for *Cyanea pilosa* to 24.6 ± 4.3 µmol · m^{-2} · s^{-1} for *Trematolobelia kauaiensis* and are significantly correlated with the average instantaneous PFD experienced by species (Fig. 6: $y = 0.034x + 1.32$, $r^2 = 0.80$, $P < 0.0001$ for 9 df). Given how ICPs are calculated, this trend is consistent with the observed increase in dark respiration with PFD across species and the near constancy of quantum yield (mean $\phi = 0.086 \pm 0.017$). Instantaneous compensation points lie far below the average and minimum PFDs to which individual species are exposed (Fig. 6). Thus, variation in ICP alone cannot account for the differential distributions of lobeliads along the light gradient.

Calculated values of the ecological compensation point—the photon flux density at which the instantaneous photosynthetic rate just balances day and nighttime leaf respiration, the cost of leaf construction amortized over leaf lifetime, and the cost of nonleaf organs amortized over their lifetimes—increase significantly with light availability and are always below a species' average PFD (Fig. 6: $y = 0.78x - 74.3$; $r^2 = 0.75$, $P < 0.001$ for 9 df). Compared with ICPs, calculated ECPs are much closer to (and yet still below) each species' average PFD and often exceed the average PFDs of other species (Fig. 6). However, ECPs exceed the minimum observed PFDs for all but three species, usually by small amounts (12–76 µmol · m^{-2} · s^{-1}) except for *Brighamia* and *Trematolobelia* (ECP = 0.95 min PFD $+ 69.1$; $r^2 = 0.45$, $P < 0.05$ for 9 df). On the other hand, leaf compensation points are always substantially below the minimum observed PFDs ($y = 0.094x + 1.25$; $r^2 = 0.86$, $P < 0.0001$ for 9 df). These data suggest that the actual minimum light requirements of individual species are close to the minimum average PFDs observed.

Mesophyll photosynthetic capacity and related traits—As average PFD rises across species, there are significant increases in carboxylation efficiency (α), the area-based maximum rate of carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}), and maximum rate of photosynthesis at saturating c_i (A_{satCO_2}). Variation in these characteristics appears to be closely coordinated, with strong correlations among most traits (Table 4), the strongest being that between electron transport capacity J_{max} and A_{satCO_2} ($r = 0.96$***). A_{max} is most strongly correlated to α ($r = 0.95$***), k to A_{satCO_2} ($r = 0.90$***), and R to V_{cmax} ($r = 0.80$***) (Fig. 7). Leaf absorptance shows no significant relationship to PFD, but is strongly tied to leaf N_{area} ($r = 0.97$***) and LMA ($r = 0.87$***). The values of N_{area}

TABLE 3.　In situ physiological, morphological, and phenological leaf characteristics of the 11 species of Hawaiian lobeliads investigated.

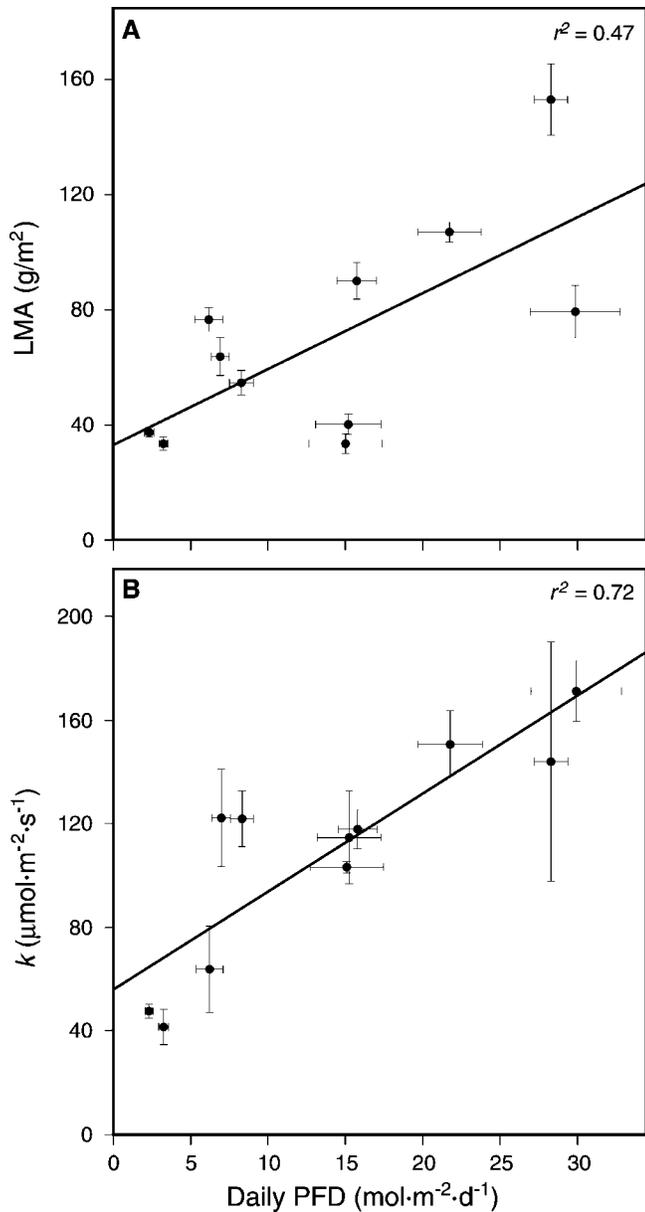|	Area-based measures										
Species	A_{max} (μmol· m^{-2}·s^{-1})	R (μmol· m^{-2}·s^{-1})	k (μmol· m^{-2}·s^{-1})	ICP (μmol· m^{-2}·s^{-1})	LCP (μmol· m^{-2}·s^{-1})	ECP (μmol·m^{-2}· s^{-1})	ϕ	Absorptance	N (g/m^2)	α	J_{max} (μmol· m^{-2}·s^{-1})
Cyanea floribunda	6.28	0.54	47.8	4.4	10.9	39.5	0.089	0.850	1.02	0.234	46.1
Cyanea pilosa	6.30	0.39	41.4	2.8	6.7	21.4	0.121	0.847	1.06	0.221	36.4
Cyanea hirtella	8.21	0.40	63.8	3.6	9.3	26.6	0.056	0.874	2.46	0.352	97.0
Cyanea leptostegia	13.87	0.88	122.1	8.2	18.4	72.7	0.102	0.888	2.75	0.466	103.9
Clermontia parviflora	13.24	1.09	121.7	10.4	28.5	104.6	0.093	0.872	1.89	0.442	99.6
Lobelia yuccoides	10.50	1.09	103.3	12.2	27.1	105.8	0.082	0.848	1.20	0.333	65.4
Delissea rhytidosperma	14.10	1.02	114.3	9.2	21.6	72.4	0.074	0.860	1.68	0.595	111.3
Clermontia fauriei	11.40	1.17	117.7	13.2	33.3	137.6	0.088	0.865	1.75	0.450	94.4
Trematolobelia kauiensis	13.46	1.84	150.4	24.6	64.9	416	0.081	0.881	2.28	0.457	106.6
Lobelia villosa	10.69	1.30	144.1	17.1	54.5	290	0.073	0.910	3.28	0.387	178.3
Brighamia insignis	18.31	2.35	171.0	24.5	64.2	581	0.081	0.870	1.64	0.656	149.9

and LMA, as well as quantum yield and stomatal conductance, have no significant relationship to PFD (Table 4).

Covariation of photosynthetic adaptations in relation to PFD—The PCA of all photosynthetic parameters produces three statistically significant axes, based on a comparison of eigenvalues with null expectations. The first of these explains 45.1% of the variance in the data set and is strongly correlated with daily PFD (Fig. 8: $r = 0.91^{***}$). Most area-based parameters are essentially collinear with axis 1, reflecting close coordination with PFD and each other in moving from *Cyanea pilosa* and *Cy. floribunda* in the shadiest microsites to *Brighamia insignis*, *Lobelia villosa*, and *Trematolobelia kauaiensis*

in the sunniest microsites (Fig. 9). Most mass-based variables are collinear with axis 2, which accounts for 28.0% of the total variance. Specific leaf area and LMA run skew to these area- and mass-based axes, as expected given that they are ratios of leaf mass and area. Leaf N content per unit mass and area show a similar pattern of covariation, nearly paralleling the directions of increase of SLA and LMA, respectively (Fig. 9). Leaf absorptance closely parallels N per unit area, as expected ($r = 0.97^{***}$), as well as LMA ($r = 0.871^{***}$). Leaf lifespan runs perpendicular to this SLA/LMA nexus, increasing as most area- and mass-based photosynthetic parameters decrease. Carboxylation efficiency α and A_{max} per unit area increase in nearly the opposite direction, skew to axes 1 and

TABLE 4.　Correlations among photon flux density (PFD) and physiological, morphological, and phonological characteristics of leaves from field populations of 11 representative species of Hawaiian lobeliads. For data and units, see Table 3. Significant correlations ($P < 0.05$) are shown in boldface type.

	Area-based measures											
	A_{max}	R	k	ICP	LCP	ECP	ϕ	Absorptance	N	α	J_{max}	V_{cmax}
PFD	**0.711**	**0.914**	**0.873**	**0.924**	**0.928**	**0.895**	−0.395	0.446	0.316	**0.686**	**0.783**	**0.860**
A_{max}		**0.833**	**0.895**	**0.726**	**0.672**	**0.691**	−0.180	0.355	0.271	**0.950**	**0.656**	**0.817**
R			**0.908**	**0.969**	**0.939**	**0.951**	−0.207	0.338	0.177	**0.742**	**0.649**	**0.803**
k				**0.896**	**0.887**	**0.809**	−0.269	0.602	0.483	**0.811**	**0.816**	**0.864**
ICP					**0.986**	**0.944**	−0.251	0.432	0.279	0.626	**0.657**	**0.775**
LCP						**0.943**	−0.276	0.530	0.367	0.579	**0.727**	**0.776**
ECP							−0.222	0.397	0.229	0.605	**0.658**	**0.732**
ϕ								−0.338	−0.402	−0.322	−0.513	−0.470
Absorptance									**0.967**	0.317	**0.830**	0.511
N										0.267	**0.750**	0.432
α											**0.677**	**0.893**
J_{max}												**0.833**
V_{cmax}												
A_{satCO2}												
g_{max}												
LMA												
SLA												
Leaf lifespan												
Γ												
A_{max}												
R												
N												
J_{max}												
V_{cmax}												
A_{satCO2}												
g_{max}												

TABLE 3. Extended.

V_{cmax} (µmol·m^{-2}·s^{-1})	A_{satCO2} (µmol·m^{-2}·s^{-1})	g_{max} (µmol·m^{-2}·s^{-1})	Neither area- nor mass-based				Mass-based measures						
			LMA (g/m²)	SLA (cm²/g)	Leaf lifespan (mo)	Γ (Pa)	A_{max} (µmol·g^{-1}·s^{-1})	R (µmol·g^{-1}·s^{-1})	N (mg/g)	J_{max} (µmol·g^{-1}·s^{-1})	V_{cmax} (µmol·g^{-1}·s^{-1})	A_{satCO2} (µmol·g^{-1}·s^{-1})	g_{max} (µmol·g^{-1}·s^{-1})
13.7	14.7	0.112	37.3	268.4	10.1	5.3	0.168	0.0144	27.3	1.23	0.367	0.413	0.0030
11.2	15.4	0.355	33.3	305.2	9.2	3.7	0.190	0.0118	32.0	1.10	0.341	0.442	0.0107
24.7	28.1	0.234	76.4	131.3	8.5	6.1	0.108	0.0053	32.5	1.28	0.325	0.370	0.0031
26.6	30.9	0.171	63.7	164.7	8.3	4.5	0.236	0.0138	44.0	1.74	0.450	0.517	0.0027
27.2	35.4	0.249	54.3	189.0	3.8	4.0	0.249	0.0200	34.5	1.90	0.519	0.694	0.0046
19.6	22.5	0.231	33.1	318.6	6.5	6.4	0.336	0.0328	37.2	2.16	0.639	0.737	0.0070
43.8	35.6	0.183	39.9	258.4	6.0	5.1	0.350	0.0256	43.0	3.01	1.200	0.886	0.0046
38.4	35.1	0.267	89.9	113.5	9.8	4.8	0.130	0.0130	19.5	1.03	0.428	0.381	0.0030
40.1	40.2	0.329	106.9	94.0	7.5	6.1	0.126	0.0172	21.3	1.00	0.375	0.375	0.0031
39.8	51.1	0.199	152.7	66.9	7.3	9.8	0.075	0.0085	21.8	1.21	0.267	0.346	0.0013
49.5	45.6	0.179	79.0	148.7	4.1	6.0	0.242	0.0298	23.4	2.02	0.693	0.632	0.0023

2 in quadrant 1 (Fig. 9). Logarithmic transformation does not alter the slightly eccentric position of A_{max} per unit area. Axis 3 explains 10.8% of the total variance and is not significantly associated with PFD or any leaf trait.

The PCA of the area-based parameters, SLA, leaf lifespan, and Γ resolves two significant axes, with the first explaining 59.4% of the variance and strongly correlating with daily PFD ($r = -0.92$***). Axis 2 accounts for 15.7% of the variance, indicating an essentially one-dimensional covariance structure associated with the first, PFD-related axis. Fifty of 91 pairwise correlations among the 14 purely area-based parameters are statistically significant before correction for multiple comparisons (Table 4); after correction, 47 (52%) are significant, all with $|r| > 0.648$. Ten of the 14 area-based parameters (71%) have significant correlations with PFD after correction for multiple comparisons. Leaf absorptance, quantum yield φ, maximum stomatal conductance g_{max}, and N content per unit area are aberrant in having almost no significant correlation with each other or PFD; the remaining area-based parameters have significant correlations, often highly so, with each other in 46 of 57 instances and with daily PFD in all 10 instances. Only two of 112 pairs of area- vs. mass-based parameters are significantly correlated after correction for multiple comparisons.

The PCA of the mass-based variables, SLA, leaf lifespan, and Γ also produces two significant axes, with the first ex-

TABLE 4. Extended.

Area-based measures		Neither area- nor mass-based measures				Mass-based measures						
A_{satCO2}	g_{max}	LMA	SLA	Leaf lifespan	Γ	A_{max}	R	N	J_{max}	V_{cmax}	A_{satCO2}	g_{max}
0.839	**−0.008**	**0.624**	**−0.518**	**−0.502**	**0.593**	**−0.035**	**0.413**	**−0.487**	**0.158**	**0.234**	**0.101**	**−0.446**
0.725	−0.159	0.238	−0.374	**−0.732**	0.039	0.363	0.561	0.029	0.508	0.516	0.469	−0.429
0.750	−0.007	0.458	−0.460	−0.596	0.314	0.066	0.527	−0.447	0.159	0.231	0.162	−0.432
0.896	−0.068	0.587	−0.604	−0.624	0.383	0.064	0.398	−0.265	0.240	0.246	0.197	−0.560
0.771	0.099	0.596	−0.552	−0.480	0.439	−0.091	0.403	−0.547	0.003	0.087	0.005	−0.452
0.825	0.092	**0.697**	−0.623	−0.464	0.531	−0.199	0.294	−0.606	−0.064	0.006	−0.076	−0.494
0.724	0.029	0.561	−0.528	−0.478	0.420	−0.151	0.344	−0.583	−0.038	0.032	−0.059	0.440
−0.446	0.325	−0.410	0.436	0.192	−0.603	0.167	0.004	0.154	−0.180	−0.174	−0.015	0.608
0.786	−0.103	**0.871**	**−0.847**	−0.158	**0.616**	−0.504	−0.402	−0.233	−0.209	−0.309	−0.360	**−0.686**
0.689	−0.072	**0.800**	**−0.807**	−0.070	**0.564**	−0.481	−0.477	−0.087	−0.181	−0.290	−0.353	−0.634
0.729	−0.212	0.234	−0.389	−0.648	0.042	0.335	0.477	0.037	0.566	0.633	0.480	−0.471
0.962	−0.237	**0.790**	**−0.751**	−0.484	**0.664**	−0.215	0.012	−0.281	0.152	0.108	−0.006	−0.704
0.899	−0.105	0.585	−0.634	−0.482	0.368	−0.013	0.264	−0.319	0.287	0.417	0.179	−0.605
	−0.055	**0.799**	**−0.784**	−0.522	0.564	−0.209	0.071	−0.370	0.111	0.126	0.007	**−0.652**
		0.080	−0.051	0.080	−0.225	−0.220	−0.168	−0.232	−0.403	−0.277	−0.238	0.564
			−0.909	−0.004	**0.741**	**−0.710**	−0.410	**−0.642**	−0.443	−0.416	−0.559	**−0.655**
			0.038	−0.475		**0.690**	0.445	0.565	0.420	0.377	0.537	**0.769**
				−0.062		−0.517	**−0.652**	−0.181	−0.637	−0.510	**−0.681**	0.085
						−0.394	−0.107	−0.409	−0.130	−0.202	−0.275	−0.494
							0.827	**0.718**	**0.890**	**0.821**	**0.953**	0.389
							0.244	**0.723**	**0.707**	**0.811**	0.178
								0.676	0.506	**0.646**	0.345
									0.929	**0.959**	0.078
										0.896	0.088
											0.257

Fig. 5. Leaf mass per unit area (LMA) and the Michaelis-Menten constant k as a function of average daily PFD for 11 representative species of Hawaiian lobeliads. Lines represent LMS regressions: (A) LMA = 2.67PFD + 33.1, r^2 = 0.47 ($P < 0.02$ for 9 df); (B) k = 3.75PFD + 56.7, r^2 = 0.72 ($P < 0.001$ for 9 df). See Fig. 2 for sequence of species from left to right.

Fig. 6. Light compensation points–instantaneous (ICP), leaf (LCP), and whole-plant or ecological (ECP)–as a function of average daily PFD. Dots represent ECPs and actual mean PFDs for individual species (see Fig. 2 for sequence from left to right); error bars represent the standard errors of mean PFDs. For clarity, data for individual species are not shown for calculated ICPs and ECPs. The dashed line running 45° across the figure is CP = PFD. Note that the traditional ICPs are far below the actual light levels inhabited by species, while ECPs are much closer to (but still below) the mean PFD occupied by each species.

plaining 57.6% of the variance and the second 20.9%. Axis 1 is strongly associated with daily PFD (r = 0.83**), although more weakly than the relationship seen for area-based parameters. Across mass-based parameters, 13 (62%) of 21 pairwise correlations are statistically significant. Maximum stomatal conductance per unit leaf mass is aberrant in having no significant correlations with any of the other mass-based parameters. Even though axis 1 of the mass-based PCA is significantly correlated with PFD, no individual mass-based parameter is significantly correlated with daily PFD. Based on these results, there appears to be a greater degree of physiological integration based on leaf area than on leaf mass. This tendency is especially striking if one focuses only on A_{max}, R, k, the

various light compensation points, A_{satCO_2}, V_{cmax}, and J_{max}. In that case, PCA axis 1 recovers 83.8% of the total variance, is essentially collinear with each of the included photosynthetic parameters, and correlates nearly perfectly with daily PFD (r = 0.94***).

Adaptive vs. nonadaptive cross-over of static light responses—As expected from the fact that A_{max}, k, and R increase with average daily PFD, many pairs of species show adaptive cross-over, with species from sunnier conditions having a higher photosynthetic rate at high PFD and a lower rate at low PFD (see Fig. 2, Table 5). Of the 55 distinct pairwise comparisons among species, 38 display cross-over in their area-based photosynthetic light responses; 36 of these cross-overs are adaptive, a highly significant deviation from the null expectation and toward the prediction by economic theory ($P < 4.5 \times 10^{-4}$, permutation test). There are 43 cross-overs for mass-based rates, of which 30 are adaptive, a marginally nonsignificant tendency in the same direction ($P > 0.066$, permutation test).

Structural and environmental determinants of maximum photosynthetic capacity—Across a wide range of angiosperms and gymnosperms, photosynthesis per unit leaf mass, leaf N content on the same basis, SLA, and leaf longevity all show strong log-log relationships to each other (Reich et al., 1997, 1999; Ackerly and Reich, 1999). Moreover, variation in photosynthetic rate can be largely explained by variation in leaf N content and SLA (Reich et al., 1997). As predicted by Givnish (1979, 1986) and Gutschick (1988, 1999), leaves with less mass per unit area (and, often, thinner cross-sections) have

Fig. 8.   Axis 1 score of the PCA ordination of photosynthetic parameters as a function of average daily PFD received by each species.

Fig. 7. A_{max}, k, and R in Hawaiian lobeliads are closely related to parameters of mesophyll photosynthetic capacity based on A vs. c_i curves. Lines represent LMS regressions. (A) A_{max} = 25.9carboxylation efficiency + 0.68, r^2 = 0.90 ($P < 0.0001$ for 9 df); (B) $k = 0.48A_{satCO_2}$ + 15.9, r^2 = 0.85 ($P < 0.0001$ for 9 df); (C) $R = 0.37V_{cmax}$ − 0.04, r^2 = 0.64 ($P < 0.005$ for 9 df).

lower photosynthetic rates at a given leaf N content, presumably as a result of the increased internal shading, diffusional limitations, and competition among chloroplasts for CO_2 inside thicker leaves with greater SLA.

Among the Hawaiian lobeliads, leaf longevity is not significantly related to $A_{max,mass}$, N_{mass}, or SLA. However, $A_{max,mass}$ has a strong positive correlation to N_{mass} and SLA (Fig. 10). The proportions of variance explained by the log-log regressions and their slopes were generally much less than those reported by Reich et al. (1999), as would be expected if the Hawaiian lobeliads simply resample the data distribution across vascular plants within a much narrower range of each variable. Within the Hawaiian lobeliads, leaf lifespans vary from 3.8 ± 0.3 mo in *Clermontia parviflora* to 10.1 ± 0.4 mo in *Cyanea floribunda*, representing a 2.7-fold variation, 30 times less than that in the global data set. By contrast, leaf N content and SLA vary by 2.3- and 4.6-fold in the Hawaiian lobeliads, only 4.2 and 6.7 times less than the variation in the global data set. The much lower proportional variation in leaf lifespan in lobeliads, combined with the lower slopes of the power-law regressions on leaf lifespan vis-à-vis N_{mass} and SLA in the global data set, probably account for the lack of significant relationships of lobeliad leaf lifespan to A_{max}, leaf N content, and SLA (see also Diemer et al., 1992; Reich, 1993; Diemer, 1998).

Across the lobeliads studied, only 63% of the variation in maximum photosynthetic capacity on a mass basis is explained by variation in leaf N content and SLA:

$$A_{max} = 0.084 \ln SLA + 0.125 \ln[N] − 0.65 \qquad (3)$$

($P < 0.005$ for 8 df). Neither parameter had a significant effect in this regression, however. Given the strong relationships of several physiological parameters to A_{max} and to average daily PFD (see earlier), we asked whether including daily PFD in a multiple regression—as a proxy for the effects it has on other physiological factors, and hence, on A_{max}—would increase our ability to predict A_{max}. Indeed, including daily PFD allows us to account for fully 96% of the variance in A_{max} across species:
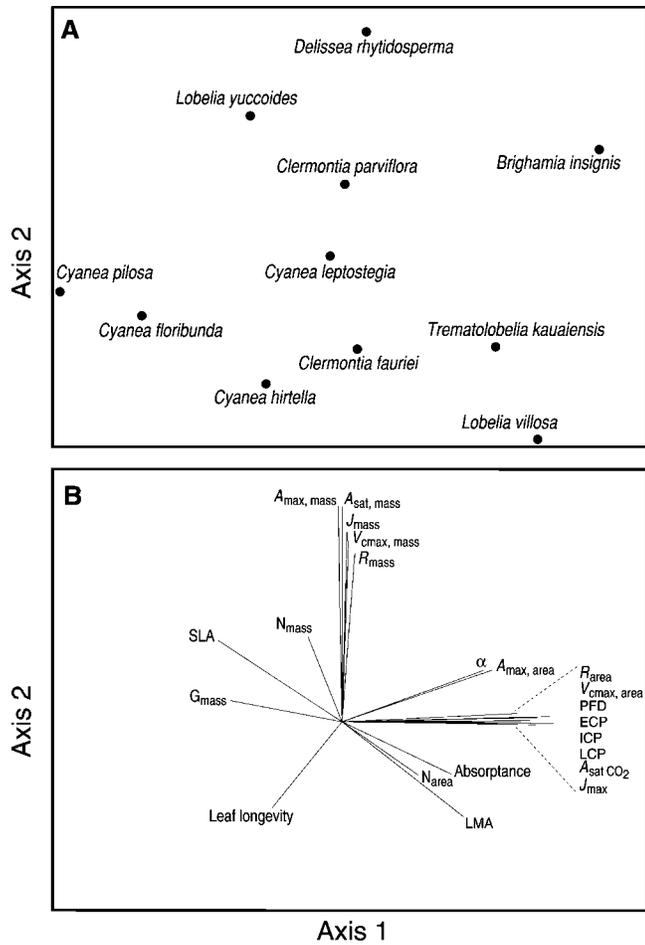
Fig. 9. (A) PCA ordination of Hawaiian lobeliad species by photosynthetic parameters. (B) Joint plot of photosynthetic parameters and PFD; direction and length of the vectors corresponding to each measurement correspond to the strengths of the correlation (r) between that measurement and scores on axis 1 and 2 of the PCA ordination. Note the near colinearity of several area-based parameters with each other, PFD, and axis 1, and the near colinearity of several mass-based parameters with each other and axis 2.

$$A_{max} = 0.153 \ln SLA + 0.127 \ln[N]$$

$$+ 0.075 \ln PFD - 1.19 \qquad (4)$$

($P \ll 0.0001$ for 7 df). This regression explains 89% of the residual variance in Eq. 3 and results in SLA, leaf N content, and PFD all having highly significant effects in the expected directions. Photosynthetic capacity per unit leaf mass increases with PFD, leaf N content, and SLA. The last effect involves

A_{max} per unit mass rising as leaf mass per unit area (LMA = 1/SLA) decreases and with it, presumably, internal shading and competition for light and CO_2.

DISCUSSION

Adaptive radiation is a recurring evolutionary process on oceanic islands, where extreme isolation permits but a few colonists to arrive from mainland source areas, and intense competition among the closely related, functionally similar descendants selects for ecological divergence (Lack, 1940, 1947; Carlquist, 1965, 1970; Grant, 1986; Givnish, 1997, 1998; Schluter, 2000; Losos et al., 2003). The Hawaiian Islands, with their tremendous present-day diversity in elevation and rainfall, unsurpassed isolation from continental areas, and a geological history spanning at least 80 Myr, have a fauna and flora whose composition and ecology have been shaped fundamentally by adaptive radiation (Carlquist, 1970; Robichaux et al., 1990; Wagner et al., 1990; Gillespie et al., 1994, 1997; Carson and Clague, 1995; Givnish et al., 1995; Baldwin, 1997; Kambysellis and Craddock, 1997; Givnish, 1998; Weller et al., 1998; Lovette et al., 2002; Remsen and O'Grady, 2002; Shaw, 2002; Carlquist et al., 2003). Examples include the Drepanidae, with a range of bill morphologies comparable to that seen across almost all other passerine families; Drosophilidae, *Laupala*, and *Megalagrion* among the insects; *Tetragnatha* among spiders; and the Hawaiian lobeliads, silversword alliance, mints, spurges, and pinks among the vascular plants. Fully half of the native vascular flora is derived from 20 initial colonists (Wagner et al., 1990), and the Hawaiian lobeliads alone account for nearly a quarter of the species derived from these leading radiations.

The last decade has seen revolutionary advances in our understanding of the origins and phylogeny of several Hawaiian groups, but little is yet known about the functional and ecological significance of phenotypic divergence within putative radiations. Exceptions include work on the light responses of *Euphorbia* species from habitats with different light regimes and rainfalls (Robichaux and Pearcy, 1980; Pearcy et al., 1982), water-use efficiencies of *Euphorbia* and *Scaevola* species from areas with different rainfall (Robichaux and Pearcy, 1984), turgor maintenance and hydraulic elasticity in the silversword alliance (Robichaux, 1984; Robichaux and Canfield, 1985; Robichaux et al., 1986, 1990), shifts in leaf longevity, nutrient use efficiency of P vs. N, and cold tolerance of populations of *Metrosideros polymorpha* at different elevations and on substrates of different age (Cordell et al., 1998, 2000, 2001a, b), and outcrossing mechanisms in *Alsinodendron/Schiedea* (Weller et al., 1995, 1998, 2001; Sakai et al., 1996); research on drought tolerance in the latter group has also be-

TABLE 5. Observed vs. expected numbers (mean ± SD, based on 10 000 permutations) of pairs of species-specific photosynthetic light responses showing adaptive cross-over, nonadaptive cross-over, non-cross-over with high-light species superior, or non-cross-over with low-light species superior. The observed numbers for each category, as well as the mean numbers emerging from the random permutations, sum to 55 in each case.

Photosynthetic light responses compared	Adaptive cross-overs	Nonadaptive cross-overs	No cross-over: high-light species higher	No cross-over: high-light species lower
Area-based responses, observed	36	2	4	13
Area-based responses, expected	18.98 ± 5.57	19.02 ± 5.57	8.49 ± 2.66	8.51 ± 2.66
Mass-based responses, observed	30	13	3	9
Mass-based responses, expected	21.47 ± 5.31	21.53 ± 5.31	6.00 ± 1.96	6.00 ± 1.96
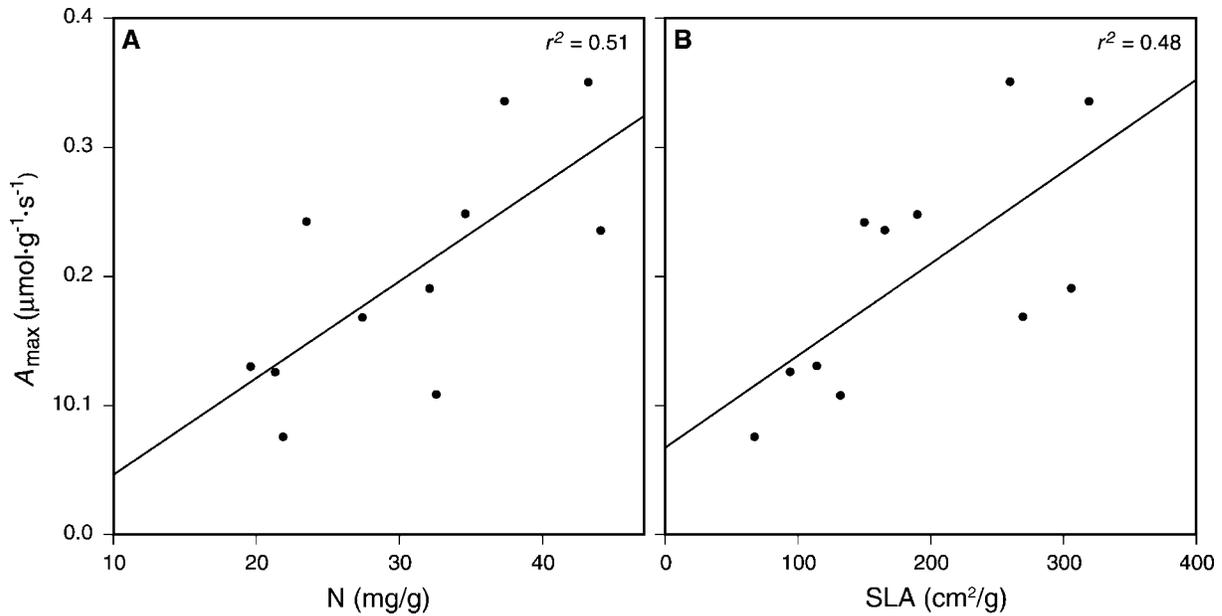
Fig. 10.   Values of A_{max}-mass as a function of (A) leaf N content per unit leaf mass and (B) specific leaf area. Lines represent LMS regressions: $A_{max} = 0.0075[N] - 0.029$, $r^2 = 0.51$ ($P < 0.02$ for 9 df); $A_{max} = 0.00071SLA + 0.06729$, $r^2 = 0.48$ ($P < 0.02$ for 9 df).

gun (T. Dawson, University of California at Berkeley, personal communication).

In all but the second of these cases, there is some evidence that phenotypes are correlated with habitat in ways that seem likely to enhance plant performance within a species' native habitat. The most notable study in our context is that of Robichaux and Pearcy (1980), who showed that forest-dwelling *Euphorbia forbesii* had lower rates of photosynthesis and respiration per leaf area, and lower light saturation and compensation points, than open-habitat *Euphorbia celastroides* and *E. degeneri*, when all were grown at ca. 500 μmol · m⁻² · s⁻¹ with ample water and nutrients. *Euphorbia hillebrandii* from partly open slopes was intermediate in all respects. This was an important pioneering study, demonstrating adaptive crossover of area-based photosynthetic rates in five of six species pairs, even though it lacked data on species photosynthesis and whole-plant growth in the field, on the quantitative distribution of species along light gradients, on the relationship between various photosynthetic parameters and native PFD, and on the phylogenetic relationships of the taxa surveyed. Our paper reports the first stage of a parallel but more extensive investigation, involving the largest adaptive radiation among Hawaiian plants, and lineages that have invaded the entire light gradient under similar, moist conditions. Taken together, the data presented here provide evidence for an adaptive radiation in photosynthetic physiology that is strongly correlated with—and indeed may help determine—the light regime that each species inhabits.

Light regimes and static light responses—Species representing each lineage of Hawaiian lobeliads occupy dramatically different light habitats, with daily PFDs varying from 2.3 mol · m⁻² · d⁻¹ in *Cyanea floribunda* to 30.7 mol · m⁻² · d⁻¹ in *Brighamia insignis*, nearly the entire range for native moist and wet habitats (Table 2). Some orange-fruited species of *Cyanea* occupy the shadiest understories on Hawaii, but these are still roughly nine times brighter than those in the under-

stories of continental tropical forests in Central and South America and Malesia (Chazdon and Fetcher, 1984; Bellingham et al., 1996; Valladares et al., 1997; Montgomery and Chazdon, 2001).

The static photosynthetic light responses of the 11 lobeliad species studied provide striking support for several predictions of classical economic theory. Maximum photosynthetic rate per unit area increases with the average PFD incident on species, as does dark respiration, the Michaelis-Menten constant k, leaf mass, and several measures of photosynthetic capacity per unit area (Figs. 2–7). Species in brightly lit environments thus respire at higher rates at low PFD, require more light to achieve a zero net rate of carbon uptake and to saturate photosynthesis, and achieve higher rates of photosynthesis at high PFD—all on a leaf-area basis—than species found in shadier habitats. A similar pattern is seen in net photosynthesis per leaf mass if species of boggy habitats or with substantial water storage tissue in their leaves are excluded. Taken together, these data are unparalleled in documenting adaptive patterns of variation in photosynthetic traits across species distributed along quantified light gradients.

Leaf lifespan and structural determinants of photosynthetic rate—Across the Hawaiian lobeliads, leaf lifespan shows only weak, nonsignificant relationships to A_{max} and leaf N content on a mass basis or to SLA (Table 4). The weakness of these relationships, relative to that seen across plants from several biomes (Reich et al., 1997, 1999), may simply reflect the limited variance in leaf lifespan across the Hawaiian lobeliads (see Results). Alternatively, these weak relationships might mean that leaf lifespan is more strongly affected by A_{max}, leaf N content, and LMA than vice versa, given the strong correlations among these last three variables in the same limited number of species and the strong correlations they have with other measures of photosynthetic capacity and PFD. High rates of photosynthetic return per unit leaf mass guarantee rapid overtopping of old leaves by new leaves and favor short

leaf lifespans (Reich et al., 1992; Ackerly, 1999; Givnish, 2002; Kitajima et al., 2002). This paradigm, however, must be modified to take into account the apparent increase in allocation to nonleaf tissue among the slowest growing species with the longest-lived leaves, often found on infertile sites (Givnish, 2002). The low fraction of variance in A_{max} explained by ln N and ln SLA, compared with the nearly complete explanation when ln PFD is included (Eq. 4), suggests that there are one or more important structural determinants of leaf photosynthetic capacity not captured in leaf N content and LMA. Identification of these additional determinants should be a high priority, given the potential utility of the relationship of A_{max} to leaf N content and SLA already established (Reich et al., 1997).

Instantaneous vs. whole-plant compensation points and partitioning of the light gradient—Instantaneous leaf compensation points range from 0.1 to 1.2% full sunlight, much lower than the ecological (whole-plant) compensation points of 1.1–29.0% sunlight calculated based on photosynthetic parameters, leaf longevity, and allocation to leaf vs. nonleaf tissue (Fig. 6). The ECPs are much closer to the lower limits of PFD actually experienced by lobeliads, suggesting they—unlike the traditional, instantaneous compensation points—may play an important role in restricting species distributions. This is the first study to test Givnish's (1988, 1995) ECP theory and demonstrate a relationship between whole-plant compensation points and the distributions of species along light gradients.

Ecological compensation points should constrain species' occurrences at the low end of their PFD range. Greater growth by competitors may limit their occurrence at high PFDs, as suggested by the adaptive cross-over of static light responses in many pairs of taxa, in which the species from shadier conditions has a higher rate of photosynthesis at low PFD, while the species from sunnier conditions has a higher rate at high PFD (Fig. 2; Table 5). Of 55 species pairs, 36 display adaptive cross-over in their area-based light responses, while 30 show adaptive cross-over in their mass-based responses. The fraction of adaptive vs. nonadaptive cross-overs is significantly greater than expected for area-based rates ($P < 4.5 \times 10^{-4}$) and marginally nonsignificant ($P > 0.066$) for mass-based rates. Greater leaf thickness and LMA, as well as higher leaf N content and associated metabolic capacity, should each tend to increase maximum photosynthesis, dark respiration, and the amount of light needed to saturate photosynthesis (Björkman et al., 1972; Björkman, 1981; Givnish, 1988, 1995). If A_{max}, k, and R were thus to increase in lock-step with each other as PFD increases, we would expect all species pairs to exhibit adaptive cross-over in their light response curves. The best measure of deviation from an ''expected'' number of cross-overs of any form may thus be the tightness of fit of the regressions of A_{max}, k, and R against PFD. For area-based measures, the values of r^2 for these regressions are significantly greater than the null expectation in each instance, and A_{max}, k, and R are all strongly correlated with each other ($0.83 < r < 0.91$).

Integration and adaptive cross-over of photosynthetic parameters on an area vs. mass basis—It is surprising that many components of photosynthetic capacity show greater integration with each other (Fig. 9) and apparent adaptation to PFD (Figs. 2–8) based on leaf area rather than mass. Givnish (1988, 1995) argued that competition in a given habitat should favor plants that maximize energetic returns per unit investment in leaf mass, leaf N content, or (best) whole-plant energy content. Returns per unit of energy invested should be more important than returns per unit leaf area, because competitive ability should be tied more closely to whole-plant growth and, hence, to returns on investment. Givnish (1988) showed that the paradigmatic study of Björkman et al. (1972) on *Atriplex triangularis* grown at three different PFDs supported the claim of adaptation only if photosynthetic rates per unit leaf area were reanalyzed on the basis of leaf mass or soluble protein content. Only then did plants grown at each of the conditioning PFDs exhibit adaptive cross-over, with each group having a photosynthetic advantage only at or near the light levels at which they were grown.

Several studies over the past decade have shown a similar shift in the ranking of species by photosynthetic rate or whole-plant growth in moving from low to high PFD. Kaelke et al. (2001) found a reversal in the relative growth rates (RGR, in grams per gram per day) of field-grown seedlings of *Populus tremuloides* vs. *Acer saccharum* and *Quercus rubra* in moving from 2.6 to 69% sunlight in Wisconsin, with sun-adapted *Populus* outgrowing *Acer* and *Quercus* above 2.5 mol/d PFD. Growth rates were related weakly to photosynthesis per leaf area, strongly to photosynthesis per leaf mass, and most strongly to photosynthesis per total plant mass. Similar reversals in species' growth ranks of temperate tree seedlings have been reported by Pacala et al. (1994), Walters and Reich (1996, 2000), and Reich et al. (2003). In tropical rain forest, Montgomery and Chazdon (2002) recently demonstrated cross-over in whole-plant growth (in grams per gram) by seedlings of *Dipteryx panamensis*, *Virola koschnyii*, and *Brosimum aliscastrum* transplanted along a light gradient from 0.2 to 6.5% full sunlight at La Selva, Costa Rica. *Virola* and *Brosimum* outgrow *Dipteryx* below ~2.5% full sunlight, while *Dipteryx* outgrows *Brosimum* and *Virola* above that level. All tree species survive at similar rates above 2.5% sunlight, but in denser shade the survival of *Dipteryx* and *Brosimum* falls below that of *Virola*. When Kobe (1999) took both survival and growth into account, he was able to show that seedlings of each of four closely related tree species (*Trophis racemosa*, *Castilla elastica*, *Pourouma aspera*, *Cecropia obtusifolia*), transplanted along almost the entire light gradient at La Selva (<1% to ca. 85% full sunlight), have an advantage in realized growth relative to competitors along a specific part of that gradient.

In each of the eight studies mentioned in the two preceding paragraphs, species (or acclimated clones) show adaptive cross-over in energetic return on investment, whole-plant growth, or realized whole-plant growth as a function of light availability. This pattern of behavior should permit species to partition the light gradient, with each having a range of conditions where it has an advantage in growth and, presumably, competitive ability (see also Horn, 1971; Canham and Marks, 1985; Latham, 1992). The results of our study parallel those of these previous studies in showing a substantial tendency toward adaptive cross-over in photosynthesis per leaf mass (30 of 55 cases), but our data display an even stronger tendency (36 of 55 cases) toward adaptive cross-over based on photosynthesis per leaf area.

What might account for this deviation from expectation? Several possibilities suggest themselves, based on differences among species in (1) resource allocation and whole-plant growth; (2) survival; (3) adaptations to area-based factors cor-

related with PFD; (4) photoinhibition and dynamic light responses; and, most importantly, (5) plasticity and growth in different light regimes.

1. Factors other than photosynthesis per leaf mass or area help determine whole-plant growth—To move from photosynthesis to whole-plant growth, one must incorporate the costs of tissue construction and maintenance, tissue turnover, and the fractional allocation to leaf vs. nonleaf tissue (Mooney, 1972; Givnish, 1988; Poorter and Lambers, 1991). Whole-plant growth can show adaptive cross-over even if photosynthesis—however expressed—does not, given the right differences in tissue fractions, longevities, or construction costs. Each of these factors can vary with PFD (e.g., Kaelke et al., 2001), and most of the species we studied grew in habitats with significantly different daily PFDs (see Table 2). Furthermore, we lack allocational data. To pursue the issue of adaptive cross-over further, a common garden experiment must be conducted in which photosynthesis, resource allocation, and whole-plant growth are measured in each species transplanted into a set of light environments that span those occupied collectively by our species in the field. We have such an experiment underway and will report its results elsewhere in the near future.

2. Differences in survival rates as well as growth must be considered in searching for adaptive cross-over and the partitioning of light gradients it facilitates—Many studies have failed to show any reversal in species' rankings by photosynthesis or whole-plant growth at different light levels, with shade-intolerant taxa retaining an edge even under low light (e.g., Loach, 1970; McClendon and McMillen, 1982; Ramos and Grace, 1990; Chazdon, 1992; Walters et al., 1993a, b; King, 1991; Kitajima, 1994; Beaudet and Messier, 1998; Poorter, 1999; Valladares et al., 2000). Some of these studies need reevaluation, because plants were grown under artificial conditions in "low" light conditions that were actually fairly high relative to those seen in the field. In more carefully designed investigations, in which realistically low light levels have been included in field manipulations, cross-overs have been observed (e.g., Kobe, 1999; Kaelke et al., 2001; Montgomery and Chazdon, 2002). Yet, even in well-designed studies, it has been common to find not an adaptive cross-over in photosynthesis or growth among species, but instead a trade-off between high growth under high light and low survival in low light (Kitajima, 1994; Pacala et al., 1996; Veneklaas and Porter, 1998). This same trade-off has also sometimes been seen in studies that do find a reversal of species' growth rates in high vs. low light (Walters and Reich, 1996; Kaelke et al., 2001; Lin et al., 2002). Previous investigators have suggested that this trade-off might arise from fundamental constraints due to herbivory and respiratory costs. Traits that yield high growth in sunny conditions (e.g., thin, soft, N-rich leaves, or light, poorly defended wood) may expose plants to high rates of herbivory, which could greatly increase mortality in moist, unproductive forest understories (Augspurger, 1984; Coley, 1988; Kitajima, 1994; Chazdon et al., 1996), especially when shade causes stocks of carbohydrates to run low (Kobe, 1997; Canham et al., 1999). Similarly, it has been argued that high respiration rates are necessarily coupled to high photosynthetic rates, so that sun-adapted plants may run marginal energetic accounts in shade and thus be subject to high mortality rates (Pacala et al., 1996; Walters and Reich, 1996, 1999, 2000;

Kaelke et al., 2001). Clearly, survival and growth are both components of fitness, in sun or shade, and both must be taken into account in any analysis of optimal physiology and allocation.

3. Differences in leaf morphology and photosynthetic physiology among plants found in sunny vs. shady microsites may reflect adaptations to environmental differences other than light availability—Several factors (e.g., relative humidity, heat load, wind speed) vary along light gradients, and shifts in plant characteristics may partly reflect adaptations to these nonlight conditions (Givnish, 1988; Valladares and Pearcy, 2002). Sunny conditions may favor thicker leaves with greater LMA partly because evaporation rates per leaf area are higher in open sites, selecting for a reduction in leaf surface area/volume ratio and resulting water loss, albeit at the cost of reduced photosynthetic capacity per unit leaf mass (Givnish, 1979). Indeed, perhaps the most repeated response of plants to greater PFD is an increase in LMA (see Jurik, 1986; Givnish, 1988; Sims and Pearcy, 1994; Pattison et al., 1998; Baruch et al., 2000; Kaelke et al., 2001; Montgomery, 2003). Accompanying this pattern is a tendency for A_{max} and R to increase with PFD more clearly based on leaf area, not mass (e.g., Sims and Pearcy, 1994; Kaelke et al., 2001; Montgomery, 2003). The difference between patterns based on leaf area vs. mass is clearly driven by LMA, which in turn may be adapted to reduce water loss in sunny microsites that are also effectively hotter and drier. To the extent that transpiration rates—and associated root costs—are closely related to leaf area, not leaf mass, and that natural selection favors maximization of the difference between photosynthetic profits and transpirational costs, patterns could be generated in area-based measures of photosynthetic capacity as PFD and external drivers of transpiration (e.g., relative humidity, heat load, wind speed) covary along light gradients. Transpirational costs should be included in the calculus of adaptive cross-over in whole-plant growth.

This principle may, in retrospect, be illustrated by the study of Sims and Pearcy (1994), who measured the photosynthetic physiology, resource allocation, and whole-plant growth of *Alocasia macrorrhiza* grown at low and high PFD. Simulations showed that the resulting differences in physiology and (especially) allocation resulted in low-light plants having a growth advantage in low light (Sims et al., 1994). High-light plants, however, appeared to be at a slight disadvantage in high light, as a result of their greater allocation to roots. Overall, root biomass was strongly correlated with daily whole-plant rates of transpiration (Sims and Pearcy, 1994). This exemplary study did not, however, analyze the impacts on photosynthesis and growth that would have resulted from growing thin-leaved, lightly rooted, shade-grown *Alocasia* under sunny conditions, as a result of the drops in leaf water potential and photosynthetic capacity that would be expected under such conditions. We believe that the shifts in LMA, leaf physiology, and root vs. leaf allocation observed in *Alocasia* may in fact be adaptive in both sun and shade and that a reversal of ranks in whole-plant growth would be evident in this and other cases if the analyses were broadened to incorporate the effects of root vs. leaf allocation and transpiration per leaf mass on leaf water potential and mesophyll photosynthetic capacity (see Givnish, 1986).

4. Photoinhibition and dynamic photosynthetic light responses must be considered—Shade-adapted plants may suffer

from photoinhibition in brightly lit environments (Osmond, 1983; Anderson et al., 1988; Demmig-Adams and Adams, 1992; Chazdon et al., 1996). If leaves are exposed to high PFD when other conditions (e.g., temperature, water/nutrient availability, carboxylation capacity) limit carbon uptake, damage can occur to the photosynthetic apparatus, especially photosystem II, reducing quantum yield and future CO_2 uptake. Photoinhibition can thus help give plants adapted or acclimated to brightly lit conditions a relative advantage over shade-adapted or shade–acclimated plants under sunny conditions. However, the Hawaiian lobeliads show little evidence of photoinhibition under field conditions, so this factor can be excluded from consideration for now (Montgomery and Givnish, 2002).

Shady environments are not uniformly dark, but punctuated by sunflecks that move across the forest floor as the sun moves across the sky. Much (30–80%) of the PFD intercepted by understory plants in tropical forests comes in sunflecks of relatively short duration (Chazdon and Pearcy, 1986a, b, 1991; Chazdon, 1988, 1992; Pearcy, 1988; Chazdon et al., 1996). This presents a fundamental challenge to understory plants, because most of their Rubisco is not activated (Seemann et al., 1988). Understory species often show higher rates of induction, and remain induced longer, than gap or canopy species (Kursar and Coley, 1993; Poorter and Oberbauer, 1993). Dynamic light responses can be critical to sun vs. shade adaptation. Valladares et al. (1997) found that six rubiaceous shrubs along a tropical forest understory-gap gradient showed little difference in steady-state photosynthesis at high or low PFD, but quite large differences in rates of induction and induction loss. The dynamic light responses of Hawaiian lobeliads are generally in accord with predictions, with species of shaded understories having faster induction than those of open habitats (Montgomery and Givnish, 2001). The implications of such dynamic light responses for carbon gain under the light regimes experienced by different species are, in fact, fairly small (R. A. Montgomery et al., unpublished manuscript).

5. Plasticity of photosynthetic light responses requires common garden studies to determine the extent to which species differences are genetic and truly adaptive—Leaf anatomy, biochemistry, and photosynthetic light responses are developmentally plastic, shifting with the light regime under which leaves develop (Jurik et al., 1979; Strauss-Debenedetti and Bazzaz, 1991, 1996; Oberbauer et al., 1993; Kitajima, 1994; Walters and Reich, 1996; Valladares et al., 2000). Consequently, the most important limitation of the data presented in this paper (and most others in the field) is that they are based on the growth and development of different species in different light regimes. Common garden experiments are required to determine the extent to which the physiological differences we have observed among species in the field are genetic vs. environmentally induced and the extent to which plasticity within species decreases (or increases) the observed, adaptive differentiation among them in response to light availability. By comparing the leaf anatomy, lifespan, biochemistry, and light responses of different species under the same light habitat, we can analyze the extent to which differences among are heritable. We can also conduct a "soft" test of adaptation by seeing if various measures of photosynthetic capacity under the same light environment increase with the average PFD different species inhabit in the field. By comparing photosynthesis and whole-plant growth within species across light regimes, we can infer the extent to which species exhibit adaptive plas-

ticity and address the fundamental question of whether the observed reaction norms result in adaptive cross-over among species and partitioning of the light gradient they inhabit. Experiments along precisely these lines are now underway.

The plasticity of photosynthetic light responses also makes it is inappropriate, in our view, to apply phylogenetically structured analyses to field data, despite the fact that a number of investigators have begun to do so (e.g., Ackerly and Reich, 1999; Ackerly et al., 2000; Wright et al., 2002). Surely the underlying premise of phylogenetically structured analyses is that similarities in morphological, physiological, or behavioral traits reflect, at least in part, the *genetic transmission* of such traits from shared ancestors, and that the potential dependence of trait similarity on evolutionary relationship must thus be included in comparative studies (e.g., see Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991; Schluter et al., 1997; Mooers and Schluter, 1999). For traits that are potentially plastic, we believe that phylogenetically structured analyses should be applied to phenotypic traits only using data from common garden studies, in which the effects of genetic and environmental differences among species can be rigorously separated and evolutionary shifts in heritable characters can thus be identified.

Applying such analyses to field measurements on species that occupy different environmental conditions, involving plastic traits that are highly responsive to such conditions, could produce erroneous or misleading results. Such analyses could identify "significant" differences among species, even if all species showed identical norms of reaction in response to a particular environment factor (e.g., PFD). The use of phylogenetically structured analyses at least implies that evolutionary change has taken place in the characters of interest; this may not be true. Furthermore, without actual data on norms of reaction from common garden studies, it is impossible to disentangle the effects of ecology and phylogeny on traits that have developed under different conditions in different species in the field. Even if there were a genetic basis to phenotypic differences observed among species in different habitats—and such differences were adaptive in the sense of increasing whole-plant growth in particular environments—but differences in PFD were strongly associated with membership in particular lineages, such analyses might identify these phenotypic differences as phylogenetic legacies (e.g., see Westoby, 1995a, b; Givnish, 1997). In this case, the lack of an adaptive difference would also be misleading.

These pitfalls can be avoided by obtaining functional data from related species grown under a series of common garden conditions and then analyzing such data in relation to the ecological conditions and phylogenetic relationships peculiar to each species. Conversely, to ensure that the common garden conditions chosen are ecologically meaningful and produce realistic phenotypes, such studies must be complemented by field investigations—like the one presented here—in which species distributions along environmental gradients are quantified and their phenotype and physiological performance at different points along the gradient are measured and compared with the predictions of economic theory. Phylogenetically structured analyses of *the ecological conditions occupied by species in the field* can also shed important light on the evolution of ecology within lineages. Furthermore, a comparison between the expressions of traits (and their contributions to competitive ability) in species under various common garden conditions with those seen in the field can provide deep in-

sights into the bases of differences in phenotype *and* ecology among species and into the lineal ''inheritance'' of ecology.

Our field data demonstrate that the Hawaiian lobeliads have, in fact, radiated into a wide range of light regimes on mesic sites and that the physiological differences among species appear well integrated and adapted to the light regimes each species occupies. Common garden studies now underway will examine the extent to which our field data represent genetic vs. environmental effects on photosynthetic physiology and test the extent to which differences among species in their pattern of photosynthetic plasticity adapt them to the range of light conditions they, in fact, occupy in nature.

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