

## LETTER

# Universal foliage-stem scaling across environments and species in dicot trees: plasticity, biomechanics and Corner's Rules

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## Abstract

Trees range from small-leaved, intricately branched species with slender stems to large-leaved, coarsely branched ones with thick stems. We suggest a mechanism for this pattern, known as Corner's Rules, based on universal scaling. We show similar crown area–stem diameter scaling between trunks and branches, environments, and species spanning a wide range of leaf size and stem biomechanics. If crown and stem maintain metabolically driven proportionality, but similar amounts of photosynthates are produced per unit crown area, then the greater leaf spacing in large-leaved species requires lower density stem tissue and, meeting mechanical needs, thicker stems. Congruent with this scenario, we show a negative relationship between leaf size and stem Young's modulus. Corner's Rules emerge from these mutual adjustments, which suggest that adaptive studies cannot consider any of these features independently. The constancy of scaling despite environmental challenges identifies this trait constellation as a crucial axis of plant diversification.

## Keywords

Adaptation, allometry, biomechanics, Corner's Rules, leaf size, mixed models, phenotypic accommodation, phenotypic plasticity, scaling, stem size.

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## INTRODUCTION

Organism–environment correlations and covariation between traits across species are the fundamental sources for inferences of adaptation (Lewontin 1977; Larson & Losos 1996). Within the woody plants, cross-species patterns of covariation between characters have been identified on regional and even global scales (Carlquist 1984; Westoby *et al.* 2002; Rosell *et al.* 2007). A central goal of plant evolutionary ecology is to generate hypotheses regarding the mechanisms underlying these patterns (McGill *et al.* 2006; Wright *et al.* 2007). For example, a negative relationship between secondary xylem vessel diameter and the number of vessels per unit xylem cross section is ubiquitous, both within and between species. This relationship is generally interpreted as involving an adaptive tradeoff between rapid conduction in wide vessels and embolism resistance in narrow ones (Carlquist 2001). Many such patterns have been repeatedly observed in different areas of the world and in different plant groups but lack convincing causal hypotheses.

The leaf size–twig size spectrum is one of the earliest-known and best-documented of these global patterns, and is also one that lacks a satisfactory mechanistic explanation (Corner 1949; Bond & Midgley 1988; Cornelissen 1999; Westoby *et al.* 2002; Preston & Ackerly 2003; Westoby & Wright 2003; Wright *et al.* 2007). Also known as Corner's Rules, this spectrum has two main components. First, individuals with large leaves have thick twigs, whereas those with small leaves have thin twigs. Second, thick-twigged trees branch sparingly, whereas slender-twigged trees branch intricately (White 1983; Ackerly & Donoghue 1998). Virtually all authors agree that greater spacing between leaves and sparse branching could be explained by selection favouring avoidance of self-shading as leaf size increases (White 1983; Ackerly & Donoghue 1998; Westoby *et al.* 2002; Sun *et al.* 2006). In addition, it is clear that stems must meet the conductive and mechanical demands of the leaves they support (White 1983; Westoby *et al.* 2002; Wright *et al.* 2006), so large leaves cannot be borne on slender stems (cf. Cornelissen 1999). However, the ideas just outlined offer no reason to think that a thick stem could not meet the

mechanical and conductive needs of small leaves, yet such a combination is probably observed only in a few extreme xerophytes. Current hypotheses also do not explain why densely branched, thick-stemmed species should be virtually non-existent (White 1983; Ackerly & Donoghue 1998; Westoby *et al.* 2002; Wright *et al.* 2007). We suggest that, to explain the pervasive pattern of trait covariation that constitutes Corner's Rules, we must identify a pervasive underlying mechanism, one that explains not only why the pattern is observed but also why alternative trait combinations are not observed.

This paper proposes a novel mechanism for Corner's Rules involving two main components. The first is the role of universal metabolic scaling between leaves and stems (West *et al.* 1999; Enquist 2002), and the second is the expectation that a given amount of crown area should assimilate more or less the same amount of carbon across species (Enquist *et al.* 1999). 'Universal scaling' refers to organismal attributes that change in predictable ways with size across many groups. It is thought to be the result of natural selection acting in similar ways on similar organismal traits in response to physical constants that apply to all organisms (West *et al.* 1997, 2000). We propose that Corner's Rules originate from the ways in which differing selective environments shape adaptive trait combinations via metabolic scaling between foliage and stems and the dynamic interplay between stem tissue density, mechanical behaviour, storage and fluid conductivity, resulting in a similar amount of carbon assimilation per unit crown area across species (Enquist *et al.* 1999). We test both of the main components of our model here.

### Universal crown–stem scaling

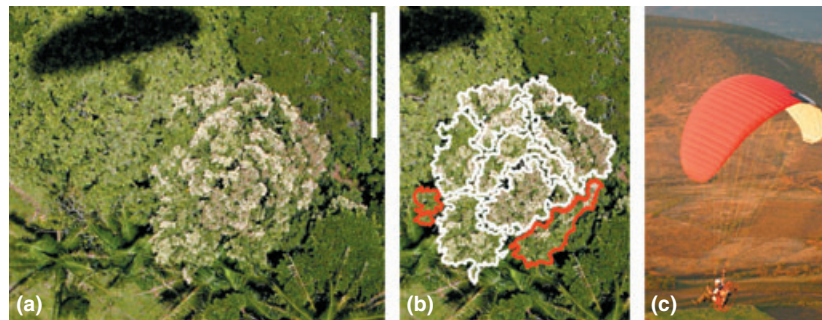
We test the prediction that stems should scale universally with the foliage that they support, and examine the role of

such scaling in producing Corner's Rules. Scaling between leaves and stems is expected partly as a result of the mechanical and conductive demands of a mass of leaves on its stem. It is also the result of the metabolic demands of the living cells of the wood and bark on the leaves. We assume that both leaf area as well as metabolically active wood and bark cells are maximized as a function of one another (Niklas 1994; Enquist 2002; Enquist & Niklas 2002; Wright *et al.* 2006).

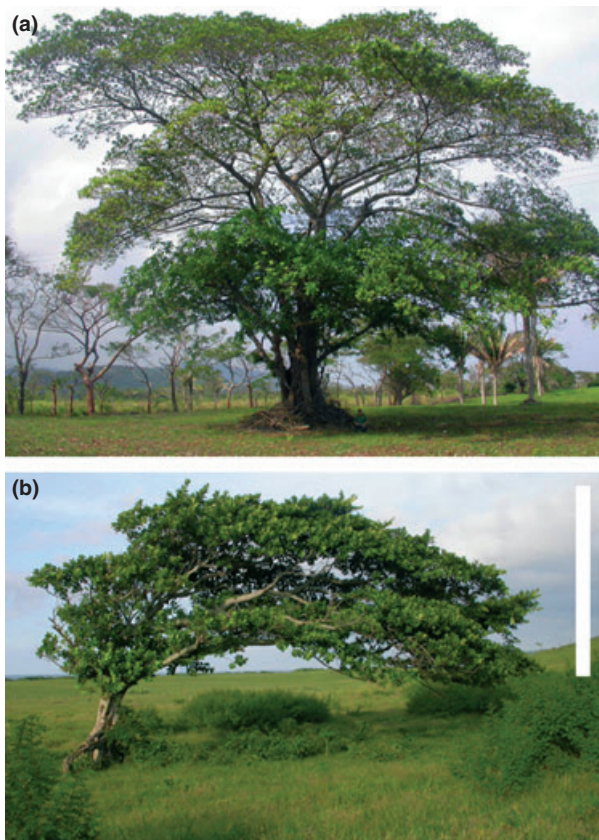
For universal foliage-stem scaling to be a viable mechanism for Corner's Rules, it must be truly pervasive, that is, apply within individuals, across individuals within species, and across species. To test for such scaling, we examined the relationship between stem diameter and crown area, the polar-projected area of the polygon described by the foliage presented to the sky by a given stem, i.e. masses of leaves as seen from aloft (Fig. 1). The arrangement of branches and leaves that trees present to the sun should be a feature of fundamental functional and adaptive importance (Horn 1971). A view from above allowed us to measure crown area–stem diameter scaling from the whole trunk to branches as a means of testing for pervasive scaling.

We examined three main universal scaling predictions. First, scaling arguments imply that, although differences between individuals across environments may be extreme (Fig. 2), natural selection should favour ontogenetic mechanisms that maintain crucial trait relationships in the face of environmental challenges (cf. West *et al.* 1997, 1999). We asked whether crown area–stem diameter scaling differs between environments or remains invariant within species between the drastically different shapes of trees in sheltered and salt-pruned coastal situations (Fig. 2).

Second, universal scaling predicts a constancy in the fractal nature of tree form (West *et al.* 1999; Enquist 2002). That is, not only are trees expected to fill space with fractionary rather than integer dimensions, but they should



**Figure 1** Tree crown mapping. (a) White-flowered tree at centre is *Cordia alliodora* in mixed forest; the aircraft shadow can be seen at upper left. (b) This crown is composed of two trees, one of which is separated into two sections (red polygons). The crowns and constituent branches were decomposed into series of nested polygons. (c) We captured these images using a slow, portable aircraft called a powered paraglider (photo Jim Webb). Scale bar = 9.5 m in (a) and (b).



**Figure 2** Phenotypic plasticity in shape and size of sheltered vs. salt-pruned trees: *Ficus tecolutensis*. (a) Sheltered individual showing large stature and symmetry of the flat crown about the trunk. Darker leaves toward the base are of the strangler *F. obtusifolia*. (b) *F. tecolutensis* on a coastal flat showing the smaller stature and cantilevered crown of salt-pruned individuals. Scale bar = 9.5 m in A, 7 m in B.

also be self-similar. That is, as a result of selection favouring minimization of transport distances and maximization of exchange surfaces, we expect similar relationships between the foliage of the entire crown of a tree and the trunk as between individual branches of the same tree and the leaves they support (West *et al.* 1997). We tested the idea of self-similarity in tree architecture with the prediction that the crown area–stem diameter relationship should be similar between trunks and branches.

Third, we tested perhaps the most improbable-sounding universal scaling prediction, that despite the remarkable range of tree shapes and sizes, all species should show similar crown area–stem diameter scaling exponents (West *et al.* 1999; Enquist 2002). To test this prediction we sampled tree diversity with 11 species spanning the core eudicots, the clade containing the majority of the flowering plants. The species selected spanned a wide range of leaf size and stem mechanical properties, and included

representatives from Caryophyllales, sister to the rest of the core eudicots, as well as Rosales, Sapindales, Ericales and the Euasterids. We tested the expectation that crown area–stem diameter scaling should be similar across species, even though leaf size and stem mechanical properties range over orders of magnitude, variation that would easily seem capable of influencing crown–stem proportionality (Niklas 1992; King 1998; Niinemets *et al.* 2006).

### Similar rates of carbon assimilation across species

In addition to testing for universal foliage–stem scaling, we provide a comparative test of the second major component of our proposed mechanism, the assumption that similar amounts of carbon should be assimilated per unit of crown area per unit time across species (Enquist *et al.* 1999). This property is likely to be a major contributor to Corner's Rules because, for comparable crown areas, large-leaved species have greater rates of stem elongation than small-leaved species due to the greater leaf spacing in larger leaved species (Wright *et al.* 2006). Despite different rates of elongation, all should have at their disposal similar amounts of photosynthates per unit crown area, meaning that fast-growing species must allocate less dry mass per unit of stem volume. We test the expectation that large leaves should be associated with stem tissues with less material per unit volume and low mechanical resistance to bending (Wright *et al.* 2007; Swenson & Enquist 2008). We argue that (1) if crown area scales with stem diameter and (2) if selection maintains a constant carbon assimilation rate per unit of crown area, then the spectrum of possible leaf size–twig size combinations is severely constrained and the pattern known as Corner's Rules emerges.

### METHODS

Our study site was the coastal plain below the Los Tuxtlas research station of the Instituto de Biología in Veracruz, Mexico, in remnants of tropical moist forest that provided a phylogenetically and morphologically diverse range of species in salt-pruned and sheltered locales (Table 1). We classed trees into two microsite types: coastal situations subject to salt laden sea breezes that pruned windward branches, or situations sheltered from these breezes. Trees ranged in distance from the ocean from 0.05 to 2 km, and all occurred on fine volcanic soil. Sheltered plants were often found on the leeward sides of coastal forest patches that included salt-pruned trees on their windward sides. Because of the proximity of the trees studied, any phenotypic differences observed are almost certainly due to the presence or absence of salt pruning (Boyce 1954) and not to other environmental differences. Voucher specimens were deposited at the National Herbarium of Mexico (MEXU).



**Table 1** Phylogenetic and morphological diversity of the sampled species

| Species and authority                            | Family        | Order/major clade | Leaf phenology, morphology | Leaf(let) length, mm | $E_{\text{stem}}$ (MPa) |
|--|---------------|-------------------|----------------------------|----------------------|-------------------------|
| <i>Coccoloba hondurensis</i> Lundell             | Polygonaceae  | Caryophyllales    | E, S                       | 6.8                  | 4311.0                  |
| <i>Cordia alliodora</i> (Ruiz & Pav.) Oken       | Boraginaceae  | Euasterid I       | D, S                       | 13.5                 | 3410.7                  |
| <i>Cordia stenoclada</i> I. M. Johnst.           | Boraginaceae  | Euasterid I       | D, S                       | 9.0                  | 3907.5                  |
| <i>Cupania glabra</i> Sw.                        | Sapindaceae   | Sapindales        | S, C                       | 6.8                  | 5273.4                  |
| <i>Ficus obtusifolia</i> Kunth                   | Moraceae      | Rosales           | E, S                       | 16.0                 | 2243.7                  |
| <i>Ficus tecolutensis</i> (Liebm.) Miq.          | Moraceae      | Rosales           | S, S                       | 15.9                 | 3325.2                  |
| <i>Ficus trigonata</i> L.                        | Moraceae      | Rosales           | E, S                       | 16.7                 | 2281.3                  |
| <i>Lonchocarpus schiedeanus</i> (Schltdl.) Harms | Fabaceae      | Rosales           | D, C                       | 4.0                  | 4510.9                  |
| <i>Pouteria squamosa</i> Cronquist               | Sapotaceae    | Ericales          | E, S                       | 13.4                 | 2951.3                  |
| <i>Spondias radlkoferi</i> Donn. Sm.             | Anacardiaceae | Sapindales        | D, C                       | 12.4                 | 1981.8                  |
| <i>Trichilia bavanensis</i> Jacq.                | Meliaceae     | Sapindales        | E, C                       | 6.3                  | 3179.1                  |

Leaf phenology and morphology are indicated as follows: the letter preceding the comma indicates whether the species is evergreen (E), deciduous (D), or semideciduous (S; the ground becomes visible through the crown in the dry season, but not all leaves are lost); the letter following the comma distinguishes simple (S) from compound (C) leaved species.

From 2003 to 2007, we took digital photographs from a powered paraglider 100 m above the canopy (Fig. 1), and measured branch diameters with the aid of rappelling gear. We mapped each measured branch as seen in the canopy photograph and delineated foliage contours on the digital images using Adobe Photoshop (Fig. 1b) and converted them to black islands of foliage (see also Fig. S1). The brush size in each case corresponded to 2× mean leaf length of the individual, based on measurements of  $c. 35$  leaves (Table 1). We measured leaflet lengths for compound-leaved species, because leaflets represented the terminal photosynthetic units. We measured crown area using IMAGEJ v. 1.39 d (<http://rsb.info.nih.gov/ij/>), thresholded at 0 white and 134 black, with all images treated at the same resolution. This approach resulted in many branch data per tree and few measurements of total crowns. Therefore, we measured  $c. 25$  additional individuals per species, using the major and minor axes of the crown ellipse. We coded each stem as a main trunk or a branch, measuring the diameters of trunks and branches and their associated crown areas from 355 individuals, with 578 crown areas ranging from 683 to 0.03 m<sup>2</sup> from stems spanning a range in diameter of 163–0.5 cm (data are available in Appendices S1 and S2).

To determine stem biomechanical properties, we collected three-five randomly selected branches from three-four trees of each species. These branches were divided into one-four segments  $c. 45$  cm in length and 2 cm in diameter for a 1 : 20 diameter: length ratio (Vincent 1992). Segments were wrapped in plastic and kept cool, transferred to the laboratory, and tested on the day subsequent to collection in three-point bending with an Instron 3345 mechanical test machine with a 5 kN load cell (Instron Corporation, Canton, MA, USA). Stem Young's moduli ( $E_{\text{stem}}$ ), which varied from 1981.8 to

5273.4 MPa (Table 1), were calculated using INSTRON SYSTEM IX/s software, using the average of the major and minor diameters of both segment extremes in the calculation of the second moment of area  $I$  (Niklas 1992).

### Statistical methods: translating scaling predictions into statistical terms

Our inferences were based on the fitting of a mixed multiple regression model predicting crown area based on stem diameter and other variables, using all of our data. The inclusion of these other variables involved a multi-step process which we detail here, before highlighting the most important points in Results. We begin by describing how we translated our predictions into statistical terms.

We used interaction terms in the multiple model to test for similar crown area–stem diameter scaling in three situations: between trunks and branches, salt-pruned and sheltered plants, and between species. To test for a similar crown area–stem diameter relationship between branches and trunks, we incorporated a binary stem type variable (trunk/branch) and an interaction term defined as the product between stem diameter and stem type into the model. A significant interaction term would indicate differing crown area–stem diameter scaling between trunks and branches. Similarly, to test for common scaling between environments, we included a binary environment variable (salt-pruned/sheltered), along with the environment  $\times$  stem diameter interaction term. We used the same approach to test for scaling differences between species.

Our single global model was more efficient than the alternative of fitting and comparing separate models for each species, because testing for differing intercepts and

slopes was straightforward and additional statistical techniques were unnecessary (see Appendices S3 and S4; Kleinbaum *et al.* 2007). Also, parameters common to all the models were estimated once using all the data (Goldstein 2003). This is an advantage because the separate models approach uses relatively few data for each model and can inflate Type I error rates. Appendix S3 provides R code (<http://www.R-project.org>) for fitting multiple models and models for each species, the results of which are compared in Appendix S4.

### Intermediate models

Before testing the significance of the interaction terms, it was necessary to fit several intermediate models. Because species are categorical, we represented them as dummy variables. However, we also wished to test the prediction that crown area–stem diameter scaling should be similar across species despite variation in leaf size and  $E_{\text{stem}}$ . We took both  $E_{\text{stem}}$  and leaf size to be constant within species, so including species along with these variables would be a source of collinearity. Of these three variables, species was the most strongly associated with crown area and was essential for testing the prediction of constant scaling between species. Therefore, we included species in the preliminary model, along with  $\ln$  stem diameter, stem type, and environment, as explanatory variables of  $\ln$  crown area.

Comparing the signs of the regression coefficients and the significance levels of the dummy variables, three groups of species differing in mean crown area ( $y$ -intercept) emerged. Group A was made up of *Trichilia havanensis*, *Coccoloba hondurensis*, *Pouteria squamosa* and *Spondias radlkoferi*; group B, *Ficus trigonata*, *Cupania glabra* and *Lonchocarpus schiedeannus*; and group C, *Cordia stenoclada*, *C. alliodora*, *F. obtusifolia* and *F. tecolutensis*. These groups did not correspond to phylogenetic affinity, phenology, leaf size, or  $E_{\text{stem}}$ , but instead represented size classes, with category A comprising the species with the smallest mean crown area, B intermediate ones and C the largest (see also Appendix S4). With considerably fewer parameters, this model with species groups was easier to interpret and led to a markedly smaller number of interaction terms. Grouping species also allowed us to incorporate leaf size and  $E_{\text{stem}}$ , showing that neither played a significant role in explaining variation in crown area (see Appendix S4).

Having identified the main model effects, we could now include all possible first-order interaction terms, and test our predictions through their significance. Of these, only stem type  $\cdot$  species group A, and stem diameter  $\cdot$  species group A were significant (Table 2). Stem type  $\cdot$  stem diameter was not significant ( $P = 0.96$ ), nor was environment  $\cdot$  stem diameter ( $P = 0.12$ ), showing constant scaling between stem types and environments.

**Table 2** Estimated linear mixed model describing the relationship between crown area and stem diameter while accounting for the effect of stem type (trunk vs. branch), environment (salt-pruned/sheltered) and species group

| Variable                       | Coefficient (SE) | P-value (95% CI)          |
|--------------------------------|------------------|---------------------------|
| $y$ -Intercept                 | -2.09 (0.10)     | < 0.0001 (-2.29 to -1.88) |
| $\ln$ Stem diameter            | 1.63 (0.03)      | < 0.0001 (1.58–1.68)      |
| Stem type (trunk)              | 0.32 (0.07)      | < 0.0001 (0.19–0.46)      |
| Environment (salt-pruned)      | -0.16 (0.05)     | 0.0015 (-0.26 to -0.06)   |
| Species group (C)              | 0.27 (0.06)      | < 0.0001 (0.15–0.39)      |
| Species group (A)              | -0.98 (0.19)     | < 0.0001 (-1.36 to -0.60) |
| Stem type $\cdot$ Group A      | 0.37 (0.14)      | 0.0105 (0.09–0.66)        |
| $\ln$ Diameter $\cdot$ Group A | 0.14 (0.05)      | 0.0023 (0.05–0.23)        |

For binary variables, the category shown in parentheses was coded as one.

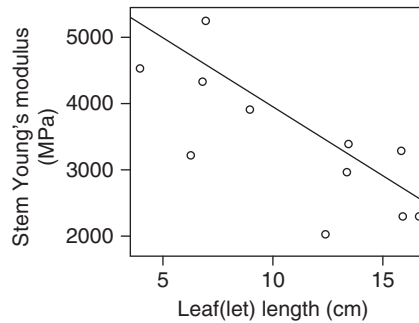
SE, standard error; CI, confidence interval.

### Final model

All of the parameters mentioned to this point were of the type known as fixed effects. Our models also included a random effect, which allowed us to take into account that branches within the same tree are likely to resemble one another more than branches from other individuals, a nested structure potentially violating assumptions of independence among data. Models with fixed and random effects, called mixed models, permit the variance to be partitioned into different levels to take into account this possible non-independence (Raudenbush & Bryk 2002; Goldstein 2003). Moreover, we included separate error terms for trunks and branches because, unlike branches, the majority of trunk crowns were measured using ground based methods, likely violating the assumption of homogeneous variance. The addition of these random terms significantly improved the fit of the model. The product of the procedure described above was our final model predicting crown area–stem diameter scaling between environments, stem types, and species, which had the general form:

$$y = \beta_0 + \sum \beta_j x_j + \beta_k x_j x_l + u_r + \text{trunk } \varepsilon_t + \text{branch } \varepsilon_b \quad (1)$$

The response variable was the  $\ln$  crown area (hereafter simply crown area) supported by a given stem. The systematic component of the model was defined by the explanatory variables,  $x_j$ , and consisted of the intercept, the main effects, and the first-order interactions. The random component of the model was defined by the random effect for trees,  $u_r$ , and the error terms for trunks,  $\varepsilon_t$ , and branches,  $\varepsilon_b$ . The random effect and the error terms were considered mutually independent random variables of normal distribution, zero mean, and common unknown variance (Goldstein 2003).



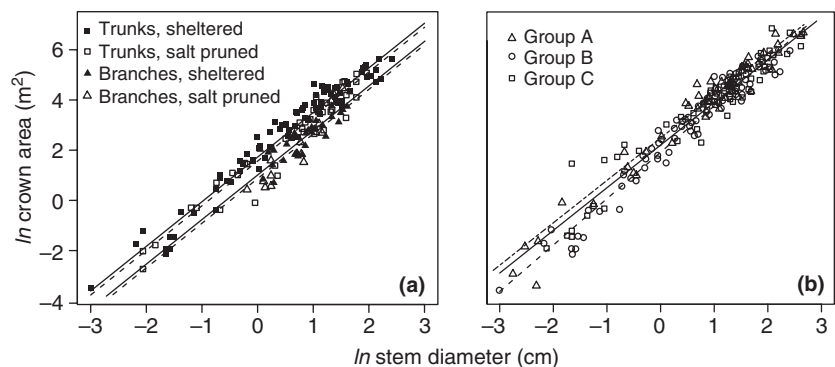
**Figure 3** Stem Young's modulus is negatively related to leaf size. Given universal crown area–stem diameter scaling, this negative relationship is congruent with the hypothesis of similar rates of carbon assimilation per unit crown area across species regardless of leaf size.

## RESULTS

The final estimated mixed model is shown in Table 2. This model did not include  $E_{\text{stem}}$  or leaf size, implying that, no matter how flexible or stiff the stem material of a given species, a stem of a given diameter supported the same crown area (Appendix S4). Similarly, whether with few large leaves or many small ones, stems of a given diameter bore similar crown area. Although  $E_{\text{stem}}$  and leaf size did not predict crown area, an ordinary least-squares regression showed that they were significantly related to one another (Fig. 3,  $n = 11$ ,  $F_{1,9} = 11.32$ ,  $P = 0.008$ ,  $R^2 = 0.56$ ,  $\beta_{\text{leaf size}} \pm \text{SE} = -170.08 \pm 50.54$ ,  $P = 0.008$ ), congruent with the notion that similar crown areas produce similar amounts of photosynthates per unit time.

Across environments, we found significantly smaller crown areas in salt-pruned individuals ( $P = 0.002$ ; Tables 2 and 3) along with patently different shapes between sheltered and salt-pruned trees (Fig. 2). Nevertheless, no matter how divergent salt-pruned and sheltered individuals were, the scaling relationship between crown area and stem diameter was maintained within the species of each group

**Figure 4** Crown area–stem diameter scaling relationships across environments and species. (a) The crowns of trunks and branches, both salt-pruned and sheltered, scaled with stem diameter with different  $y$ -intercepts but identical slopes. Species were classified into three groups; this example is given from the A species group. (b) Groups B and C shared a slope of 1.63, slightly, but significantly, different from that of group A at 1.78. Data shown are from trunks of sheltered trees.



**Table 3** Slopes and intercepts for salt-pruned and sheltered trunks, and branches of all three species groups

| Species group | Stem type | Environment | Slope (95% CI)   | Intercept |
|---------------|-----------|-------------|------------------|-----------|
| A             | Trunk     | Sheltered   | 1.78 (1.70–1.85) | –2.40     |
|               | Trunk     | Salt-pruned |                  | –2.53     |
|               | Branch    | Sheltered   |                  | –3.07     |
|               | Branch    | Salt-pruned |                  | –3.23     |
| B             | Trunk     | Sheltered   | 1.63 (1.58–1.68) | –1.77     |
|               | Trunk     | Salt-pruned |                  | –1.93     |
|               | Branch    | Sheltered   |                  | –2.09     |
|               | Branch    | Salt-pruned |                  | –2.25     |
| C             | Trunk     | Sheltered   |                  | –1.49     |
|               | Trunk     | Salt-pruned |                  | –1.65     |
|               | Branch    | Sheltered   |                  | –1.82     |
|               | Branch    | Salt-pruned |                  | –1.98     |

CI, confidence interval; group A, *Trichilia havanensis*, *Coccoloba hondurensis*, *Pouteria squamosa*, *Spondias radlkoferi*; group B, *Ficus trigonata*, *Cupania glabra*, *Lonchocarpus schiedeana*; group C, *Cordia stenoclada*, *C. alliodora*, *F. obtusifolia*, *F. tecolutensis*.

(Fig. 4a). The final model did not include an interaction term between stem diameter and stem type, implying that crown area–stem diameter scaling did not differ between trunks and branches. Across species, crown area scaled with stem diameter with a mean slope of  $c. 1.7$ ; the slope was 1.78 for the four species with smallest crown area and 1.63 for the remainder (Fig. 4b, Table 3). Although very similar, these slopes were significantly different given that the 95% confidence interval for the difference of the two scaling parameters (0.05, 0.23) did not include zero.

## DISCUSSION

### Perturbation, plasticity, and universal scaling

Given the strikingly different appearances between sheltered and salt-pruned trees (Fig. 2), and significantly smaller crown areas in salt-pruned individuals, it would not have

been surprising to find equal disparity in foliage-stem scaling between environments. Nevertheless, no matter how divergent the overall appearances of salt-pruned and sheltered individuals, the crown area–stem diameter scaling relationship was identical (Fig. 4a).

Identical scaling between microsites raises the question of how these constant relationships are maintained even as other features vary with environmental differences and disturbance (e.g. strangler fig attack on tree in Fig. 2a, broken branches at left in Fig. 2b). Developmental canalization is often invoked to explain features that are consistently produced despite perturbation during ontogeny (Waddington 1953; cf. Murren 2002). In canalized traits, even though perturbations may have the potential to deviate ontogeny, connections between elements (Waddington's 'genes') result in areas of developmental space that are inaccessible, represented pictorially as ridges in a landscape. In such diagrams, valleys represent the most likely, easily accessed paths through developmental space. Although the regression slopes that we recovered represent clear indications of a preferred ontogenetic path despite the perturbing effects of differing environments, canalization cannot explain the allometry we observed. This is because the foliage area–stem size ontogenetic landscape is a flat one: perturbations, e.g. wind breakage or gnawing animals, constantly deviate the 'ideal' crown area–stem size relationship. If no ridges prohibit movement to any part of this space, a mechanism other than canalization must be responsible for maintaining the favoured scaling relationship.

Phenotypic plasticity is usually thought of as manifested by different morphologies in different environments. However, plasticity has a counterpart role in the buffering of environmental challenges, actively maintaining crucial relationships between parts. This aspect of plasticity is known as phenotypic accommodation (West-Eberhard 2003). With respect to the crown–stem relationship, this ontogenetic buffering includes replacement of lost foliage by rapid shoot growth, and replacement of wounds to the trunk by locally accelerated cambial activity (Hejnovicz 1997; Gibert *et al.* 2006; Kramer 2006; Schulgasser & Witztum 2007). Recent studies show evidence for phenotypic accommodation in a variety of other stem traits, including hydraulics, biomechanics, and biomass accumulation rates (Tateno & Bae 1990; Weitz *et al.* 2006; Rosell & Olson 2007; Zeleznik 2007). Within species, the question of how ontogenetic buffering mechanisms maintain crown–stem scaling and other vital proportionalities offers a nexus to unite studies of signalling and growth regulation in a single adaptive theme (Niklas 2005; Telewski 2006). Across species, similar patterns of crown–stem scaling provide a mechanistic account for the leaf size–stem size spectrum.

### Universal foliage-stem scaling and Corner's Rules

We show that crown area scales similarly across species separated by some 100 million years despite marked variation in leaf size and stem biomechanics. We predicted this scaling based on the expectation that a given amount of crown area should require a similar amount of stem conductive, mechanical, and storage tissue whether it is a single large leaf or many small ones (West *et al.* 1999; Enquist 2002). The living cells of the trunk and roots require a certain amount of leaves as photosynthate sources, a metabolic dependency that presumably determines the 'ideal' relationship between leaves and the rest of the plant (Niklas 1992; Westoby & Wright 2003; cf. Kruger & Volin 2006). Despite resembling one another closely in their crown–stem proportionalities (Tables 2 and 3; Fig. 4), the species studied here differed in important ways, most notably in stem biomechanics and leaf size (Table 1).

Although crown area–stem diameter scaling is similar in species with different leaf sizes, species with larger leaves bear them more widely spaced than do those with small leaves (White 1983). Greater leaf spacing requires greater rates of stem elongation. However, trees of all leaf sizes fix similar amounts of carbon per unit of crown area per unit time (Enquist *et al.* 1999), a situation with important mechanical repercussions. If similar crown areas produce only a given amount of photosynthates per unit time regardless of leaf size, then the greater stem elongation associated with leaf spacing in large-leaved species must be accomplished by lower stem tissue density than in smaller leaved species of similar crown area (Enquist *et al.* 1999; cf. Valladares *et al.* 2002). Stem tissue density is positively associated with  $E_{\text{stem}}$  (Niklas 1992; Swenson & Enquist 2008), so that species with stems that elongate rapidly have more flexible tissue than do those that elongate slowly. A stem with low-density tissue obtains mechanical viability via increased diameter and abrupt taper relative to one with dense tissue (Niklas 1992). This relationship can be expressed by the mechanical properties of stem materials as described by Young's modulus  $E_{\text{stem}}$ , and by stem second moment of area  $I_{\text{stem}}$ , which describes the deployment of material in space in terms of how well-placed it is to resist bending (Niklas 1992). The product  $EI_{\text{stem}}$  describes the mechanical behaviour of a branch as a whole in bending. For a given  $EI_{\text{stem}}$ , branches with low  $E_{\text{stem}}$  must be thicker, that is, have higher  $I_{\text{stem}}$ , than branches with high  $E_{\text{stem}}$ . At the same time, branches should be shorter, though petioles longer, in species of low  $E_{\text{stem}}$  (King 1998; Niinemets *et al.* 2006). Because large leaves are borne widely spaced on thick stems, they should be associated with rapid stem extension rates, low stem tissue density, and low  $E_{\text{stem}}$  (Pickup *et al.* 2005; Wright *et al.* 2006, 2007; Swenson & Enquist 2008), an expectation we confirmed (Fig. 3).



Our data are compatible with the two main predictions of our proposed mechanism underlying Corner's Rules. We interpret the negative leaf size– $E_{\text{stem}}$  relationship as congruent with the idea that similar amounts of carbon are fixed per unit of crown area across species, and we confirmed our predictions of similar crown–stem scaling between trunks and branches, environments, and species. Universal metabolic crown–stem scaling together with similar rates of carbon fixation per crown area across species explain why a given tree crown may be composed of many small leaves borne on stems of high-density tissues, gradual taper, and slow stem growth, or composed of few large leaves on stems of low density, abrupt taper, and rapid stem growth. Our hypothesis provides a testable causal account for Corner's Rules, in addition to explaining the link between wood density, leaf size and stem growth rate, a relationship not traditionally regarded as part of Corner's Rules (Westoby & Wright 2003; Wright *et al.* 2006; cf. Swenson & Enquist 2008).

#### Underdetermination and specific scaling values

Our study involved predictions of similar scaling between branches and trunks, and across environments and species, but was not predicated on any specific scaling value. However, most universal scaling studies focus on these values because different constants can imply differing underlying causes (West *et al.* 1999; Reich *et al.* 2006). Studies including ours report constants between crown area or total leaf area and stem diameter or area in the range of 1.2–1.9 (Table 3; Preston & Ackerly 2003; Westoby & Wright 2003; Muller-Landau *et al.* 2006; Sun *et al.* 2006). These data can support both an inference of slightly negative leaf area–leaf mass allometry as well as one suggesting isometric or slightly positive allometry, a difference with important evolutionary consequences. We present these different interpretations as an example of underdetermination, when empirical evidence is compatible with more than one explanation (Dietrich & Skipper 2007).

On one hand, our results can be interpreted as suggesting that crown area is proportional to leaf area over all size classes, leading to a pattern of 'diminishing returns'. This scenario implies that ever greater investment in leaf biomass brings ever smaller increments in important leaf traits such as leaf area (Niklas *et al.* 2007; Niklas & Cobb 2008). That is, if instead of the intuitive leaf area  $\propto$  leaf mass (cf. Sun *et al.* 2006), leaf area  $\propto$  leaf mass<sup>*c*</sup>, where  $0 < c < 1$ , then ever greater investment in leaf mass will bring proportionally ever smaller increases in leaf area. Such negative allometry in photosynthetic area with increasing leaf mass would represent an important upper bound to plant function across habitats (Niklas *et al.* 2007; Niklas & Cobb 2008; cf. Milla & Reich 2007). Based on our results, crown area  $\propto$

stem diameter<sup>7/4</sup>; assuming that leaf mass  $\propto$  stem diameter<sup>2</sup> (Niklas 1994; Enquist 2002), then crown area (and leaf area)  $\propto$  leaf mass<sup>7/8</sup>, a scaling exponent  $< 1$  and consistent with diminishing returns. Critically, this inference is based on the assumption that leaf area  $\propto$  crown area, suggested by our finding of identical scaling between branches and trunks (Fig. 4a, Tables 2 and 3; cf. West *et al.* 1999). If trees are self-similar, with each meristem and branch segment maintaining similar relationships with respect to neighbours, it could be expected that the proportion of self-shaded leaves per unit crown area remains constant across tree size classes, leading to leaf area–crown area isometry and an inference of diminishing returns.

On the other hand, another plausible interpretation leads to a different inference regarding leaf area–leaf mass proportionality. Above we assumed that leaf area  $\propto$  crown area, but if canopies become deeper with increasing size, it is possible that degrees of self-shading could also become larger, that is, the amount of leaf area per unit crown area increases with increasing plant size (cf. Horn 1971). Congruent with this idea is that our species group A, which comprised the species with smallest crown areas, also had the steepest slope (Table 3, Fig. 4b). Similarly, Muller-Landau *et al.* (2006) found steeper crown area–trunk diameter slopes in their 'small' crown size class. At the same time, there is some evidence that leaf area  $\propto$  crown area<sup>*c*</sup>, where  $c > 1$ , for example the 5/4 of Grace & Fownes (1998). Their value with our results yields leaf area  $\propto$  stem diameter<sup>11/5</sup> and leaf area  $\propto$  leaf mass<sup>11/10</sup>, suggesting the isometry predicted by Enquist (2002) or slightly positive allometry. Overcoming the ambiguity between diminishing returns and isometry scenarios will at the very least require globally comparable crown area–stem size measurements and analyses.

#### CONCLUSION

A classic criticism of adaptationist studies is that organisms should not be arbitrarily atomized into independent traits (Lewontin 1977). We have offered a testable hypothesis regarding the causal links between stem size, branching frequency, leaf size, stem tissue density, stem growth rate, and carbon assimilation rates, and suggest that this interplay produces the well-known pattern Corner's Rules. This constellation of trait relationships implies that, for example, leaf size evolution cannot be studied independently of factors such as stem biomechanics or growth rate (cf. Westoby *et al.* 2002). Does the neotropical pioneer *Cecropia* have large leaves because of selection directly favouring greater leaf size, selection for its thick, hollow stems, or because of selection favouring rapid height growth? Selection on any one of these factors individually or in combination could lead to an increase in leaf size (cf.



White 1983; Cornelissen 1999; Kruger & Volin 2006; Olson & Rosell 2006; Kleiman & Aarssen 2007; Milla & Reich 2007). Mapping such constellations of trait covariation and identifying their underlying causes makes possible studies of adaptation that view organisms not as collections of independent traits but as integrated systems (Lewontin 1977; cf. Bonser 2006; Enquist *et al.* 2007).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Crown mapping: additional detail

**Appendix S1** Crown area–stem diameter dataset

**Appendix S2** Key to dataset headers

**Appendix S3** R code for fitting a multiple mixed model and per-species models

**Appendix S4** Comparisons between multiple models and per-species models

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