BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 40(6): 686–691 2008 10.1111/j.1744-7429.2008.00434.x

Scaling of Frond Form in Hawaiian Tree Fern *Cibotium glaucum*: Compliance with Global Trends and Application for Field Estimation

Naomi Arcand[1,2], **Aurora K. Kagawa**[3], **Lawren Sack**[4,5], and **Thomas W. Giambelluca**[2]

[1] University of Colorado, Department of Geography, 260 UCB, Boulder, Colorado 80309, U.S.A.

[2] University of Hawai'i at Mānoa, Department of Geography, 445 Saunders Hall, 2525 Maile Way, Honolulu, Hawai'i 96822, U.S.A.

[3] University of Hawai'i at Mānoa, Department of Botany, 3190 Maile Way, Honolulu, Hawai'i 96822, U.S.A.

[4] Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, California 90095-1606, U.S.A.

ABSTRACT

Large-fronded tree ferns are critical components of many tropical forests. We investigated frond and whole-plant allometries for Hawaiian keystone species *Cibotium glaucum*, for prediction and to compare with global scaling relationships. We found that *C. glaucum* fronds maintain geometric proportionality across a wide range of plant and frond sizes. These relationships result in strong allometries that permit rapid field estimation of frond size from simple linear dimensions. *C. glaucum* frond allometries complied with intra- and interspecific global trends for leaf area versus mass established for much smaller-leafed species, indicating 'diminishing returns' in photosynthetic area per investment in mass for larger fronds. The intraspecific trend was related to declining water content in larger fronds, but not to a significantly larger investment in stipe or rachis relative to lamina. However, *C. glaucum* complied with the global interspecific trends for greater allocation to support structures in larger leaves. Allometries for frond number and size versus plant height showed that as plants increase in height, frond production and/or retention progressively declines, and the increases of leaf size tend to level off. These frond and whole plant-level relationships indicate the potential for estimating frond area and mass at landscape scale to enrich studies of forest dynamics.

Key words: allometry; Cibotiaceae; forest plots; leaf mass per area; leaf size; leaf traits; pteridophyte; rain forest; specific leaf area.

TREE FERNS ARE KEYSTONE SPECIES IN MANY WET FORESTS INSIDE and outside the tropics, often dominating the subcanopy layer with tall caudexes (trunks) and crowns of large fronds (Walker & Aplet 1994, Durand & Goldstein 2001b, Grubb 2003, Coomes *et al.* 2005, Roberts *et al.* 2005). *Cibotium glaucum* (Sm.) Hook & Arn., one of four endemic Hawaiian *Cibotium* species (Cibotiaceae; Palmer 2003, Smith *et al.* 2006) can achieve densities of up to 5000 mature individuals per hectare in *Metrosideros polymorpha* forest on Hawai'i Island, constituting 77 percent of subcanopy cover (Mueller-Dombois *et al.* 1981, Drake & Mueller-Dombois 1993).

Quantification of tree fern frond area and mass in the forest subcanopy would enrich studies of vegetation structure, dynamics, and ecohydrology (*e.g.*, Arens & Baracaldo 1998, Condit 1998, Lehmann *et al.* 2002, Derroire *et al.* 2007, Jones *et al.* 2007). However, direct measurements are a challenge for tree ferns such as *C. glaucum*, which can reach heights of over 6 m, with individual fronds of 4 m^2 in area (Nelson & Hornibrook 1962, Wick & Hashimoto 1971; Durand & Goldstein 2001a). We tested allometries for the relationships among frond dimensions in plants of a range of sizes. These allometries would enable simple field prediction of frond area and mass and could thus be implemented in studies of individual tree ferns and in plot censuses.

The large size of *C. glaucum* fronds additionally permitted testing of global leaf scaling allometries. Studies of large sets of much smaller-leafed species established that, both intra- and interspecifically, leaf mass per area (LMA) is greater in larger leaves, leading to 'diminishing returns' in photosynthetic area (Milla & Reich 2007, Niklas *et al.* 2007). This trend arises in part due to increasing allocation to petiole and midrib (Howland 1962; Niinemets *et al.* 2007). We assessed whether the very large fronds of *C. glaucum* complied with these trends.

We additionally tested plant-level allometries to determine the scaling of frond size and number versus plant height. These allometries provide a quantitative description of the ontogenetic trajectory of the growth form, and indicate the potential for predicting average values for frond traits from measurements of caudex height.

METHODS

SPECIES, STUDY SITES, AND MEASUREMENTS.—We measured *C. glaucum* in four wet *M. polymorpha*-dominated forests on Hawai'i Island at 1000–1200 m elevation: Hōnaunau Forest (HF; 19.48° N, 155.87° W), Laupāhoehoe Forest (LF; 19.80° N, 155.27° W), 'Ōla'a Forest (OF; 19.48° N, 155.21° W), and Hawai'i Volcanoes National Park Thurston Tube Forest (TF; 19.42° N, 155.24° W). The mean annual temperature, precipitation, and relative humidity of the four sites are HF: 17.7°C, 1533 mm, 82.9 percent; LF: 14.3°C, 3725 mm, 80.0 percent; OF: 16.5°C, 3642 mm, 82.7 percent; and TF: 15.7°C, 2545 mm, 81.7 percent (T. W. Giambelluca & L. Cuo, unpubl. data.).

Received 31 December 2007; revision accepted 9 April 2008.

[5] Corresponding author; e-mail: lawrensack@ucla.edu

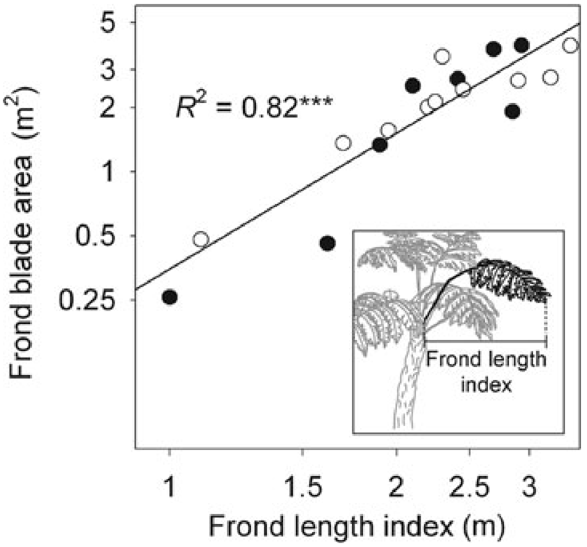

FIGURE 1. Allometry for *Cibotium glaucum* frond area versus frond leaf index (FLI), a linear dimension rapidly measured in the field, useful for prediction (see Table 1 for parameters); inset: schematic showing the measurement of FLI. Values are shown on log axes and fitted with the standard major axis (SMA). Symbols: Black, ‘Ōla‘a Tract Forest; White, Hōnaunau Forest.

We collected one representative frond for each of 8–10 tree ferns of a range of caudex heights in OF and HF from November 2005 to October 2006. We sampled fully mature, unbrowsed fronds, exposed to understory irradiance levels. We measured stipe (petiole) diameter for each frond just above caudex insertion and frond length index (FLI), a simple, rapid measurement of the distance from the caudex to the frond tip, parallel to the ground (Fig. 1, inset). We harvested these fronds and measured linear dimensions, *i.e.*, stipe, blade, and frond (stipe plus blade) lengths, and frond maximum width; areal dimensions, *i.e.*, the areas of whole blades, and of detached pinnules (including their midveins) separated from rachises (with a LI-3100C meter; LI-COR, Lincoln, Nebraska); and the mass of components after drying at 70°C for 5 d. For fronds sampled from another 10 tree ferns of a range of sizes at OF, we measured stipe diameter and, after rehydration, water content at saturation [WCS = (saturated mass − dry mass)/saturated mass] for a segment of rachis and pinnules branching off the primary rachis.

STATISTICS.—We tested for trait differences between forests using *t*-tests (Minitab Releases 14 and 15; State College, Pennsylvania; Sokal & Rohlf 1995). To test predictive allometries, *i.e.*, which could be used to estimate *y* from *x*, we fitted lines by least squares to log-transformed data, determining regression coefficients and parameters *a* and *b* for $\log y = a + b \times \log(x)$. We compared fits among forests using analyses of covariance, comparing slopes and intercepts (Genstat 6th Edition, VSN, Hemel Hempstead, UK).

To test functional allometries, *i.e.*, the intrinsic linkages between independent traits, we used standard major axes (SMA; Sokal & Rohlf 1995; Sack *et al.* 2003) using *SMATR* in R (http://www.bio.mq.edu.au/ecology/SMATR/index.html; Warton *et al.* 2006; Warton & Ormerod 2007; R Development Core Team 2007). The use of SMA treats both *x* and *y* as independent variables with natural variation and measurement error, and is thus most appropriate for determining their functional interrelationship (Smith 1980; Sokal & Rohlf 1995; Sack *et al.* 2003). We present SMA parameters α and β for $\log y = \alpha + \beta \times \log(x)$. We tested whether SMA slopes differed from those expected according to geometric similarity, the scenario in which proportions are maintained as leaf size increases; linear dimensions should scale with β of 1, as should areal dimensions, and areal dimensions should scale with linear dimensions with β of 2 (Niklas 1994; Sack *et al.* 2003).

In this study we sampled plants of a range of sizes, as we were interested in testing allometries useful across that range. However, we also wished to compare the intraspecific allometry of blade area versus mass with published allometries that sampled leaves of different sizes across individuals of a limited range of size. Thus, for the scaling of blade area versus mass we tested the degree to which the correlation between these traits might have derived only from both variables scaling with tree fern size. Using partial correlation analysis (using Minitab Release 14, and formulas in Zar 1999; see also Shipley 2004), we tested the bivariate relationships among frond area, frond mass and caudex height, partialling out the third variable. This analysis allowed us to determine whether blade area and blade mass were correlated regardless of their linkage with plant size.

RESULTS

SCALING OF FROND DIMENSIONS: GEOMETRIC SIMILARITY, AND PREDICTION.—The tree ferns sampled at OF and HF ranged in heights from 0.21 m to 2.8 m (mean ± SE of 0.96 ± 0.18 m), and the sampled plants from the two forests did not differ statistically in caudex height or in the measured frond traits (*t*-tests; P values > 0.15). Fronds varied 17-fold in blade area, 42-fold in blade dry mass, and threefold in frond mass per area (see ranges in Table 1). Values for WCS ranged 60–79 percent.

The scaling of frond dimensions (*i.e.*, those listed in Tables S1 and S2) supported geometric similarity. All linear frond dimensions generally scaled isometrically ($r = 0.82$–0.98; $P \leq 0.016$; $N = 10$–20). The relationships among stipe diameter and the lengths of stipe, blade and frond had β of 0.80–1.25, with 95% CIs including unity; only frond width scaled nonisometrically with stipe diameter, with $\beta = 0.60$ and 95% CIs 0.38–0.94, although it scaled isometrically with other linear dimensions—the average β for these relationships was 1.03 ± 0.055 ($N = 20$; common SMA slopes for HF and OF). Areal dimensions also scaled isometrically, with β of 0.98–1.02 ($r = 1.0$; $P < 0.001$; $N = 18$), with 95% CIs including unity; the average β was 1.00 ± 0.0063 ($N = 6$). Linear and areal dimensions scaled with β of 1.69–3.21 ($r = 0.72$–0.94; $P \leq 0.044$; $N = 8$–18), with 95% CIs including 2; the average β was 2.23 ± 0.16 ($N = 12$).

TABLE 1. *Allometries for prediction of individual frond blade and pinnule area in* Cibotium glaucum *from an easy-to-measure frond length index (see Fig. 1). Values in square brackets following traits are the ranges of values sampled to develop the allometries, with mean value in bold; note large maximum frond sizes. Parameters fitted for log (Frond length index) = a + b × log (x), by ordinary linear regression (OLS; parameters reported ± SE, with R^2 and significance level, and n in parentheses). For all relationships, the lines fitted by OLS for 'Ōla'a Tract Forest (OF) and Hōnaunau Forest (HF) were coincident in slopes and intercepts (ANCOVA; P-values for differences > 0.05). ***$P < 0.001$. †Only data from HF were available.*

x-variable	Frond length index [1.0–**2.3**–3.4]
Blade area (m^2) [0.26–**2.2**–3.9]	$b =$ **2.13** ± 0.244; $a = -0.466 \pm 0.089$ $R^2 = 0.82^{***}$ (18)
Pinnule area (m^2) [0.25–**2.1**–3.8]	$b = 2.134 \pm 0.246$; $a = -0.480 \pm 0.0896$; $R^2 = 0.81^{***}$ (18)
Frond dry mass† (g) [56–**486**–1134]	$b = 2.38 \pm 0.366$; $a = 1.72 \pm 0.140$; $R^2 = 0.87^{***}$ (7)
Blade dry mass (g) [16–**244**–671]	$b = 2.51 \pm 0.416$; $a = 1.38 \pm 0.152$; $R^2 = 0.72^{***}$ (15)
Pinnule dry mass (g) [14–**188**–575]	$b = 2.36 \pm 0.368$; $a = 1.33 \pm 0.134$; $R^2 = 0.70^{***}$ (18)

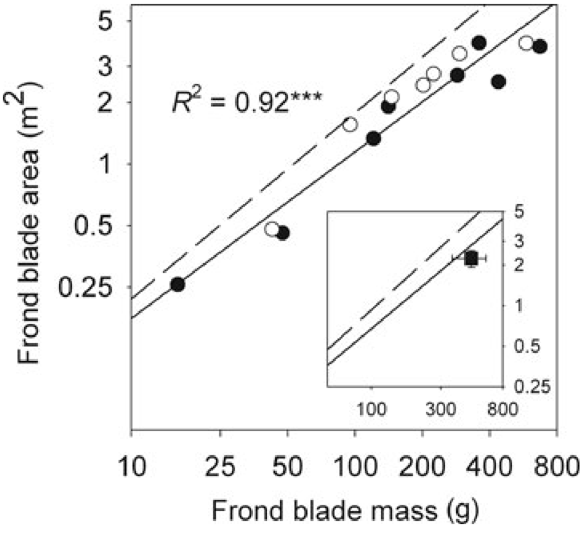

FIGURE 2. Allometries for *Cibotium glaucum* frond blade area versus mass, and comparison with global trends for leaf design. The solid line represents the standard major axis (SMA) for *C. glaucum*: log (area) = –1.57 + 0.814 × log (mass), and the dotted line represents the global intraspecific trend for leaves varying in size on mature plants of 157 angiosperm species with much smaller leaves, < 0.03 m^2 (SMA slope from Milla & Reich 2007, with intercept of *C. glaucum* used; see text for discussion); inset: square represents average value for *C. glaucum* fronds, and solid and dotted lines represent the extrapolation of global interspecific trends determined, respectively for much smaller leaves of 70 fern species up to 0.011 m^2, and for 1943 vascular plant species up to 0.25 m^2 (for ferns, log[leaf area] = 2.02 + 0.904 × log[dry mass]; for vascular plants, log[leaf area] = 2.01 + 0.979 × log[dry mass]; Niklas *et al.* 2007). Symbols as in Figure 1.

We found that FLI provided an allometric basis for predicting area and dry mass for frond, blade, and pinnules ($R^2 = 0.70–0.87$; $P < 0.001$; Fig. 1; Table 1). Frond lengths, blade lengths, and stipe diameter also had predictive potential ($R^2 = 0.56–0.98$; $P < 0.001$; Tables S1 and S2).

COMPLIANCE OF FROND SCALING RELATIONSHIPS WITH GLOBAL TRENDS FOR DIMINISHING RETURNS.—*Cibotium glaucum* fronds complied with global intraspecific allometries, extending trends derived for smaller leaves. Larger fronds showed lower area relative to dry mass, *i.e.*, a diminishing return in photosynthetic area with increasing mass. For fronds, blades, and pinnules, the β values for area versus dry mass were 0.75–0.83, with 95% CIs excluding unity ($r = 0.94–0.98$; $P < 0.001$; $N = 7–18$). This trend was within the range determined for 157 species of diverse angiosperms with leaves < 0.03 m^2, which had β values of 0.57–1.29 (Fig. 2), though the diminishing return in our study was stronger than the average for the species in that study, $\beta = 0.91$, and 95% CIs 0.88–0.92 (Fig. 2; Milla & Reich 2007). Notably, the trend we studied for *C. glaucum* was an ontogenetic allometry, *i.e.*, holding across plants of different sizes. One concern might be that the relationship of blade area and mass might be driven secondarily by their respective relationships with plant size. However, our partial correlation analysis showed that this was not the case. We found partial *r* values of 0.82, –0.59, and 0.92 ($P < 0.05$) for, respectively, height and blade mass (partialling out blade area), height and blade area (partialling out blade mass), and blade mass and area (partialling out height). Thus, larger plants have fronds of larger mass, but if that ontogenetic pattern were 'removed', then larger plants would in fact have smaller fronds, because frond blade mass and area are intrinsically allometrically linked, even at a constant plant size.

The diminishing returns observed in the intraspecific scaling of blade area with blade mass did not arise from significantly greater allocation to support structures in larger fronds. The scaling of stipe and rachis mass with pinnule, blade, and frond mass did not differ from isometry ($\beta = 0.99$ to 1.42, with 95% CIs including unity; $r = 0.88–0.99$; $P \leq 0.009$; $N = 7–15$); the average β was 1.24 ± 0.069 ($N = 6$). The greater LMA in larger fronds would arise from a greater thickness or density, and the latter would be associated with lower WCS (Sack *et al.* 2003). Indeed, WCS declined with increasing frond size (assessed using stipe diameter; $\beta = -0.14$; 95% CIs = –0.078 to –0.25; $r = -0.64$; $P = 0.048$; $N = 10$).

Cibotium glaucum also complied with *interspecific* trends for larger leaves to have higher LMA, greater allocation to support, and lower WCS. *Cibotium glaucum* fell close to the extrapolated line for area versus dry mass for fern species with pinnules or fronds up to 0.011 m^2 (Niklas *et al.* 2007; Fig. 2, inset). This trend predicted the average frond in our sample should have an LMA of 173 g/m^2; we found 186 ± 19.8 g/m^2. Notably, ferns have relatively high LMA; the trend reported by Niklas *et al.* (2007) for vascular plants with leaves up to 0.25 m^2 predicted 111 g/m^2. The dry mass allocation to stipe and rachis was also consistent with the trend for 122 species with leaves up to 500 g fresh mass (Niinemets *et al.* 2007) (fractional allocation to petiole and midrib = 0.24 + 0.0505 × ln [leaf fresh mass]). That trend predicted that the average frond in this study would have 61 percent mass allocation to stipe and rachis; we found 59.7 ± 0.05 percent SE. *Cibotium glaucum* pinnules also complied with the trend for leaf water content, determined for 666 vascular plant species with leaf mass < 32 g (log[water content] = 0.299 + 0.982 × log [dry mass]; Niklas *et al.* 2007); that trend predicted that the average frond in our study would have a WCS of 64 percent, and we found 68.3 ± 0.65 percent.

PLANT-LEVEL ALLOMETRIES: RELATIONSHIPS BETWEEN FROND NUMBER AND SIZE, AND TREE FERN HEIGHT.—The allometries of frond number and size versus height indicated that as plants increase in height, frond production and/or retention declines, and the increases of leaf size eventually level off. The allometry of frond number versus height was significant for LF and TF ($R^2 = 0.53$–91; $P < 0.017$; $N = 9$–10), and the forests had similar slopes (ANCOVA, $P = 0.71$); β was 0.61 with 95% CIs 0.37–0.99 (Fig. 3A). However, TF had an intercept higher by 0.090 ± 0.038 ($P = 0.032$), indicating 23 percent more fronds at any height. The allometry of FLI versus height was significant for HF, LF, and OF ($R^2 = 0.47$–0.75; $P = 0.002$–0.029; $N = 7$–10), but not TF ($R^2 = 0.19$; $P = 0.21$, $N = 10$) and the forests did not differ ($P = 0.11$–0.59); β was 0.48, with 95% CIs = 0.39–0.60 (Fig. 3B).

DISCUSSION

We found strong scaling relationships at frond and plant level in *C. glaucum*, with implications for leaf design. Further, these relationships have potential for prediction of individual frond sizes and for estimation of stand-level frond area and mass.

We found that the scaling of frond dimensions followed geometric similarity for linear as well as areal dimensions. Fronds maintain their proportionality as they expand to different sizes, apparently due to constraints in primordium formation and expansion. These relationships result in several possibilities for predicting frond area from simple linear dimensions. In particular, we found that FLI is useful for rapid, nondestructive assessment at ground level of whole-frond area and mass, and can be implemented for studies of individual tree ferns and for estimation of plot-level total frond area.

We found that *C. glaucum* fronds complied with global intraspecific and interspecific allometries for diminishing returns of frond area with increasing frond mass, extending trends derived for smaller leaves. We found a β value of blade area versus mass within the range reported for the 157 species with leaves up to 0.03 m^2 in size, although the diminishing returns found for *C. glaucum* was steeper than the average value in that study (Milla & Reich 2007).

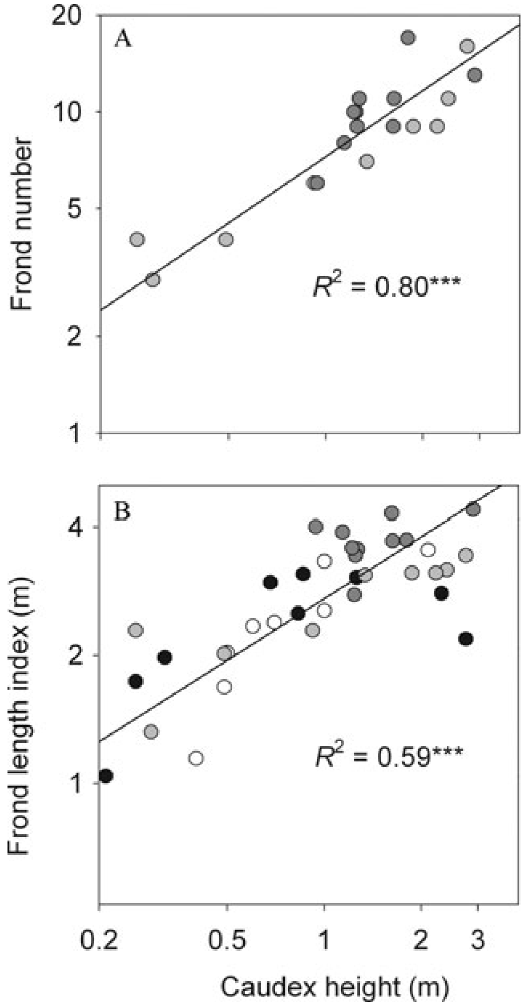

FIGURE 3. Whole-plant allometries for *Cibotium glaucum*, on log axes, and fitted with standard major axes (SMA). (A) Mean frond number versus caudex height (SMA equation: log[frond number] = 0.860 + 0.684 × log[height]; least-squares equation: log[frond number] = 0.867 ± 0.0218 SE + 0.613 ± 0.0733 SE × log [height]). (B) Mean FLI versus caudex height (SMA equation: log [FLI] = 0.417 + 0.481 × log [height]; least-squares equation: log [FLI] = 0.416 ± 0.0167SE + 0.371 ± 0.0526 SE × log [height]). ***$P < 0.001$. Symbols: Black, ʻŌlaʻa Tract Forest; White, Hōnaunau Forest; Light gray, Laupāhoehoe Forest; Dark gray, Thurston Tube Forest.

We note that this study focused on *ontogenetic allometry*, *i.e.*, trends across plants of different sizes, whereas the global study focused on *static allometry*, *i.e.*, trends across mature plants of similar size for each species. We focused on ontogenetic allometry here as we aimed to predict relationships across size-classes of plants. Our findings, and those of Milla and Reich (2007) suggest that both types of allometries can be important sources of ‘diminishing returns’ in photosynthetic area per mass allocation. More studies are needed for whether the two allometries should be the same, or whether they differ; theory and studies of animals show that ontogenetic and static allometries may be similar, or they may differ, depending on the specific relationship considered (Smith 1980; Cheverud 1982; Strauss 1993); we are not aware of any comparisons of the two types of allometry for plant functional relationships. However, for *C. glaucum*, our partial correlation analysis indicated that the ontogenetic allometry for blade area versus mass was similar in direction to the static allometry, independently of their linkage with plant size. Indeed, ontogenetic and static trends might be hypothesized to be similar for leaf trait allometries, as these relate to disposable organs of constrained design, and the differences between small and large leaves expanded in similar environments might be roughly consistent whether sampled across plants of a given size, or across plants of different sizes. Specific studies are needed to address the question of possible differences between static and ontogenetic intraspecific allometries for leaf traits (*cf.* Milla *et al.* 2008).

Notably, the intraspecific trend for diminishing returns in frond area with increasing mass allocation did not arise from greater allocation to stipe and rachis, but was associated with a declining WCS, consistent with greater blade density. This finding indicates that the modulation of traits to accommodate higher support requirements in larger leaves is achieved by adjustments within the lamina, rather than in midrib or petiole support. On the other hand, *C. glaucum* also complied strongly with *interspecific* trends for larger leaves to have higher LMA, greater allocation to support, and lower WCS (Niinemets *et al.* 2007, Niklas *et al.* 2007). The compliance of *C. glaucum* with the global interspecific trend indicates that the larger-scale diminishing returns in leaf area with increasing mass owe in part to increasing allocation to support, even to the large frond sizes in this study (Niinemets *et al.* 2006, 2007). We note that the global allometries, developed for much smaller leaves, had remarkable ability to predict area from dry mass, dry mass allocation to stipe and rachis from mass, and leaf water content from mass. Further study is needed of the scaling of other leaf traits, such as photosynthetic rates per mass and leaf life span (*cf.* Wright *et al.* 2004, Karst & Lechowicz 2007), and of the possibility that these traits might also show inter- and/or intraspecific trends with leaf size.

Finally, we found strong plant-level allometries for *C. glaucum*, *i.e.*, the scaling of frond number and size with plant height. These allometries showed forest-level variation. Still, in both forests, the scaling trends indicated that as plants increase in height, frond production and/or retention declines, and the increases of leaf size eventually tend to level off, indicating a change in form consistent with approach to a maximum leaf area.

We note that the allometries in this study have potential applications in frond- and plant-level studies. Further, the combination of these allometries could have additional applications. For example, one might combine allometries to estimate total frond area for given tree ferns of known heights by multiplying predicted frond number by average frond area, derived from predicted FLI (including bias-corrections; Baskerville 1972, Sprugel 1983). For such data generated from our allometries, the fitted least-squares line was log (total area) $= 1.31 + 1.40 \times \log$ (height), with 95% CIs $^{+240\%}_{-71\%}$ (the CIs were asymmetric, as these were calculated for functions fitted to log-transformed data; using the *rnorm* function in R version 2.6.1; R Development Core Team; Efron & Tibshirani 1993, Manly 1997). The uncertainty was very large, as this equation was derived by combining allometries for different forests, as we had collected data to demonstrate general allometries, rather than for site-specific predictions of total frond area. For precision in estimating total area, one would construct each of the allometries for a specific site (*cf.* Durand & Goldstein 2001a). This approach would enable landscape-level estimates of frond biomass and area from information of tree fern numbers and heights. Such future work would clarify the roles and dynamics of tree ferns in wet forests around the world.

ACKNOWLEDGMENTS

We thank J. Delay, M. C. Ho, F. Inman, R. Mudd, and T. Ranker for assistance with data collection, the Hawai'i Permanent Forest Plots Network team for logistical assistance, and the editors and two anonymous reviewers for improving the manuscript. This work was supported by National Science Foundation grants EAR-0309731 and IOB-0546784, by the U.S. Geological Survey Biological Resources Discipline Global Change Research Program, and by Kamehameha Schools.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

TABLE S1. *Allometries for prediction of individual frond blade and pinnule area in* Cibotium glaucum *from linear traits.*

TABLE S2. *Allometries for prediction of mass values for fronds and their components in* Cibotium glaucum *from linear traits.*

LITERATURE CITED

ARENS, N. C., AND P. S. BARACALDO. 1998. Distribution of tree ferns (Cyatheaceae) across the successional mosaic in an Andean cloud forest, Narino, Colombia. Am. Fern J. 88: 60–71.

BASKERVILLE, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2: 49–53.

CHEVERUD, J. M. 1982. Relationships among ontogenetic, static, and evolutionary allometry. Am. J. Physic. Anthropol. 59: 139–149.

CONDIT, R. 1998. Tropical forest census plots. Springer, Berlin, Germany.

COOMES, D. A., R. B. ALLEN, W. A. BENTLEY, L. E. BURROWS, C. D. CANHAM, L. FAGAN, D. M. FORSYTH, A. GAXIOLA-ALCANTAR, R. L. PARFITT, W. A. RUSCOE, D. A. WARDLE, D. J. WILSON, AND E. F. WRIGHT. 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. J. Ecol. 93: 918–935.

DERROIRE, G., L. SCHMITT, J. N. RIVIERE, J. M. SARRAILH, AND J. TASSIN. 2007. The essential role of tree-fern trunks in the regeneration of *Weinmannia tinctoria* in rain forest on Reunion, Mascarene Archipelago. J. Trop. Ecol. 23: 487–492.

DRAKE, D. R., AND D. MUELLER-DOMBOIS. 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology 74: 1012–1019.

Durand, L. Z., and G. Goldstein. 2001a. Growth, leaf characteristics, and spore production in native and invasive tree ferns in Hawaii. Am. Fern J. 91: 25–35.

Durand, L. Z., and G. Goldstein. 2001b. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126: 345–354.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, Boca Raton, Florida.

Grubb, P. J. 2003. Interpreting some outstanding features of the flora and vegetation of Madagascar. Prespect. Plant Ecol. Evol. Syst. 6: 125–146.

Howland, H. C. 1962. Structural, hydraulic, and "economic" aspects of leaf venation and shape. *In* E. E. Bernard and M. R. Kare (Eds.). Biological prototypes and synthetic systems, Volume 1, pp. 183–191. Plenum Press, New York, New York.

Jones, M. M., P. O. Rojas, H. Tuomisto, and D. B. Clark. 2007. Environmental and neighbourhood effects on tree fern distributions in a Neotropical lowland rain forest. J. Veg. Sci. 18: 13–24.

Karst, A. L., and M. J. Lechowicz. 2007. Are correlations among foliar traits in ferns consistent with those in the seed plants? New Phytol. 173: 306–312.

Lehmann, A., J. R. Leathwick, and J. M. Overton. 2002. Assessing New Zealand fern diversity from spatial predictions of species assemblages. Biodivers. Conserv. 11: 2217–2238.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. CRC Press, Boca Raton, Florida.

Milla, R., and P. B. Reich. 2007. The scaling of leaf area and mass: the cost of light interception increases with leaf size. Proc. R. Soc. Lond. B 274: 2109–2114.

Milla, R., P. B. Reich, Ü. Niinemets, and P. Castro-Díez. 2008. Environmental and developmental controls on specific leaf area are little modified by leaf allometry. Funct. Ecol. 22: 565–576.

Mueller-Dombois, D., K. W. Bridges, and H. L. Carson. 1981. Island Ecosystems: Biological Organization in Selected Hawaiian Communities. US/IBP Synthesis Series 15. Hutchinson Ross Publishing Co., Stroudsburg and Woods Hole, Massachusetts.

Nelson, R. E., and E. M. Hornibrook. 1962. Commercial uses and volume of Hawaiian tree fern. U.S. Forest Service. Pacific Southwest Forest and Range Experiment Station. Technical Paper 73.

Niinemets, Ü., A. Portsmuth, D. Tena, M. Tobias, S. Matesanz, and F. Valladares. 2007. Do we underestimate the importance of leaf size in plant economics? Disproportional scaling of support costs within the spectrum of leaf physiognomy. Ann. Bot. 100: 283–303.

Niinemets, Ü., A. Portsmuth, and M. Tobias. 2006. Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. New Phytol. 171: 91–104.

Niklas, K. J. 1994. Plant allometry. University of Chicago Press, Chicago, Illinois.

Niklas, K. J., E. D. Cobb, U. Niinemets, P. B. Reich, A. Sellin, B. Shipley, and I. J. Wright. 2007. "Diminishing returns" in the scaling of functional leaf traits across and within species groups. Proc. Natl. Acad. Sci. USA 104: 8891–8896.

Palmer, D. 2003. *Hawai'i's Ferns and Fern Allies*. University of Hawai'i Press, Honolulu, Hawai'i.

R Development Core Team. 2007. R: A language and environment for statistical computing. ISBN 3–900051-07–0, http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, N. R., P. J. Dalton, and G. J. Jordan. 2005. Epiphytic ferns and bryophytes of Tasmanian tree-ferns: a comparison of diversity and composition between two host species. Aust. Ecol. 30: 146–154.

Sack, L., P. D. Cowan, N. Jaikumar, and N. M. Holbrook. 2003. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant Cell Environ. 26: 1343–1356.

Shipley, B. 2004. Analysing the allometry of multiple interacting traits. Perspect. Plant Ecol. Evol. Syst. 6: 235–241.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider, and P. C. Wolf. 2006. A classification for extant ferns. Taxon 55: 705–731.

Smith, R. J. 1980. Rethinking allometry. J. Theoret. Biol. 87: 97–111.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W.H. Freeman, New York, New York.

Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209–210.

Strauss, R. E. 1993. The study of allometry since Huxley. *In* J. S. Huxley (Ed.). Problems of relative growth, pp. xlvii–lxxv. Johns Hopkins University Press, Baltimore, Maryland.

Walker, L. R., and G. H. Aplet. 1994. Growth and fertilization responses of Hawaiian tree ferns. Biotropica 26: 378–383.

Warton, D. I., and J. Ormerod. 2007. *smatr*: (Standardised) Major axis estimation and testing routines, R package version 2.1. http://web.maths.unsw.edu.au/~dwarton.

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. Biol. Rev. 81: 259–291.

Wick, H. L., and G. T. Hashimoto. 1971. Frond development and stem growth of tree-fern in Hawai'i. Research note PSW-237, Pacific Southwest Forest and Range Experiment Station. U.S. Forest Service.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428: 821–827.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey.