Effects of Wind on the Allometry of Two Species of Plants in an Elfin Cloud Forest

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ABSTRACT

Thigmomorphogenesis includes the effects of mechanical perturbation on plant growth. To test whether thigmomorphogenesis is evident at different scales within plants, we investigated the effect of wind on allometric relationships between specific plant parts. We chose two species from the elfin cloud forest of Puerto Rico that have contrasting growth habits, the shrub Clibadium erosum (Asteraceae) and the palm Prestoea acuminata var. montana (Arecaceae), and subjected them to barrier-protected and wind-exposed treatments. For C. erosum, we compared the allometry of stems and branches against three allometric models that predict that plant height or branch length increases at the 1, 2/3, and 1/2 power of stem diameter. Only the geometric similarity model (scaling exponent of 1) seemed to hold for plants of barrier-protected and wind-exposed treatments. For P. acuminata, we compared the allometry of leaves against geometric similarity, self-similarity, and elastic stiffness models. Mean petiole length ratios (petiole length/basal radius) of leaves of barrier-protected plants were higher on leaves of barrier-protected plants than wind-exposed plants. We suggest that alteration of the allometric relationships of plants, organs, or plant modules (stems and branches of C. erosum and leaves of P. acuminata) and alteration of the number of plant parts (leaves and branches of C. erosum) are adaptive responses resulting from the mechanical perturbation induced by wind in the elfin forest.

Key words: Clibadium erosum; leaf shape; Prestoea acuminata var. montana; Puerto Rico; scaling; thigmomorphogenesis.

IN TERRESTRIAL ENVIRONMENTS AND ESPECIALLY IN MOUNTAINS, forces caused by wind are the most ubiquitous and important cause of dynamic loading (Grace 1977). Mechanical stimulation has been tested in many vascular plants, producing reduced stem elongation and an increase in stem diameter (Grace 1977). This response, called thigmomorphogenesis by Jaffe (1980), involves the motion-induced reallocation of growth (Niklas 1992). From an ecological point of view, thigmomorphogenesis may have adaptive significance (Jaffe 1980; King 1981, 1991; Lawton 1982). It may also represent a developmental response to mechanical stress suffered by plants in windy cloud forest (Lawton 1982). Field observations suggest that the effect of wind on trees and plants of tropical and subtropical cloud forests is to produce a reduction in height and an increase in diameter (Lawton 1982, Cavelier & Mejía 1990, Dupuy et al. 1993). Lawton (1984) found that species that were more common on ridge crests had greater wood density. In general, plant diameter increases with exposure to wind (Telewski 1995), although Henry and Thomas (2002) found a decrease in diameter of Abutilon theophrasti when exposed to wind in a greenhouse. In another greenhouse study, Pruyt et al. (2000) found that mechanical perturbation caused increases in flexural rigidity due largely to an increase in cross-sectional area. Working with sunflowers, Smith and Ennos (2003) showed that the effect of wind on mechanical properties could be attributed to mechanical perturbation rather than the passage of air over the surface of the plant. Thigmomorphogenesis is likely to be especially important in windy environments such as montane terrain. Wind microclimates can vary dramatically, with important consequences for the vegetation (Clark et al. 1998). Although these studies strongly suggest that wind should affect allometry of cloud forest species, this idea has hardly been tested experimentally with plants from the cloud forest. An exception is the work of Cordero (1999) on saplings of Cecropia schreberiana, which demonstrated drastic changes in allometry, architecture, stem biomechanics, and gas exchange as a result of exposure to wind.

In a prior study (Fetcher et al. 2000), protection from wind had no significant effects on measures of growth such as total biomass, aboveground biomass, and total leaf area of Clibadium erosum, Prestoea acuminata var. montana, and Psychotria berteriana. In this paper, the effect of wind on allometric relationships between specific plant parts is analyzed on two of those species: the shrub C. erosum (Ws.) DC. (Asteraceae) and the palm P. acuminata (Willdenow) H. E. Moore var. montana (Graham) Henderson & Galeano (Arecaceae), chosen because of their contrasting growth habits. We hypothesized that thigmomorphogenesis could become evident at a scale different from that of the whole plant when subjected to barrier-protected and wind-exposed treatments.

Reinforcement of branches has been reported for Abies fraseri under wind or mechanically induced perturbations (Telewski & Jaffe 1986). Three models have been proposed to explain girth increases that are disproportionately greater for plants subjected to mechanical stimulation. The first is the elastic similarity model, also called the “elastic stiffness model” (Niklas 1992). This model, proposed by McMahon and Kronauer (1976), assumes that a branch acts as a cantilevered beam that is fixed at one end. If a branch...
conforms to the elastic similarity model, then the deflection at the tip is constant when divided by the length, and tree height or branch length (H) increases as the 2/3 power of stem diameter (D), that is, \( H \propto D^{2/3} \) (McMahon 1973, McMahon & Kronauer 1976). Furthermore, the ratio of diameter to branch length measured on any branch will serve to represent the entire tree (McMahon & Kronauer 1976). In the second model, called the geometrical similarity model, shape remains constant with an increase in size, and H varies with the 1.0 power of D (Norberg 1988), that is, \( H \propto D^1 \). A third allometric model that describes the growth of branch length and diameter to maintain mechanical stability is the constant stress model (Dean & Long 1986). This model predicts that \( H \propto D^{1/2} \) and assumes a constant maximum stress throughout the length of a cantilevered branch (Niklas 1993). In general, the elastic similarity model has been used to analyze the effects of static loading, whereas the constant stress model has been applied to analyze dynamic loading such as that induced by wind (Niklas 1992). Trees are subjected to both static and dynamic loading over their lifetimes, however, and most species are overbuilt, with a safety factor of approximately 4, indicating a response to loading by wind pressure (Niklas 1992).

We tested these models at several levels of architectural organization in our two study species. For *C. erosum*, we studied the relationships between the lengths and the diameters of main stem and branches by comparing the allometric scaling exponents to the values predicted by these three models. The allometric relationships of saplings of *P. acuminata* were studied at the scale of individual leaves. Previous studies of leaves have reported significant positive correlations between biomechanical and morphometric parameters such as petiole length and laminar mass (Niklas 1991a). Assuming that a leaf behaves as a cantilevered structure subject to static and dynamic loadings, we considered that leaves contain a prismatic structure (petiole) supporting the laminar load. Chazdon (1986) made a similar assumption in a study of the biomechanics of the leaves of three species of understory palms. She found that the leaf size appeared to be mechanically constrained and that the three species had similar factors of safety but different leaf sizes. Niklas (1991b) suggested that petioles of pinnately compound leaves can respond mechanically similarly to branches. We hypothesized that the allometry of leaves in saplings of *P. acuminata* would change if subjected to different wind regimes. Furthermore, the changes should vary depending on the type of leaf (simple vs. compound leaves) (Chazdon 1986, 1991).

**METHODS**

**STUDY SITE AND SPECIES.**—The experiment was established in 1990 along the road to Pico del Este (18°16'N, 65°45'W), Luquillo Experimental Forest (LEF), Puerto Rico, at approximately 950 m asl. This area contains a dwarf cloud forest association and falls within the lower montane rain forest life zone (Ewel & Whitmore 1973). Howard (1968, 1969) described this forest as having typically high rainfall and cloud cover, strong winds, water-saturated soils, reduced radiation, and dwarfed or stunted vegetation densely covered by epiphytes. Mean annual rainfall is 4210 mm. Mean daily wind speed measured by an anemometer (Campbell 034B, Campbell Scientific, Logan, UT, U.S.A.) at Pico del Este was 15.6 km/h or 4.3 m/s for 1998–2004, while the mean of hourly maximum wind speeds was 28.5 km/s or 15.3 m/s (Whendee Silver, pers. comm.). The anemometer was located about 300 m from the study plots with a similar exposure to prevailing winds. Over 17 percent of hourly maximum wind speeds were over 36 km/h or 10 m/s, while nearly 86 percent of the wind observations were in the NNE or ENE quadrants (Whendee Silver, pers. comm.). For a summary of climatic factors, composition of vegetation, and physiognomy see Brown et al. (1983) and Weaver (1995).

*Clibadium erosum* (Asteraceae) is a large woody shrub (1–2.5 m tall at maturity) commonly found along roadsides in the LEF. According to Howard (1968), this species recently invaded summits in the forest interior, possibly dispersed by humans. Individuals of this species grow quickly in open habitats and root readily from cuttings, which was one of the reasons we chose it for this study. *Prestoea acuminata var. montana* (Arecaceae), which grows to 10 m tall and 12 cm DBH, dominates the palm brakes slightly below the elevations of the cloud forest, where it represents 61 percent of the individuals (Recher 1970). Seedling density of *P. acuminata* in the Colorado forest association averages more than 23,000 per ha (Weaver 1992).

**EXPERIMENTAL DESIGN.**—As part of a larger experiment on the effect of elevation, population origin, and wind on the primary productivity of tropical wet forests (Fetcher et al. 2000), eight plots were established along the roadside toward Pico del Este area at LEF, Puerto Rico. Each plot was planted with eight plants 1 m apart that were randomly assigned to the four treatments obtained from the combination of two populations (two origins) and two wind treatments (barrier-protected and wind-exposed) in a complete randomized block design. Plants were protected from wind by barriers constructed from clear plastic attached to four wooden stakes (1 m tall) placed around each plant (at ca 30 cm radius). A 5–10 cm space was left at the base of the plastic to enhance air circulation inside each barrier. The barriers were replaced to accommodate the growth of plants, when they were damaged by the wind, or because of the deposition of dirt and growth of epiphylls. During the course of the experiment the plots were watered at 3–4 mo intervals. Although we did not monitor leaf temperatures, the plants were open to the sky, air temperatures were generally moderate, and there was usually some wind circulation; hence we believe that temperatures did not rise significantly inside the barriers. The barriers may have reduced lateral light somewhat, but it is likely that they acted as a neutral density filter and thus did not change light quality significantly. Wind-induced shaking of the plants was not completely eliminated by the barriers, but observations in the field indicated that it was greatly reduced.

Cuttings of *C. erosum* from a low elevation site (approximately 500 m above sea level) and from a high elevation site (more than 900 m above sea level) were previously collected and rooted in a greenhouse in San Juan, Puerto Rico. A maximum of three cuttings were obtained from the same large plant, but most of the cuttings came from individual plants. Seedlings of *P. acuminata* were collected...
from similar areas. Cuttings of *C. erosum* were maintained for 2 mo in a potting mix in the same greenhouse. The two species were planted at the same time. Two months after the initial planting, dead palms (approximately 5%) were replaced.

**Morphological measurements.**—Because of the great differences in their forms, we measured different aspects of the morphologies of the two species. For *C. erosum*, we measured total height, basal stem diameter, stem diameter 10 cm aboveground, branch diameter and length, and branch position (with respect to the length of the main axis). Plants were harvested 18 mo after planting in 1991 and all plant material was separated into leaves, branches, and stems. Leaf area by branch was immediately measured after harvest in a leaf area meter (LI-3100, Licor, Inc., Lincoln, NE, U.S.A.) and the number of branches (NB), the total number of leaves (TNL), and the number of expanded leaves (NEL) were counted.

For *P. acuminata*, entire saplings were harvested 38 mo after planting and transported to the laboratory, where plant parts were separated. Each leaf was cut at the petiole level at the nearest point from the pseudostem. Seedlings of *P. acuminata* produce simple, bifid leaves initially, followed by compound leaves. Leaves were separated into simple (bifid) leaves and pinnately compound leaves. Leaf area, leaf mass, specific leaf mass (SLM), lamina length, and the basal diameter and length of the petiole were measured for every leaf. Lamina length was considered as the mid-vein length or the rachis length for the simple or compound leaves, respectively. The petiole length ratio (PLR) was calculated as the petiole length divided by its basal radius. The leaf length ratio (LLR) was calculated as the lamina length divided by the petiole length.

In a prior study (Fetcher et al. 2000), there was no significant effect of population on several growth parameters in the two species. In addition, studies have shown that altitudinal variation in *P. acuminata* did not demonstrate significant genetic differentiation between populations, probably due to high gene flow (Carromero 1996). In the absence of strong evidence for population effects, data between populations, probably due to high gene flow (Carromero 1996). In the absence of strong evidence for population effects, data between populations were pooled to study the effect of wind protection on the allometry of both plant species.

**Statistical analyses.**—For *C. erosum*, analysis of covariance (ANCOVA) was used to identify effects of treatment on relationships between selected pairs of variables using treatment as categorical variable. For *C. erosum*, the scaling exponents $b$ (slope) of the relationship between log $H$ and log $D$ of main stem, largest branch, and the middle-most branch were calculated by least square regression (LS) and reduced major axis (RMA) regression (bent branches were avoided). RMA regression is more appropriate for analyses when the error due to measurement is approximately the same for both independent and dependent variables (McArule 1988, Cedeno et al. 1996). LS slopes are included for comparison with earlier studies. A modified $t$-test for comparing $b_{RMA}$ between treatments and against the scaling exponents of each model followed equations 9 and 10 from McArule (1988). The analyses were performed at two scales, main stem allometry and single branch allometry. The analysis for the single branches was done by choosing the longest branch and the mid-crown branch from each plant.

For *P. acuminata*, petiole length and basal diameter, laminar area and dry mass, SLM, PLR, and LLR were analyzed by analysis of variance (ANOVA). Analysis of covariance (ANCOVA) was used to identify effects of treatment on relationships between selected pairs of variables using treatment as categorical variable. The slopes of some allometric relationships were also calculated using RMA and the analysis of treatment differences between $b_{RMA}$ followed McArule (1988).

**Results**

**Allometry of Cladium erosum.**—All ANCOVA analyses showed significant relationships between the continuous variables (independent effects, Table 1), but there were not always significant treatment or interaction effects. Protection from wind appeared to produce some changes in the relationship between plant height ($H$) and basal diameter ($D$), although the results were not unequivocal (Table 2). The LS regression between $H$ and $D$ suggested that the basal diameters of wind-exposed plants increased more as plant height increased than did the diameters of protected plants (Table 2). Nevertheless, neither $b$ nor $b_{RMA}$ was significantly different between exposed and protected treatments (Table 2). For the stems of wind-exposed plants $b_{RMA}$ was not significantly different from the scaling exponents of 1 and 2/3, whereas for the barrier-protected plant stems it was different from all three scal-

| Table 1. Probability values resulting from the analyses of covariance for the relationships between several parameters at the whole plant and branch levels of Cladium erosum at Pico del Este grown in two wind regimes. Ind = independent continuous variable, TRT = treatment, Ind $\times$ TRT = interaction, $R^2$ = coefficient of determination, $D$ = stem or branch diameter, $H$ = plant height or branch length, $L A$ = leaf area, $N B$ = number of branches, $N E L$ = number of expanded leaves, $T N L$ = total number of leaves.

<table>
<thead>
<tr>
<th></th>
<th>Independent</th>
<th>Dependent</th>
<th>Ind</th>
<th>TRT</th>
<th>Ind $\times$ TRT</th>
<th>$R^2$</th>
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<tr>
<td>log $H$</td>
<td>log $D$</td>
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<td>0.664</td>
<td>0.570</td>
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<tr>
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<td>log LA</td>
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<td>0.311</td>
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<td>0.914</td>
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<td>0.560</td>
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<tr>
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<td>NB</td>
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<tr>
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<td>0.004</td>
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<tr>
<td>log $H$</td>
<td>log $D$</td>
<td>0.0001</td>
<td>0.223</td>
<td>0.361</td>
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<tr>
<td>log $D$</td>
<td>log LA</td>
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<td>0.988</td>
<td>0.085</td>
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<td><strong>Middle branch</strong></td>
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<tr>
<td>log $H$</td>
<td>log $D$</td>
<td>0.002</td>
<td>0.025</td>
<td>0.024</td>
<td>0.45</td>
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<tr>
<td>log $D$</td>
<td>log LA</td>
<td>0.021</td>
<td>0.051</td>
<td>0.032</td>
<td>0.36</td>
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</tbody>
</table>
TABLE 2. Whole-plant and branch level analyses of the relationship between basal diameter (D) and height or length (H) of plants of Clibadium erosum. The parameters \( a \) and \( b \) are the LS regression intercept and slope of the equation \( \log H = a + b \log D \), and \( R^2 \) is the coefficient of determination of the least squares regression analysis. The columns \( b = 1 \) (geometric similarity), \( b = 2/3 \) (elastic similarity), and \( b = 1/2 \) (constant stress model) represent the t-test comparison for each hypothesis, respectively. The reduced major axis slope (\( b_{RMA} \)) is also presented; different letters in the superscripts indicate significant differences between treatments (\( P < 0.05 \)). The results of ANCOVA for these relationships are in Table 1. For \( R^2 \): ns = non-significant; *, \( P < 0.05 \); **, \( P < 0.01 \).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>( N )</th>
<th>( a )</th>
<th>( b )</th>
<th>( R^2 )</th>
<th>( b = 1 )</th>
<th>( b = 2/3 )</th>
<th>( b = 1/2 )</th>
<th>( b_{RMA} )</th>
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<tr>
<td>Plant stem</td>
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</tr>
<tr>
<td>Exposed</td>
<td>21</td>
<td>0.29</td>
<td>0.55</td>
<td>0.32**</td>
<td>ns</td>
<td>ns</td>
<td>0.05</td>
<td>0.98*</td>
</tr>
<tr>
<td>Protected</td>
<td>27</td>
<td>0.48</td>
<td>0.41</td>
<td>0.32**</td>
<td>0.05</td>
<td>0.002</td>
<td>0.001</td>
<td>0.72*</td>
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<tr>
<td>Largest branch</td>
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<tr>
<td>Exposed</td>
<td>17</td>
<td>0.003</td>
<td>0.63</td>
<td>0.53**</td>
<td>ns</td>
<td>ns</td>
<td>0.01</td>
<td>0.87*</td>
</tr>
<tr>
<td>Protected</td>
<td>24</td>
<td>-0.33</td>
<td>0.78</td>
<td>0.84**</td>
<td>0.05</td>
<td>0.005</td>
<td>0.001</td>
<td>0.85*</td>
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<tr>
<td>Middle branch</td>
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<td></td>
</tr>
<tr>
<td>Exposed</td>
<td>11</td>
<td>-0.66</td>
<td>0.62</td>
<td>0.50*</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>0.88*</td>
</tr>
<tr>
<td>Protected</td>
<td>16</td>
<td>0.61</td>
<td>0.11</td>
<td>0.07**</td>
<td>0.002</td>
<td>0.002</td>
<td>0.001</td>
<td>0.39*</td>
</tr>
</tbody>
</table>

For the mid-crown branches, which were wholly contained within the barriers, both the treatment and the interaction terms were significant; the diameters of wind-exposed branches increased more for a given increase in branch length than did the protected branches (Tables 1 and 2; Fig. 1A). Mid-crown branches inside barriers increased their leaf areas in greater proportion than did the mid-crown branches of wind-exposed trees (Table 1; Fig. 1B). The slope \( b \) was significantly smaller for the protected branches, as was the value of \( b_{RMA} \) (Fig. 1).

In general, stems and branches did not show clear trends in the scaling values. Most values of \( b_{RMA} \) for the wind-exposed branches did not differ from the scaling exponents associated with the geometric and elastic similarity models. The protected treatment produced a greater number of differences from the theoretical values (Table 2). The middle branches supported the expected trend of more slender structures in the protected plants.

ALLOMETRY OF PRESTOEA ACUMINATA.—Using two-way ANOVA, we found significant \( (P < 0.01) \) effects of leaf type (simple or compound) on all variables except for PLR (Table 3). Furthermore, there were effects of the wind-protection treatment on the log-transformed values of petiole length, petiole diameter, leaf area, lamina dry mass, and PLR. Because none of the variables had significant interaction terms, the comparisons of means between treatments were done separately by leaf type for each variable.

For simple leaves, petiole length and PLR were significantly less in the wind-exposed treatment, whereas leaf length ratio was larger (Fig. 2). The other variables did not have significant differences

FIGURE 1. Relationships between the log10 of the diameter of the middle branch and the log10 of the branch length (A) and leaf area (B) of plants of Clibadium erosum grown under barrier-protected (solid lines and filled circles) and wind-exposed (dotted lines and empty circles) conditions. For (A), regression parameters and slope comparisons are given in Table 2. For (B), the least squares regression was \( \log_{10} LA = 0.15 \log_{10} D + 1.98 (R^2 = 0.005, P < 0.84) \) for the wind-exposed plants, and \( \log_{10} LA = 3.69 \log_{10} D - 0.84 (R^2 = 0.40, P < 0.011) \) for the barrier-protected plants. Values of \( b_{RMA} \) for wind-exposed and protected plants were 0.16 and 5.85, respectively (Student’s \( t = 3.84, P < 0.001 \)). Lines shown are from LS regression. ANCOVA results are shown in Table 1.
of means between treatments, but all of them showed a tendency toward a general reduction in the wind-exposed treatments (Fig. 2). For compound leaves, petiole length and diameter, leaf area, and PLR were significantly larger in the protected treatment (Fig. 2). Other variables had higher values in the barrier-protected treatment, but the differences were not significant.

Allometric relationships between pairs of these variables measured on the leaves of *P. acuminata* were compared using ANCOVA with treatment as a categorical variable. All continuous variables were significantly correlated, with the exception of log L versus PLR of simple leaves exposed to wind (Figs. 3A–D). For the simple leaves, the only significant treatment and interaction effects were for the relationship of log D with leaf length ratio (LLR) (data not shown) and between log L with PLR (Fig. 3). Likewise, values of $b_{RMA}$ for simple leaves of exposed and protected plants were not different for any allometric relationships (Table 3).

On the other hand, allometric relationships of compound leaves were significantly affected by the treatment and had significant interaction effects (Fig. 3). Specifically, the ANCOVA for the relationship between log petiole diameter and log petiole length ($R^2 = 0.68$) was significant for the interaction term and both main effects (Fig. 3E, Table 3). The values of $b_{RMA}$ for log leaf area versus petiole diameter and for log PLR versus log petiole length for compound leaves of wind-exposed plants were significantly greater than for the protected plants (Table 3). The relationship between petiole diameter and log leaf area ($R^2 = 0.90$) showed that compound leaves inside the barriers had proportionally smaller lengths or smaller leaf areas with increases in petiole diameter (Fig. 3G, Table 3). The values of $b_{RMA}$ between D and log leaf area were significantly larger for the wind-exposed leaves than for the barrier-protected leaves (Table 3). The relationship between PLR and the log petiole length in the compound leaves indicates that the petiole was disproportionately longer per unit radius in the barrier-protected leaves than in the wind-exposed treatment (Fig. 3H, Table 3).

**DISCUSSION**

**Allometry in *Cladium eramosum***.—Of the three models that predict the scaling exponent of growth between diameter and height, only the geometric similarity model seemed to hold in the most cases for the plants exposed to wind (Table 2). Norberg (1988) suggests that the geometric similarity model describes growth of herbs and small trees, whereas the elastic similarity model is better for explaining the scaling of larger trees. King (1996) and Thomas (1996) also reported that larger trees do not conform to the geometric similarity model. The branches of *C. eramosum* had a scaling exponent similar to the “nonwoody” group of species (including dicot herbs, but not the palms) studied by Niklas (1993), who pointed out the inapplicability of these models when comparing across different plant clades. However, there was not as clear-cut a difference in the scaling of branches of *C. eramosum* as there was at the level of the whole tree. Although we were expecting stems of *C. eramosum* to scale according to the predictions of the geometric similarity model (as previously found by Norberg [1988] for herbs), the small sample size did not permit us to distinguish between the geometric similarity and elastic similarity models (see also Niklas 1994).

On the other hand, allometric relationships from the middle branches showed significant effects of treatment in the relationships between branch diameter and the amount of leaf area supported (Table 1). As expected, wind-exposed branches produced less leaf area than did protected branches (Fig. 1). The main effect of wind damage may be to prevent full leaf expansion (Rushton & Toner 1989). The drag on the plant is mainly determined by the exposed surface area, which produces greater wind resistance that may provoke bending and plant breakage (Vogel 1989). Under windy conditions, reduction in growth of leaf area would reduce breakage of a branch or whole plant, especially in this broad-leaved species.

At the whole plant level, there were fewer leaves per number of branches produced by the wind-exposed plants. This shift in whole-plant allometric pattern could have resulted from a change in the number of modules as the plants grew. The absence of treatment effects on most of the whole-plant allometric relationships in this study and in the individual growth parameters from the previous one (Fetcher et al. 2000) suggest that the physiological and morphological constraints imposed by wind could be transferred to different architectural units (or scales) where the allocation...
of functions may offer greater plasticity to the plant. This explanation has been proposed for the adaptive architectural design of some growth habits. For example, it was found that the allometric relation between tree height and leaf area of *Cecropia obtusifolia* is maintained constant in smaller, younger, nonbranched trees through increments of leaf size, whereas in taller, older, branched trees it is maintained through increments in the number of smaller leaves (Alvarez-Buylla & Martínez-Ramos 1992). Studies based on metameric architecture have found that the distribution of module types is different between evergreen and summer-deciduous matorral species (Ginocchio & Montenegro 1992), which supports the notion that the proportion of modules assigned to different roles depends on the interaction with the environment (Hardwick 1986). Thus, it is possible that a size-dependent developmental factor was involved in the response of *C. erosum* to wind.

**ALLOMETRY IN *PRESTOEA ACUMINATA***.—The comparison of leaf dimensions in saplings of *P. acuminata var. montana* revealed significant effects of leaf type and treatment without significant interaction effects. It is likely that the treatment differences were due to a size-dependent effect because the compound leaves were much larger than the simple leaves. This reflects normal growth
FIGURE 3. Allometric relationships of simple (left) and pinnately compound (right) leaves of *Prestoea acuminata* var. *montana* at Pico del Este. Plants were grown under barrier-protected (solid lines and filled circles) and wind-exposed (dotted lines and empty circles) conditions. Lines shown are from LS regression. Ind, T, and Ind × T represent the source of variation for the continuous independent variable, the treatment, and the interaction effects, respectively. D = petiole diameter, L = petiole length, LA = leaf area, M = leaf mass, PLR = petiole length ratio. ns = nonsignificant, *, P < 0.05; **, P < 0.01.

because the leaf dimorphism represents a sequential pattern in the development of palm leaves. Differences due to wind exposure were less common for the simple leaves than for compound leaves. Simple leaves from the wind-exposed treatment had smaller petiole lengths and values for PLR, whereas LLR tended to be larger; there were no differences in other variables. On the other hand, the compound leaves from the wind-exposed treatments produced smaller means in four of seven variables and LLR also showed the same tendency (Figs. 2 and 3).

The general reduction of leaf dimensions in the wind-exposed plants coincides with previous observations of the reduced growth produced by mechanical perturbations such as wind (Grace 1988, Rushton & Toner 1989). In the simple leaves, petiole length, LLR, and PLR were affected by the protected treatment, but leaf area and
petiole diameter were not (Fig. 2). The PLR can be interpreted as a slenderness ratio (Niklas 1992, 1994), where higher values indicate that taller (longer) structures are supported by proportionally smaller basal diameters or radii. As expected, mean PLR was significantly higher (more slender) for petioles of both leaf types in barrier-protected plants, which means that simple and compound leaves maintained a mechanically safer petiole form (less slender) in the wind-exposed plants. Thus, petioles of *P. acuminata* can respond to wind in a way similar to plant stems, by becoming smaller and thicker (Jaffe 1980). Protection from the wind did not detectably affect leaf area in the simple leaves; this could be due to the smaller sizes of these structures. On the other hand, it has been shown that compound leaves have lower drag when compared to simple leaves (Vogel 1989). The compound trait may permit greater plasticity for leaves to adjust their growth to prevailing wind conditions.

As plants grow, the shape and the material properties of organs and tissues change during their development such that they can support themselves and support external loadings such as wind (Niklas 1990). In addition to supporting this argument, this paper also suggests that alteration of the allometric relationships of plant parts, organs, or plant modules (leaves of *P. acuminata* and branches of *C. erosum*) and alteration of the number of parts (leaves and branches of *C. erosum*) could be viable strategies to compensate for the effects of wind or other mechanical stresses.

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**LITERATURE CITED**


