FUNCTIONAL DIVERSITY OF CARBON-GAIN, WATER-USE, AND LEAF-ALLOCATION TRAITS IN TREES OF A THREATENED LOWLAND DRY FOREST IN HAWAII[1]

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We examined carbon-gain, water-use, and leaf-allocation traits for six tree species of a Hawaiian dry forest to better understand the functional diversity within this threatened ecosystem. Tropical dry forests are among the most endangered ecosystems on Earth, and in Hawaii, as elsewhere, declining biodiversity threatens ecosystem processes that may depend on forest functional diversity. We found broad variation among species including a two-fold difference for mean photosynthetic rate, a greater than three-fold difference for predawn water potential, and a nearly three-fold difference for leaf life span. Principal component analysis showed a clear separation of species based on carbon-gain vs. water-use related axes, and $\delta^{13}C$ analysis revealed differing limitations (supply vs. demand) on carbon assimilation. The broad functional variation not only spanned traditional classifications (avoiders vs. tolerators), but also included unusual strategies (e.g., fast growth with drought tolerance). Correlations among traits, including leaf life span, leaf mass per area, and %N, followed typical global patterns, but some exceptions appeared as a result of unique life-history characteristics, such as latex-rich sap and root parasitism. Elucidating functional variation provides important information that can be used to link plant biodiversity with ecosystem processes and also facilitate the management and preservation of tropical dry forests and other threatened communities.

Key words: functional diversity; Hawaiian dry forest; leaf allocation; photosynthetic gas exchange; stable isotopes; water relations.

Plant functional diversity is a primary factor affecting ecosystem processes and, subsequently, the ecosystem services upon which humans rely (Díaz and Cabido, 2001). These processes (e.g., stability and resource fluxes) may depend on different characteristics of the functional diversity, such as the range, richness, evenness, or divergence of functional variation (Mason et al., 2005), or on the functional composition of a community (Díaz and Cabido, 2001). Regardless of the measure, functional diversity has a large influence on many ecosystem characteristics, including nutrient cycling, hydrology, microclimate, disturbance, species interactions (see Eviner and Chapin, 2003), invasibility (Daehler, 2003), and stability (Díaz and Cabido, 2001).

Many plant physiological traits (e.g., photosynthesis and transpiration) can be directly linked to functions that influence such ecosystem processes. These traits are often correlated with other leaf-level traits, both morphological and physiological (Wright et al., 2005a), giving rise to trait associations commonly referred to as functional suites. For example, leaf traits, such as leaf mass per unit area (LMA), foliar nitrogen

(N), and leaf life span (LLS), have been shown to co-vary with photosynthesis (Chapin, 1993; Reich et al., 1997; Santiago and Wright, 2007) and hydraulic properties (Tyree et al., 1994; Ackerly, 2004). Furthermore, many such trait pairs have a common scaling relationship across very broad habitats, climates, and phylogenetic levels (e.g., Reich et al., 1997; Wright et al., 2005a, b). Measurement of the diversity of such functional suites and scaling relationships within a community is crucial to better understand the adaptive value of these suites and their influence on ecosystem processes. Importantly, the loss of biodiversity can mean the loss of functional properties that are ultimately important to humans and other organisms. Recognizing these potential losses is of even greater urgency in systems that are already severely fragmented, have high endemism, or have inherently low diversity and therefore an increased probability of functional loss.

Tropical dry forests are among the most threatened ecosystems of the world, due in large part to habitat loss (Murphy and Lugo, 1986; Bullock et al., 1995). Saving these forest systems is important from a biodiversity perspective, but recent studies have also demonstrated relatively high functional variation in dry forest systems (e.g., Eamus, 1999; Prior et al., 2003; Ishida et al., 2006), augmenting the importance of preserving these forests. Interestingly, this variation does not always correspond to patterns found in more mesic and well-studied forest systems (Prior et al., 2003), underscoring the need for enhanced comprehension of functional diversity in tropical, dry forest systems.

Dry forests and woodland communities of Hawaii are distinct from other forest ecosystems of the Hawaiian islands. Most notably, the ubiquitous dominant tree of nearly all other mature Hawaiian forests, *Metrosideros polymorpha*, is rare in mature (>3000 y old) dry forest ecosystems (Stemmermann and Ihsle, 1993). In addition, although Hawaii's wet and mesic forests have higher overall plant diversity (Price, 2004), the

Table 1. Relative abundances of the six tree species used in this study.

Species	Family	Abundance on Big Island	Abundance at research site
Colubrina oppositifolia	Rhamnaceae	Rare (Endangered)	Rare
Diospyros sandwicensis	Ebenaceae	Common	Common
Metrosideros polymorpha	Myrtaceae	Common	Uncommon
Pouteria sandwicensis	Sapotaceae	Rare	Rare
Psydrax odorata	Rubiaceae	Common	Common
Santalum paniculatum	Santalaceae	Rare	Common

diversity of canopy trees is significantly greater in dry forests, with 20 to 40 tree species often present (Rock, 1974; Cabin et al., 2000; Medeiros et al., 1998). The high tree diversity of these forests suggests that functional diversity may also be high, but unlike many other tropical dry forests that have both drought deciduous and evergreen species, almost all tree species in Hawaiian dry forests are evergreen (>80%), thus potentially limiting functional diversity in spite of high species diversity.

Quantification of functional diversity in Hawaiian dry forest ecosystems is especially urgent at present. On the island of Hawaii (the Big Island), less than 10% of the original dry forest ecosystems remain intact (Bruegmann, 1996), and of these, many are heavily degraded by human land use, feral ungulate browsing, and invasion by non-native plants. Such pressures have substantially reduced populations of most native trees including some federally listed endangered species. Successful management of these species and their ecosystems requires a greater understanding of their physiological functioning and the functional diversity of species within the community. Such knowledge will also contribute to our understanding of species effects on ecosystem-level processes (e.g., resource cycles and ecosystem resilience) and the consequences of their loss.

We examined functional diversity among six native Hawaiian trees in a dry forest community on the Big Island of Hawaii. In all, 13 traits were evaluated in both a wet and a dry period of the year. Physiological measurements based on leaf-level gas exchange and water potential provided direct assessment of functions related to short-term carbon gain and water use, while inferences about longer-term plant functioning were made from morphological, phenological, and leaf chemical analyses. Multiple-trait correlations and principal component analyses were used to identify trait suites and functional overlap among the species, as well as any unique attributes of individual species within this community. These evaluations also provided an opportunity to compare the functional variation of Hawaiian dry forests to that of other tropical dry forests and to global patterns of functional trait correlations (Reich et al., 1997; Wright et al., 2005a).

MATERIALS AND METHODS

Species descriptions—The six species examined in this study (Table 1) are either among the most common and dominant species in the lowland dry forest ecosystems of Hawaii or represent species believed to have been common before extensive harvests by humans. All are evergreen and endemic to Hawaii except *Psydrax odorata,* which is native to Hawaii and other Pacific islands.

Site description—All trees measured were within the Kaupulehu Dry Forest Preserve (655 m a.s.l.), located approximately 17 km north of Kailua-Kona, Hawaii County, Hawaii, USA (19°46′05″ N, 155°56′19″ W). The 2.3 ha preserve is one of the best examples of native Hawaiian dry forest remaining on the island of Hawaii (Cabin et al., 2000). It was fenced in 1956 to exclude alien ungulate browsers.

Monthly mean rainfall and temperature based on the Kailua-Kona airport weather station (~10 km SW of the preserve) are shown in Table 2. Predictability of monthly rainfall amount is low, as demonstrated by the high coefficient of variation for each month. Rainfall (1998–2005) and temperature (2003–2005) data for the Kaupulehu Preserve are limited but correlate with the general weather patterns of Kailua-Kona (Table 2), with average annual rainfall at the preserve about 60% higher than the Kailua-Kona long-term average.

The plant community of the preserve is classified as lowland dry forest and shrubland (Wagner et al., 1999) composed primarily of evergreen tree species (Cabin et al., 2000). The underlying substrate is an `a`a lava flow estimated to be 1500 to 3000 y old (Moore et al., 1987), with mean available (i.e., resin extractable) soil nitrogen (NO_3-N + NH_4-N) and phosphorus (PO_4-P) of ~40 $\mu g \cdot g^{-1}$ and ~25 $\mu g \cdot g^{-1}$, respectively (Austin and Vitousek, 1998). The forest canopy is dominated by the native tree *Diospyros sandwicensis* (A. DC), (Ebenaceae) and codominated in places by *Psydrax odorata* (A. Gray) (Rubiaceae), which is the only other tree species with a relatively high abundance within the preserve. Until recently, the forest understory throughout the preserve had virtually no native species, likely owing to decades of alien ungulate grazing. Instead, the understory was dominated by the alien invasive bunchgrass, *Pennisetum setaceum* (Forssk.) Chiov., (Poaceae; fountain grass),

Table 2. Monthly climate data for the Kaupulehu field site (1998–2005) and long-term records for Kona International Airport[a] (1980–2005), 10 km SW of Kaupulehu.

Month	Kaupulehu Dry Forest Preserve			Kona International Airport[a]		
	Monthly mean temperature (°C)[b]	Monthly mean precipitation (mm)	Precipitation coefficient of variation (%)	Monthly mean temperature (°C)	Monthly mean precipitation (mm)	Precipitation coefficient of variation (%)
January	21.2	76.0	120	23.4	48.1	90
February	20.4	61.8	136	23.5	26.6	142
March	19.2	44.6	120	24.0	33.2	103
April	21.6	28.9	97	24.7	16.3	116
May	21.8	47.3	124	25.5	19.8	98
June	22.6	24.6	92	26.2	15.4	119
July	23.7	11.0	105	26.8	17.2	96
August	24.1	29.6	135	27.1	20.5	93
September	24.9	16.9	86	27.0	19.6	85
October	23.5	59.1	94	26.6	20.7	138
November	22.4	65.2	118	25.5	31.0	119
December	20.8	22.1	128	24.0	42.5	109

[a] National Climate Weather Center Station Ke-ahole Point 68.13, Hawaii (513911)
[b] Available for 2003 through 2005 only

which typically covers 75 to 80% of the forest floor (Cabin et al., 2000). In 1995, all fountain grass was removed from the preserve in an attempt to facilitate native plant regeneration. Currently, the understory contains a mixture of native and non-native shrubs and approximately 20% cover of fountain grass (S. Cordell, personal observation).

Trait measurements—Measurements were made on five trees for each species except *Diospyros* ($N = 8–16$) and *Metrosideros* ($N = 3$). Unless otherwise noted, each set of measurements was made on the same day and done once during winter (January 2002) and once during summer (July 2002).

For assessing plant water status, predawn (Ψ_{pd}) and midday (Ψ_{md}) water potential were measured on at least two stem segments of each tree using a Scholandar-type pressure chamber (PMS, Corvalis, Oregon, USA). The Ψ_{pd} values were used as an indication of soil water availability to a plant and maximum daily water status, whereas Ψ_{md} estimated minimum daily water availability and thus maximum daily water stress. On the same day water potential was measured, carbon-gain functions were evaluated by measuring net photosynthesis (A_{net}), stomatal conductance (g_s), and internal CO_2 concentration (c_i) taken between 0900 and 1300 hours local time using a portable gas exchange system (LiCor 6400, LiCor, Lincoln, Nebraska, USA). During measurements, circulation of external air provided ambient temperature and humidity to the leaf chamber. Photosynthetic photon flux density was maintained at 1500 µmol m^{-2}·s^{-1} using a red-blue light source (LiCor 6400-02B) with the reference CO_2 concentration set at 400 ppm so that chamber CO_2 remained between 370 to 390 ppm. Because of time limitations, these measurements were performed only on two trees per species. Three leaves of the most recent fully expanded cohort were measured and averaged per tree. From these measurements, intrinsic water-use efficiency was calculated as the ratio of net photosynthesis to stomatal conductance (A_{net}/g_s).

Five to 10 leaf samples, taken from the same cohorts as those used for photosynthesis, were collected from each tree. Petioles were removed and leaves were stored in plastic bags with damp paper towels before being measured (within 72 h) for leaf area (LI-3100; LiCor). The leaves were then oven dried at 70°C to a constant mass. From these area and mass values, leaf mass-to-area ratio (LMA) was calculated. This ratio was also used to convert area-based net photosynthesis to mass-based net photosynthesis (A_{mass}).

The dried leaves were then ground to a uniform powder using a 40-mesh filter on a Wiley Mill (Thomas Wiley Laboratory Mills, Philadelphia, Pennsylvania, USA). A subsample was analyzed for carbon isotope ratio ($\delta^{13}C$), which provides an integrated long-term measurement of leaf-level carbon assimilation processes including (in C_3 plants) water-use efficiency. Higher $\delta^{13}C$ indicates greater water-use efficiency (Farquhar et al., 1989). Nitrogen isotope ratios ($\delta^{15}N$) and mass-based percentage carbon (%C) and nitrogen (%N) were also measured from these subsamples. The latter two values were used to determine the ratio of carbon to nitrogen (C/N). All four elemental analyses were done at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah.

Leaf life span (LLS) was measured on 40 buds distributed among at least five trees per species. Measurements were taken approximately every 60 d from autumn 1999 through the end of 2003. All leaves ($N = 51–165$ per species) were marked upon first emergence and thereafter classified as present, dead, or missing during each subsequent sampling period. Median LLS values were used for most comparisons, although mean LLS and median LLS were very strongly correlated ($r = 0.96$, $P < 0.01$). Where noted, mean LLS values were used in comparisons with published studies that examine relationships between LLS and leaf-allocation traits such as LMA and C/N. These last two traits represent carbon investment costs of leaves, whereas LLS is a measure of the time frame over which that investment will return dividends. The correlation between any investment trait and LLS is an economic relationship which predicts that higher investment values (e.g., greater LMA) should have a greater duration of return (longer LLS). Furthermore, LMA and C/N often correlate with one another due to the increase in leaf carbon relative to nitrogen (higher C/N) as a leaf becomes thicker (higher LMA) (Reich et al., 1999). Because nitrogen is a major component of the photosynthetic pigments and proteins, it often correlates positively with A_{net} and negatively with LMA and LLS (Reich et al., 1997, 1999; Wright et al., 2002).

Variation of water sources used by trees was determined by measuring oxygen isotope ratios ($\delta^{18}O$) of resident water in soils and tree stem samples (Dawson, 1993). For trees, three to four 3-cm stem segments per tree were cut from living branches, consolidated, and immediately sealed in a glass vial. Soils were collected from depths of 0–5 cm and 10–20 cm ($N = 8$ each) and immediately sealed in glass vials. These samples came from soil found in small pockets within the matrix of primarily solid lava. Soils at greater depths were

inaccessible, but estimates of $\delta^{18}O$ in deep-soil water of arid regions in Hawaii range from −5 to −7‰ (Hsieh, 1997; Stratton et al., 2000; D. R. Sandquist, unpublished data). Soil and stem samples were returned to the plant ecophysiology laboratory at California State University, Fullerton, where water was extracted cryogenically and isolated for isotope analysis. The $\delta^{18}O$ values of all water samples were determined at SIRFER.

Tree growth rates were estimated by the incremental growth of the trunk at approximately 1.3 m above ground level. Spring-loaded metal dendrometer bands were placed around trees in July 2001 and left undisturbed for 1 y to allow a grow-in period. In July 2002, dendrometer bands were marked. Growth incremental changes were measured as the linear distension of the dendrometer band (mm) after 2.5 y. Growth incremental changes are reported as change in diameter per year and proportional annual increase (%).

Statistical analyses—Analysis of variance (model I) was used to compare trait differences among species, and a Tukey–Kramer honestly significant difference (HSD) multiple comparisons test was used to identify significant differences of means among species (at $P = 0.05$ level). Standard least squares linear regression was employed to determine which traits were most closely associated with specific response variables (e.g., A_{net}, c_i). Values of predawn and midday water potential, diameter growth, and %N were log transformed prior to analyses to correct for non-normal distributions.

Trait correlations, based on means among species for the entire data set, were determined from a Pearson product moment correlation. Standardized major axis (SMA) analysis was applied when testing for slope and elevation differences between winter and summer groupings of pairwise trait relationships (Wright et al., 2001) using SMATR Version 2.0 software (Warton et al., 2006). All other regressions, correlations, and mean comparisons were performed using JMP statistical analysis software (SAS Institute, Cary, North Carolina, USA).

Principal component analysis (PCA) was used to examine functional variation among dry forest trees based on a suite of traits that broadly integrates water-use (Ψ_{pd}, Ψ_{md}, and $\delta^{18}O$) and carbon-gain (LMA, %N, and $\delta^{13}C$) functions. Because of unequal sample sizes among species, PCA was first run on a matrix of normalized data based on the trait means for each species. A second analysis was run on a matrix of normalized data based on values for each individual tree to visualize variation among trees within and among species. For each analysis, correlations were determined between each trait and each of the first five principal component axes. PCA was performed using PRIMER statistical analysis software (PRIMER-E Ltd., Plymouth, UK).

RESULTS

Functional diversity of carbon-gain traits—Leaf-level characteristics related to carbon-gain physiology varied greatly among the six species in this study. For those traits most closely related to carbon gain (A_{net}, g_s, c_i, %N, and $\delta^{13}C$), %N, $\delta^{13}C$, and c_i differed significantly among species. Small sample sizes within species precluded a more robust analysis of the gas exchange characters, but the general patterns of variation for these traits were similar to those for the other carbon-gain related measures (Table 3).

Within each time period, variation among species was relatively high for leaf-level gas exchange traits (A_{net}, g_s, and c_i) (Table 3). Photosynthetic rates of *Colubrina* and *Psydrax*, in particular, were approximately 50% greater than those for the other four species in January. Three species, *Colubrina*, *Psydrax* and *Santalum*, experienced a large decrease in A_{net} from January to July, while values for the other three remained essentially constant. Likewise, c_i for all species decreased from January to July, with the variation across species remaining high. Variation was also high among species for g_s in January, but these values declined sharply for all species in July, converging on low g_s values in July (Table 3), a change that reflected decreased water availability over this period (see next section).

Percentage foliar N differed significantly among species in

TABLE 3. Mean leaf-level carbon-gain trait values for the six species used in this study (± 1 SE). Significant differences ($P < 0.05$) among species within a season are depicted as different letters (Tukey-Kramer HSD multiple comparisons test). Absence of letters indicates no significant differences among species within a season.

Species	A_{net} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)		g_s ($mol \cdot m^{-2} \cdot s^{-1}$)		c_i (ppm)		$\delta^{13}C$ (‰)		Foliar N (%)	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Colubrina oppositifolia	12.55	8.20	0.13	0.07	196.67[a]	171.00	−25.06[a]	−25.22[a]	3.17	2.28[a]
	(0.70)	(0.90)	(0.01)	(0.01)	(12.67)	(7.29)	(0.42)	(0.53)	(0.19)	(0.12)
Diospyros sandwicensis	7.53	8.54	0.10	0.08	249.23[b]	188.18	−26.79[b]	−27.48[bc]	0.86	1.03[c]
	(0.56)	(0.49)	(0.01)	(0.01)	(4.39)	(9.25)	(0.28)	(0.19)	(0.08)	(0.03)
Metrosideros polymorpha	6.32	6.74	0.16	0.07	306.83[c]	218.00	−27.40[b]	−28.80[c]	0.84	0.86[c]
	(0.60)	(1.15)	(0.02)	(0.01)	(12.73)	(10.45)	(0.13)	(0.20)	(0.10)	(0.01)
Pouteria sandwicensis	6.34	6.03	0.11	0.06	268.50[bc]	212.25	−26.97[b]	−27.22[bc]	1.76	2.00[b]
	(0.69)	(0.22)	(0.01)	(0.01)	(20.53)	(14.04)	(0.39)	(0.36)	(0.20)	(0.15)
Psydrax odorata	11.19	7.33	0.14	0.07	237.33[ab]	188.25	−25.64[ab]	−26.01[ab]	1.26	1.48[b]
	(0.79)	(1.59)	(0.01)	(0.02)	(3.68)	(20.23)	(0.77)	(0.83)	(0.07)	(0.07)
Santalum paniculatum	8.50	5.80	0.13	0.05	247.00[abc]	185.50	−25.78[ab]	−26.35[ab]	1.38	1.22[b]
	(0.77)	(0.46)	(0.01)	(<0.01)	(12.06)	(10.20)	(0.23)	(0.20)	(0.11)	(0.19)

Notes: A_{net} = net photosynthesis; g_s = stomatal conductance; c_i = intercellular CO_2 concentration; $\delta^{13}C$ = stable carbon isotope ratio.

both seasons ($P < 0.001$ for both winter and summer), ranging from a low of $0.84 \pm 0.10\%$ (mean $\pm$ SE; *Metrosideros*, January) to a high of $3.17 \pm 0.19\%$ (*Colubrina*, January). There was, however, no consistent change between winter and summer months across all species (Table 3) because percentage foliar N increased ($P < 0.05$) in two species (*Diospyros* and *Pouteria*), decreased ($P < 0.05$) in one (*Colubrina*), and did not change in the other three.

Based on a full factorial regression analysis of A_{net} as a response variable to %N (a measure of assimilation capacity) and g_s (a measure of water loss and carbon supply control), regulation of gas exchange apparently shifted from co-control by both g_s and N concentration in January ($F_{1,17} = 6.9$, $P = 0.02$ and $F_{1,17} = 4.9$, $P = 0.04$ respectively; $g_s \times$ %N interaction $P = 0.44$) to control by g_s alone in July ($F_{1,17} = 73.5$, $P < 0.001$; %N and $g_s \times$ %N interaction were not significant, $P = 0.36$ and $P = 0.10$, respectively). The results were the same when using c_i instead of A_{net} as the response variable (data not shown).

Carbon isotope ratios varied among species by more than 2.3‰ in January and 3.5‰ in July and generally corresponded positively with the differences in gas exchange among species in both of these seasons (Table 3). For example, *Colubrina* always had the greatest $\delta^{13}C$, %N, and A_{net} values (Table 3), whereas *Metrosideros* always had among the lowest $\delta^{13}C$, %N, and A_{net} values (Table 3). Carbon isotope ratios of all species

decreased from January to July as did A_{net}, g_s, and water potential (see next section).

Functional diversity of water-use traits—Mean values for most water-use traits (Ψ_{pd}, Ψ_{md}, and $\delta^{18}O$) varied significantly among species (Table 4). Predawn water potentials were fairly high (ca. -0.50 MPa) in January for all but one species (*Santalum*, Table 4). By July, however, mean Ψ_{pd} decreased and variation increased substantially, ranging from -0.83 to -3.35 MPa. The change in Ψ_{pd} was most pronounced for *Psydrax* (-0.68 to -3.35 MPa), with *Pouteria* also having a large Ψ_{pd} drop (Table 4). *Colubrina*, *Diospyros*, and *Metrosideros* all had relatively small (ca. 0.50 MPa) decreases, thereby maintaining fairly high mean Ψ_{pd} (>-1.0 MPa) throughout the year. Overall, *Psydrax* and *Santalum* always had the lowest mean Ψ_{pd} (Table 4), the latter being more than two times lower than all other species in winter.

Midday water potential values in January were all quite similar among species, except for *Santalum* (Table 4). In spite of significant decreases in predawn water potential from January to July across all species ($P < 0.05$), half of the species (*Colubrina*, *Metrosideros*, and *Santalum*) had no significant ($P > 0.05$) decreases of midday water potential over this period, perhaps indicating physiological regulation to avoid severe midday water stress.

Mean $\delta^{18}O$ values were relatively low (-3.9‰ to -6.6‰)

TABLE 4. Mean values of water-use traits (± 1 SE) for the six species used in this study and oxygen isotope ratios of soil samples. Significant differences ($P < 0.05$) among species within a season are depicted as different letters (Tukey multiple comparisons test). Absence of letters indicates no significant differences among species within a season.

|	Predawn water potential (MPa)		Midday water potential (MPa)		$\delta^{18}O$ (‰)	
	Winter	Summer	Winter	Summer	Winter	Summer
Colubrina oppositifolia	−0.47[ab] (0.02)	−0.94[a] (0.09)	−1.23[a] (0.06)	−1.21[a] (0.08)	−5.38 (0.29)	−4.82[a] (0.14)
Diospyros sandwicensis	−0.37[a] (0.01)	−0.95[a] (0.06)	−1.61[b] (0.03)	−2.19[b] (0.10)	−5.06 (0.51)	−4.45[a] (0.15)
Metrosideros polymorpha	−0.47[ab] (0.02)	−0.83[a] (0.07)	−1.50[b] (0.07)	−1.33[ab] (0.06)	−3.90 (0.95)	−4.73[ab] (0.09)
Pouteria sandwicensis	−0.59[b] (0.08)	−1.49[ab] (0.19)	−1.43[ab] (0.10)	−2.46[bc] (0.20)	−6.44 (0.19)	−5.00[a] (0.51)
Psydrax odorata	−0.68[b] (0.03)	−3.35[c] (0.62)	−1.64[b] (0.07)	−4.36[d] (0.54)	−5.78 (0.69)	−3.34[b] (0.26)
Santalum paniculatum	−1.54[c] (0.08)	−2.02[bc] (0.07)	−3.54[c] (0.08)	−3.53[cd] (0.08)	−6.65 (0.38)	−4.63[ab] (0.29)
Soil at 0–5 cm					−2.35 (0.44)	1.14 (0.57)
Soil at 10–20 cm					−4.58 (0.70)	−0.41 (0.54)

Notes: $\delta^{18}O$ = stable oxygen isotope ratio.
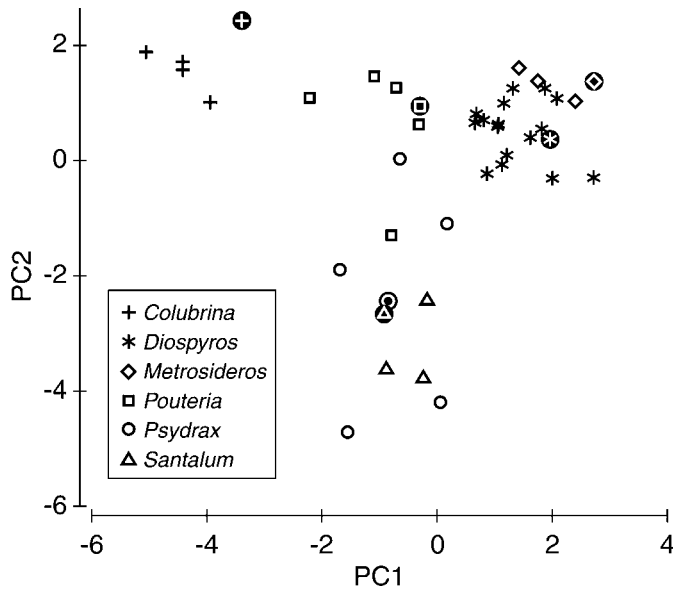
Fig. 1. Bi-plot of the first two principal components from the PCA of carbon-gain and water-use traits in six Hawaiian dry forest species. Data are results from two separate analyses: circled symbols represent PCA based on mean trait values for each species; uncircled symbols represent PCA based on trait values for individual trees. PC scores for means and individuals of each species are very similar but are slightly offset because of unequal sample sizes among species. For both analyses, the traits that most strongly influenced PC1 were those related to carbon gain (and had negative correlations), while those most strongly affecting PC2 were water-use traits (positively correlated).

TABLE 5. Eigenvector coefficients for each carbon-gain and water-use trait constituting the first five principal components (PC1–5) derived from the principal component analysis of these traits in six dry forest tree species. Analysis based on species mean values.

Carbon-gain or water-use trait	Eigenvector coefficient				
	PC1	PC2	PC3	PC4	PC5
Summer $\delta^{13}C$	−0.413	−0.081	0.101	0.123	0.424
Summer LMA	0.404	−0.157	−0.137	−0.033	−0.051
Winter $\delta^{13}C$	−0.389	−0.093	0.085	0.427	0.277
Winter %N	−0.377	0.246	−0.043	0.022	−0.068
Winter LMA	0.370	−0.160	0.197	−0.217	0.561
Summer %N	−0.364	0.191	0.064	−0.442	−0.150
Winter $\delta^{18}O$	0.258	0.266	0.223	0.604	−0.288
Summer $\delta^{18}O$	−0.200	−0.325	0.540	0.250	−0.014
Summer Ψ_{pd}	0.129	0.418	−0.303	0.117	0.487
Winter Ψ_{pd}	0.115	0.358	0.466	−0.140	0.245
Summer Ψ_{md}	0.073	0.479	−0.159	0.202	0.034
Winter Ψ_{md}	0.029	0.358	0.493	−0.240	−0.135

Notes: $\delta^{13}C$ = stable carbon isotope ratio; LMA = leaf mass per area; %N = percent foliar nitrogen; $\delta^{18}O$ = stable oxygen isotope ratio; Ψ_{pd} = predawn water potential; Ψ_{md} = midday water potential.

and were not significantly different among species in January (Table 4). These values indicate that all plants used soil-saturating winter rainwater (low $\delta^{18}O$ ratio). The high water potentials during this period indicate ample water in the soil column, and $\delta^{18}O$ values through the soil profile (Table 4) converged within the first 20 cm on the estimated deep-soil $\delta^{18}O$ values of −5 to −7‰ (Hsieh, 1997; D. R. Sandquist, unpublished data). By July, however, mean $\delta^{18}O$ values increased for all species (except *Metrosideros*), reflecting uptake of water with higher $\delta^{18}O$ values, i.e., water from summer rain and surface soil water exposed to evaporation (Table 4). *Psydrax* had the greatest mean $\delta^{18}O$ value at this time, an indication of greater surface water use, while *Pouteria* and *Colubrina* had the lowest values, suggesting less use of surface water and more dependence on deeper water.

Integrated analysis of water-use and carbon-gain traits—PCA was used to examine functional variation among species based on a composite of carbon-gain and water-use traits over both periods of the year. The PCA based on mean values for each species showed a strong separation among species within the first two components (Fig. 1). These two defined 77% of the variation (PC1 = 44%; PC2 = 33%), with 100% of the variation fully explained over the first five components.

A second PCA, used to examine variation among all trees sampled in the study, agreed with the first. Individual trees were clustered largely within species groups along the first two axes (Fig. 1). Again, the first five principal components

explained almost all of the variation (88%), and the first two components explained 60% (PC1 = 34%; PC2 = 26%).

For both analyses, carbon-gain traits loaded most strongly on PC axis 1, such that functions associated with greater carbon gain decreased along axis 1 (Table 5). Carbon isotope ratios were the best overall trait for predicting separation on PC axis 1. Water-use traits most strongly defined axis 2 (Table 5), with greater water status corresponding to more positive values of PC2. Summer water potentials (both predawn and midday) followed by winter water potentials had the greatest effect on this axis (Table 5).

In both PCA evaluations (Fig. 1), *Colubrina* was set apart from all other species at the high carbon-gain, high water-status corner of the ordination. *Metrosideros* and *Diospyros* clustered together at the low carbon-gain, high water-status corner, and *Pouteria* ranked as intermediate along axis 1, but had high water-use values along axis 2. *Psydrax* overlapped with *Santalum,* being intermediate along axis 1 (carbon gain) and having the lowest values along axis 2 (water status). At the individual level, the greatest variation was for *Psydrax* water status (PC2). All other species clustered fairly close together along both axes.

Variation of allocation and growth patterns—As for leaf carbon-gain and water-use traits, there was fairly broad variation of allocation related traits (LMA, C/N, LLS, and increment growth) among the six tree species. LMA and C/N were significantly lower in *Colubrina* than in most other species during both seasons (Table 6), a result that corresponds with the other productivity measures for this species. *Diospyros* and *Metrosideros* had the two highest LMA and C/N values in both January and July. LMA declined from January to July for all species except *Santalum* and *Colubrina* (Table 6).

Interspecific variation was very high for median leaf life span (LLS) (Table 6). *Psydrax*, which had the greatest LLS (1085 d), exceeded that of the next longest (*Diospyros* and *Metrosideros*) by 30% and retained leaves for 700 d longer than *Colubrina*, which had the shortest median LLS (385 d). *Psydrax* also had the greatest annual growth increase (8.9

TABLE 6. Mean values (±1 SE) of leaf mass per area (LMA) and carbon-nitrogen ratio (C : N) for the six species used in this study. For leaf life span, values shown are medians, and in parentheses are the 1st and 3rd quartile of leaf life span distribution for each species. Significant differences ($P < 0.05$) among species within each season/column are depicted as different letters (Tukey multiple comparisons test).

Species	LMA (g·m⁻²)		C/N		Median leaf life span (days)	Increment growth (mm·y⁻¹)
	Winter	Summer	Winter	Summer		
Colubrina oppositifolia	84.3[a]	113.0[a]	12.46[a]	18.43[a]	385	5.0[ab]
	(13.2)	(13.9)	(1.00)	(0.75)	(324–481)	(1.0)
Diospyros sandwicensis	305.3[d]	220.1[b]	54.78[c]	44.99[d]	840	1.7[c]
	(7.8)	(9.3)	(2.64)	(1.38)	(607–960)	(0.5)
Metrosideros polymorpha	248.0[c]	237.8[b]	55.00[c]	51.33[d]	815	3.6[abc]
	(9.9)	(29.4)	(5.40)	(1.50)	(652–1000)	(0.8)
Pouteria sandwicensis	210.8[bc]	186.6[b]	25.46[ab]	23.98[ab]	694	2.5[bc]
	(6.1)	(14.8)	(2.08)	(1.66)	(534–1000)	(0.7)
Psydrax odorata	237.8[bc]	178.8[b]	37.28[b]	32.74[bc]	1085	8.9[a]
	(17.6)	(10.4)	(1.98)	(1.43)	(786–1337)	(1.4)
Santalum paniculatum	182.1[b]	203.5[b]	33.68[b]	36.48[c]	465	3.4[bc]
	(13.8)	(2.8)	(2.95)	(3.34)	(349–566)	(0.9)

mm·y⁻¹; 9.6%), with *Colubrina* having the second highest rate (5.0 mm·y⁻¹; 1.7%). *Diospyros* trunk diameter showed the least annual increase (1.7 mm·y⁻¹; 1.1%), but there was significant overlap of growth among all the species, so that there were no clear groupings based on this parameter (Table 6).

Integration of allocation and physiological function traits—Pairwise correlations of all 13 traits for both winter and summer sample periods are presented in Appendix S1 (see Supplemental Data accompanying online version of this article). The expected relationship between lower water availability and higher $\delta^{13}C$ values (indicating greater water-use efficiency) held true for all species in July except for *Colubrina*, which had both high $\delta^{13}C$ and high water potential values (Tables 3 and 4). *Psydrax* had the greatest $\delta^{13}C$ values and the lowest overall water potential, with *Metrosideros* ranking at the opposite end of the spectrum. The $\delta^{13}C$–water potential relationship was not observed in January, likely owing to all but one species having indistinguishable water potential values at this time of high water availability (Table 4).

Among species, LLS was positively related to both LMA and C/N (Fig. 2). These relationships were the same whether mean or median LLS was used, but mean LLS is presented in Fig. 2 for comparison to other studies. Notably, plants at the high end of the spectrum (*Diospyros*, *Metrosideros*, and *Psydrax*) had decreased LMA and C/N values from winter to summer, whereas plants at the low end of the relationship actually had an increase (*Colubrina* and *Santalum*). In spite of these apparent differences in plasticity, all species occupied the same relative position within each correlation.

Although LMA and %N alone were highly variable among species, the LMA–%N relationship was markedly uniform across all species. A strong negative relationship occurred between LMA and %N in both January and July (Fig. 3), and the slopes calculated from SMA for both months were similar (−0.0116 and −0.0129, respectively) and not significantly different from each other ($P = 0.747$). The only species that appeared to stray from this strong trend was *Pouteria*, which had high %N relative to its LMA.

DISCUSSION

Functional diversity and distinguishing traits of Hawaiian dry forest trees—It has long been recognized that taxonomic diversity of tree species in Hawaiian dry forests exceeds that of
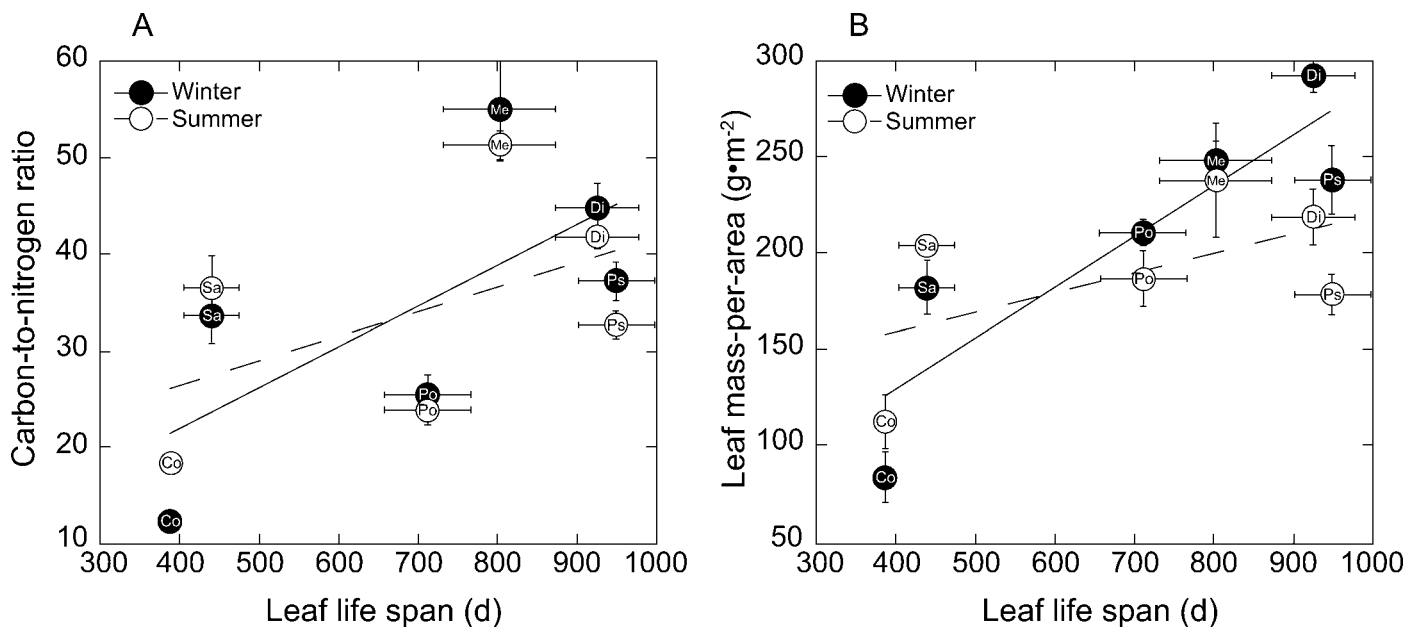

Fig. 2. Relationships between leaf life span and (A) leaf carbon-to-nitrogen ratio and (B) leaf mass-per-area for six Hawaiian dry forest species in winter and summer. Error bars = ±1 SE. Letters within symbols represent each tree species: *Colubrina* (Co), *Diospyros* (Di), *Metrosideros* (Me), *Pouteria* (Po), *Psydrax* (Ps), *Santalum* (Sa).
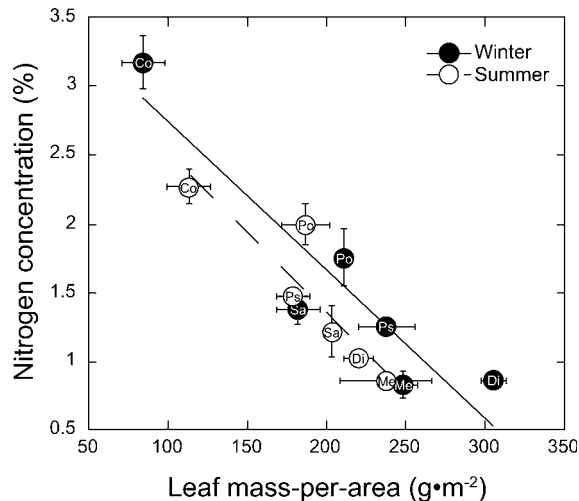
Fig. 3. Relationship between mean leaf mass-per-area and mean foliar nitrogen concentration (%) for six Hawaiian dry forest species in winter and summer. Error bars = ±1 SE. Letters within symbols represent each tree species: *Colubrina* (Co), *Diospyros* (Di), *Metrosideros* (Me), *Pouteria* (Po), *Psydrax* (Ps), *Santalum* (Sa).

Hawaiian wet forests (Rock, 1974), but only one other set of studies to date (Stratton et al., 2000; Stratton and Goldstein, 2001) has examined the degree to which this species diversity confers functional diversity—the measure of diversity that more directly influences ecosystem processes (Díaz and Cabido, 2001) and is potentially of greater importance for conservation. For the primary tree species of the North Kona dry forest ecosystem of Hawaii, we found a high degree of variation for virtually all functional traits measured, and this functional diversity likely begets a diverse ecosystem in terms of resource processes. These results underscore the importance of preserving the species composition of these threatened forests.

It is beyond the scope of this study to identify the causal factors for the variation we found, but low predictability of annual rainfall and high spatial variability on these young volcanic substrates creates a highly patchy environment in both space and time. This patchiness may provide many opportunities for niche specialization. Additionally, during the evolution of these species, low competition and herbivore pressures (which are reduced in many island systems) may have also allowed for greater variability of functional traits and suites. Regardless of the mechanisms, we saw high interspecific variability across most carbon-gain functions (e.g., 98% difference in winter A_{net}), water-use functions (e.g., 304% difference for summer Ψ_{pd}), and leaf-allocation functions (e.g., 182% difference for LLS), and such variation was found in both wet (January) and dry seasons (July). Among-species differences were also largely conserved between these two periods (e.g., Figs. 2 and 3).

This breadth of function is not unusual in tropical dry forests and savannas, but it has normally been found in dry forest studies that span evergreen through drought deciduous life forms (e.g., Sobrado, 1991; Eamus et al., 1999; Prior et al., 2003). Hawaiian dry forests, however, are different from most other tropical dry forests in that the latter are often dominated by drought deciduous species, whereas almost all tree species

in Hawaiian dry forests are evergreen (>80%). Given this limited variation of life form, the range of values found across the Hawaiian species was surprisingly high—comparable in some cases to global variation (Wright et al., 2005a). For example, the ranges for LMA (84 to 305 g·m⁻²) and %N (0.8 to 3.2%) nearly spanned the 5th though 95th percentiles found in a global survey of LMA in evergreen species (55 to 485 g·m⁻²) and %N in non-nitrogen fixing species (0.6 to 3.6%) (Wright et al., 2005a). That such breath is seen within a small number of Hawaiian dry forest species (see also Stratton et al., 2000) might reflect the high environmental heterogeneity and evolutionary divergence for which the Hawaiian archipelago is well known (Wagner and Funk, 1995).

The principal component analysis demonstrated that the functional differentiation among the six species was strongly associated with variation of carbon-gain (PC1) and water-use (PC2) traits (Fig. 1). Examination of individual carbon-gain and water-use characteristics supported this finding while also helping to identify unique attributes found within species and the limitations on their productivity.

Colubrina, at the upper end of the carbon-gain spectrum, had high net photosynthetic rates with correspondingly high foliar nitrogen content. Photosynthetic carbon gain is limited by the balance between CO_2 supply, determined largely by stomatal conductance, and CO_2 demand, which is controlled primarily by biochemical capacity (Farquhar et al., 1980). The high A_{net} and %N values for this species suggest that it has a relatively high biochemical capacity for carbon gain. In contrast, its low c_i values, and correspondingly high $\delta^{13}C$, suggest that stomatal limitations (i.e., low CO_2 uptake) are instead the greater constraint on carbon gain in this species. However, in spite of this result the water status of *Colubrina* was consistently high and did not substantially change from January to July. The modest shift in $\delta^{18}O$ values from January to July (0.55‰) suggests that the water source for this species is not strongly influenced by variation in seasonal rainfall and is probably deep (as indicated by low $\delta^{18}O$). But even though this species has high rates of carbon gain and ample water, it appears to still be limited by carbon supply and is thus operating at below maximum capacity.

At the other end of the carbon-gain spectrum was *Metrosideros*. It had low but consistent photosynthetic rates and the lowest foliar nitrogen concentrations of any species (Table 3). Carbon isotope ratios were also lowest in this species, indicating an accumulation of CO_2 in the intercellular space (c_i) (shown also by direct measurements; Table 3) most likely induced by the particularly low carboxylation rates. These low rates did not appear to be caused by water availability or stomatal conductance because both were among the highest measured for any species in the study. As such, potential carbon gain in *Metrosideros* appears to be limited less by carbon supply than by carbon demand (biochemical capacity), a fundamentally different mechanism than the limitation for *Colubrina*. Despite both species being evergreen, this contrast mirrors differences often found between drought deciduous and evergreen species in other tropical dry forests (Eamus et al., 1999; Ishida et al., 2006).

Metrosideros was the only species with relatively enriched $\delta^{18}O$ values in winter and relatively depleted values in summer, potentially indicating a shift in use of water sources (Table 4). This species is largely confined to patches of young lava substrates (Stemmermann and Ihsle, 1993) that are likely to have higher surface-water $\delta^{18}O$ values in winter owing to

evaporation and low vegetation cover. In summer these sites are even drier, likely causing *Metrosideros* to rely more on deep soil water, a result also found by Stratton et al. (2000) for *Metrosideros* during drought.

Like *Metrosideros*, *Pouteria* had very low photosynthetic rates and $\delta^{13}C$ values (and high c_i values), suggesting it also has a low carboxylation capacity. However, *Pouteria* had the second greatest foliar nitrogen concentration, which generally correlates with higher carboxylation capacity. This high nitrogen, however, is probably due to the milky (latex) sap in this and many other species of the Sapotaceae family (Kalita and Saikia, 2004) and is therefore not related to carboxylation as in other species. The large seasonal shifts in $\delta^{18}O$ and modest seasonal changes in both predawn and midday water potential (Table 4) indicate a dynamic water source for this species, but this variation did not appear to substantially alter carbon-gain functions, which remained consistent among seasons (Table 3).

Overall mean water potentials for *Diospyros*, the most common tree in this forest, were similar to those of the three previously mentioned species, but declined seasonally. In spite of this decreased water status, photosynthetic rate increased slightly (Table 3). This resulted in *Diospyros* going from having one of the lowest winter A_{net} values to the highest summer value. There was little to no change in stomatal conductance, carbon isotope ratio, or oxygen isotope ratio, but surprisingly, foliar nitrogen content increased, which likely accounts for the slightly higher summer A_{net} rates. This dynamic suggests an interesting shift from limitation by carboxylation capacity in winter to that of carbon supply (stomatal conductance) in summer; changes in c_i value also support this finding. This dynamic seems out of phase with seasonal water status but results in a conservative persistence of A_{net} throughout the year, much like the nutrient- and water-stress tolerant species of other tropical dry forests (e.g., Ishida et al., 2006) and other low-resource environments (Chapin, 1980). This tolerance may account for the dominance of *Diospyros* in many Hawaiian dry forests.

Psydrax, the second most common tree of this system, had the second highest overall photosynthetic rate and mean $\delta^{13}C$ values (behind *Colubrina*), but unlike *Colubrina*, foliar nitrogen in *Psydrax* was relatively low (Table 3). The mean water potential values of *Psydrax* were also distinctly different from all other species in that they decreased dramatically from winter to summer (Table 4), with a concomitant increase of mean $\delta^{18}O$—these changes appeared to track the large changes in surface soil water $\delta^{18}O$. Together these water-use traits indicate a close coupling between *Psydrax* water status and surface water availability. Photosynthetic rates also dropped by about 35% from winter to summer (Table 3), but they remained relatively high (mean = 7.33 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in spite of the predawn water potential change of −2.67 MPa (almost 400%). This trait relationship demonstrates relatively high drought tolerance by this species. (By comparison, photosynthesis in *Colubrina* decreased 35% over a water potential drop of only −0.47 MPa, 100%.) Such tolerance may help explain the unusual combination of very long-lived leaves and high growth rates in this species. That is, leaf retention along with drought tolerance provides the possibility of opportunistic plant growth—much like that found in forest gap species, especially in the absence of herbivory (Coley, 1988).

Santalum had carbon-gain functions that were almost always intermediate to all other species. It appeared to be water-stress sensitive, having very low photosynthetic rates in summer (Table 3) that correlated with a significant drop in predawn water potential (Table 4). *Santalum* also had remarkably low midday water potential values that persisted throughout the year, even during favorable winter conditions (Table 4). This unusual behavior may reflect the fact that *Santalum* often parasitizes roots of other species (Wagner et al., 1999) and by having continually low midday water potential, the maintenance of sap flow from the host plant into this parasite is ensured (Radomiljac et al., 1999).

Integration of leaf-economic traits and relevance to adaptive functioning—Leaf-economic (i.e., allocation) traits concurred with carbon-gain and water-use variation for the most highly productive species, *Colubrina*, in having the lowest LMA, LLS, and C/N (Table 6), as would be expected based on global patterns of correlation among these traits (Reich et al., 1997; Wright et al., 2004). For the other five species, there was also general agreement with these correlations (e.g., Fig. 3). For example, the low-productivity species *Metrosideros* had relatively high LMA, LLS, and C/N, and *Diospyros*, the slowest growing species, also had high LMA and long LLS. However, some species did not follow these patterns, and the departures appeared to be related to the unusual life-history characteristics described earlier (e.g., high growth and A_{net} rates with long LLS in *Psydrax*).

In spite of these departures, the leaf-economy relationships, when viewed at the community level, generally conformed to those expected based on other regional and global studies (e.g., Reich et al., 1999; Wright and Westoby, 2002). However, seasonal changes in these relationships were evident. The LLS–LMA correlation (Fig. 2), for example, was quite strong in January ($r = 0.879$; $P = 0.02$) but was not significant in July ($r = 0.564$; $P = 0.24$). This change conflicts with studies showing limited environmental effects on this global relationship (Wright et al., 2002). In most other studies of these relationships, however, environmental variability was based on regionally ascribed climate differences (spatial variation), whereas our measure of environmental variation was seasonal (temporal variation); thus, our study includes phenotypic plasticity of trait correlations, while the global patterns do not.

The seasonal change we observed was a result of long-LLS plants (high LMA) having a large reduction of LMA from January to July, whereas LMA for those with shorter LLS (lower LMA) slightly increased (Fig. 2). This latter response is expected under conditions of increasing drought, indicating that the plants with shorter LLS responded more synchronously with the environment. The display of high plasticity for LMA in longer-LLS species is surprising given that their leaves generally persist through extended periods of climate variation, and a more stable LMA would be expected. However, the minimum LMA of these species was still equal to or greater than that of the shorter-LLS species (Table 6), which suggests that the latter may be poorly adapted to summer drought conditions—a circumstance that may beget the shorter life span of these leaves. Within the longer-LLS species, separate leaf cohorts might have different longevities that are tied more or less closely with climate (e.g., Evans and Black, 1993). Such polymorphism could account for the contradiction of having long LLS and being highly variable, but more detailed intra-annual measurements of LLS are necessary to determine the cause of this unexpected pattern.

There was also a very strong negative relationship between

LMA and %N in both January and July (Fig. 3). The slope of this relationship, which was nearly identical to that reported for trees in other studies (Prior et al., 2003; Wright et al., 2005a), did not change between seasons in spite of the variable plasticity in LMA among species. The consistent LMA–%N relationship is expected based on allometric and functional constraints: i.e., only so much nitrogen can be put into the cells of a leaf (Shipley et al., 2006), and additional nitrogen might impact biochemical function and efficiency, such as light use (Reich et al., 1997). Thus, species that do not align on the LMA–%N relationship may have discrete functional differences associated with nitrogen economy. In this study, *Pouteria* had consistently greater %N relative to leaf LMA, which, as previously noted, is probably due to higher foliar nitrogen values from the milky sap of this Sapotaceous species (Kalita and Saikia, 2004).

The broad spread of mean values for LLS, LMA, %N, and C/N among the species of this study (Table 6) suggests a diverse set of carbon- and nutrient-economy functions within this Hawaiian dry forest. In comparison to global data sets, the overall mean for %N was among the lowest, whereas that for LMA was relatively high (Reich et al., 1997; Wright et al., 2001, 2005a). Such values suggest that tree-influenced process rates (e.g., nutrient cycling and transformations) in this ecosystem are relatively slow, especially given that the most abundant species, *Diospyros*, has high LMA, LLS, and C/N, and very low foliar N.

The environmental challenges of this low-resource dry forest ecosystem might be expected to constrain the variation of trait combinations in the tree species, but the variation found was broader than expected and may even support emerging evidence for evolution of alternative functional designs within narrowly defined niche space (Marks and Lechowicz, 2006). Many of the species had typical coupling among functional traits (suites) that would classify them in traditional schemes for woody perennial plants. For example, *Colubrina* is a highly productive (high A_{net} and growth) drought avoider (high Ψ, deep water sources), whereas *Pouteria* is slow growing (with low A_{net}) and tolerates relatively low midday water potentials (albeit having deep water sources). Other trees of this forest, however, have unexpected combinations: *Psydrax* has surprisingly rapid growth and high A_{net} rates given its remarkably long LLS, very low Ψ, and apparent reliance on unpredictable surface water. This species might be best classified as an "opportunistic drought tolerator," similar to some desert species (e.g., cacti). Another uncommon combination was that of conservative productivity (slow growth, consistent A_{net}, high LMA, and LLS) with relatively high water status, as seen in *Diospyros* and *Metrosideros*. This might be considered the "conservative drought avoider" suite. Such uncommon trait combinations result in functional syndromes that amplify the already apparent functional diversity of this forest and further reinforce its distinctness.

Implications of functional diversity and changing composition on ecosystem processes, restoration, and management—One of the greatest threats to biodiversity worldwide, and on the island of Hawaii in particular, is invasion by alien grasses (D'Antonio and Vitousek, 1992; Vitousek, 1994). In the Hawaiian dry forests, the alien bunchgrass *Pennisetum setaceum* inhibits recruitment of native species and alters ecosystem nutrient cycles (Cabin et al., 2000; Litton et al., 2006). By most indications, the two species that are most

successful in the presence of this invader are *Diospyros* and *Psydrax*, but for apparently different reasons. By having low productivity, unchanging δ^{18}O, and generally high overall water potentials, *Diospyros* appears to partially escape competition with *Pennisetum* via a deep rooting system and a conservative growth strategy. *Psydrax*, on the other hand, appears to interact more directly with *Pennisetum* because of its surface-water dependence (as indicated by fluctuating δ^{18}O and water potential values), but because it appears to grow rapidly under favorable conditions and also to tolerate very low water availability, its abundance may result from an ability to compete effectively with *Pennisetum*. These functional characteristics of *Psydrax* and *Diospyros* may buffer these two species against the deleterious effects of *Pennisetum* and other alien plants, and may explain why these are two of the most common species in remnant Hawaiian dry forests (Litton et al., 2006). Both species, however, would have higher productivity in the absence of *Pennisetum* (Litton et al., 2006), and a greater presence of species like *Colubrina* would certainly increase dry forest production.

Compared to the diversity in continental systems, the taxonomic diversity of the North Kona dry forest ecosystem would not be considered high. However, in comparison to the more productive mesic and wet forests of Hawaii, the tree diversity is much greater, and our findings indicate that the functional diversity accompanying this species diversity spans a surprisingly broad spectrum. In spite of our enhanced understanding of functional diversity and competitive potential in these dry forest trees, many questions remain about why certain species appear to dominate the remnants of this unusual forest while others are conspicuously rare. Our findings indicate that the trees of this system have some degree of overlap for many individual traits, thereby conferring some redundancy, but overall, each species appears to occupy fairly separate functional space (niche). As such, potential shifts in the composition of these forests caused by invasion, disturbance, or climate change are likely to have significant consequences on the properties of, and services provided by, this important ecosystem. In particular, the conversion from a functionally diverse forest to a homogeneous *Pennisetum* grassland would undoubtedly alter and potentially eliminate many of the characteristic processes of this unique and culturally important ecosystem.

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