

Relationships Among Ecologically Important Dimensions of Plant Trait Variation in Seven Neotropical Forests

IAN J. WRIGHT^{1,*}, DAVID D. ACKERLY², FRANS BONGERS³, KYLE E. HARMS^{4,13},
GUILLERMO IBARRA-MANRIQUEZ⁵, MIGUEL MARTINEZ-RAMOS⁵, SUSAN J. MAZER⁶,
HELENE C. MULLER-LANDAU⁷, HORACIO PAZ⁵, NIGEL C. A. PITMAN⁸,
LOURENS POORTER^{3,9}, MILES R. SILMAN¹⁰, CORINE F. VRIESENDORP¹¹, CAM O. WEBB¹²,
MARK WESTOBY¹ and S. JOSEPH WRIGHT¹³

¹Department of Biological Sciences, Macquarie University, New South Wales 2109, Australia, ²Department of Integrative Biology, 3060 Valley Life Sciences Building, University of California, Berkeley, Berkeley, CA 94720-3140, USA, ³Forest Ecology and Forest Management, Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands, ⁴Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1715, USA, ⁵Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Patzcuaro 8701, Ex-Hacienda de San José de la Huerta, 58190, Morelia, Michoacán, México, ⁶Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 931067, USA, ⁷Department of Ecology, Evolution and Behavior, 100 Ecology Building, 1987 Upper Buford Circle, St Paul, MN 55108, USA, ⁸Department of Botany, Box 90339, Duke University, Durham, NC 27708-0339, USA, ⁹Instituto Boliviano de Investigación Forestal, Casilla 6204, Santa Cruz, Bolivia, ¹⁰Department of Biology, Wake Forest University, Winston-Salem, NC, USA, ¹¹Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago IL 60605, USA, ¹²Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect St., P. O. Box 208106, New Haven, CT 06520-8106, USA and ¹³Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Republic of Panama

Received: 10 October 2005 Returned for revision: 14 November 2005 Accepted: 5 January 2006 Published electronically: 4 April 2006

• **Background and Aims** When ecologically important plant traits are correlated they may be said to constitute an ecological ‘strategy’ dimension. Through identifying these dimensions and understanding their inter-relationships we gain insight into why particular trait combinations are favoured over others and into the implications of trait differences among species. Here we investigated relationships among several traits, and thus the strategy dimensions they represented, across 2134 woody species from seven Neotropical forests.

• **Methods** Six traits were studied: specific leaf area (SLA), the average size of leaves, seed and fruit, typical maximum plant height, and wood density (WD). Trait relationships were quantified across species at each individual forest as well as across the dataset as a whole. ‘Phylogenetic’ analyses were used to test for correlations among evolutionary trait-divergences and to ascertain whether interspecific relationships were biased by strong taxonomic patterning in the traits.

• **Key Results** The interspecific and phylogenetic analyses yielded congruent results. Seed and fruit size were expected, and confirmed, to be tightly related. As expected, plant height was correlated with each of seed and fruit size, albeit weakly. Weak support was found for an expected positive relationship between leaf and fruit size. The prediction that SLA and WD would be negatively correlated was not supported. Otherwise the traits were predicted to be largely unrelated, being representatives of putatively independent strategy dimensions. This was indeed the case, although WD was consistently, negatively related to leaf size.

• **Conclusions** The dimensions represented by SLA, seed/fruit size and leaf size were essentially independent and thus conveyed largely independent information about plant strategies. To a lesser extent the same was true for plant height and WD. Our tentative explanation for negative WD–leaf size relationships, now also known from other habitats, is that the traits are indirectly linked via plant hydraulics.

Key words: Fruit size, leaf size, phylogenetically independent contrasts, plant height, plant strategies, seed size, specific leaf area, tropical rainforest ecology, wood density.

INTRODUCTION

Interspecific correlations among ecologically important plant traits capture the attention of evolutionary ecologists because they may reflect two distinct phenomena. First, they may indicate physical, physiological or developmental ‘constraints’ that limit the independent variation and evolution of the focal traits. Second, the correlations may be the adaptive outcome of natural selection favouring

particular combinations of traits over others, in which case the set of traits are often described as forming an ecological ‘strategy’ dimension (Westoby *et al.*, 2002). Distinguishing between these explanations and understanding the basis for trait-based strategy dimensions is important because it gives us insight into life-history trade-offs that operate within and between environments, and thus also into phenomena such as niche differentiation, species coexistence and the broad shifts in plant traits that occur along geographic gradients. Furthermore, emergent

* For correspondence. E-mail iwright@rna.bio.mq.edu.au

properties of ecosystems such as rates of net primary productivity and nutrient cycling are not only determined by site properties (e.g. rainfall, temperature, irradiance), but also by the traits and relative abundances of the species occurring therein (Reich *et al.*, 1997; Perez-Harguindeguy *et al.*, 2000; Garnier *et al.*, 2004).

The position of a species along a strategy dimension should relate to how the species makes a living or where it is most competitive (Grime *et al.*, 1997; Weiher *et al.*, 1999; Westoby *et al.*, 2002; Ackerly, 2004; Diaz *et al.*, 2004). Rankings of species along a dimension should be consistent (at least approximately) in the face of within-species variation due to plasticity, acclimation or ecotypic variation. Four trait-based strategy dimensions identified to date (each described below) describe variation in (1) leaf structure and physiology, (2) seed size and seed output, (3) leaf size and twig size, and (4) typical maximum plant height (Westoby *et al.*, 2002). In this study we compiled data for focal traits from each of these dimensions, as well as for wood density, for more than 2100 woody species from seven Neotropical forests. Wood density (WD) was of particular interest: while it has been suggested to be involved in several different strategy dimensions (see below), to date there have been few large-scale quantifications of its relationship to other key plant traits.

We had three aims. First, to quantify the pattern of ‘cross-species’ (interspecific) correlations among these ecologically important traits and, by implication, the correlation structure among the strategy dimensions that they represent. Convincingly demonstrating that two trait dimensions are orthogonal (not correlated) is at least as important for understanding plant ecological strategies as demonstrating that they are correlated: orthogonal dimensions convey independent information about plant strategies (Ackerly, 2004). Second, using ‘phylogenetic’ analyses (Felsenstein, 1985), we tested whether evolutionary divergences in trait-pairs showed similar correlation patterns as the cross-species analysis. Where results from the two types of analyses differ this may indicate that taxonomic biases in the dataset contributed substantially to the cross-species results. Third, we assessed how general the trait-relationships were by comparing cross-species trait correlations calculated for each of the seven forests separately. Below, we describe in more detail the trait-dimensions that were studied via their focal (representative) traits.

Plant species are arrayed along a ‘leaf economics spectrum’ running from high to low specific leaf area (leaf area per dry mass; SLA), leaf N and P concentration and gas exchange rates, but from short to long average leaf lifespan (Grime *et al.*, 1997; Reich *et al.*, 1997; Reich *et al.*, 1998; Wright *et al.*, 2004). Although many herbs and grasses and species native to fertile soils occur towards the high-SLA end of the spectrum, and many evergreen species from infertile habitats occur towards the low-SLA end, a range of leaf economic strategies can still be seen within growth forms, plant functional types and biomes (Reich *et al.*, 1997; Wright *et al.*, 2004; Wright *et al.*, 2005). Leaf economic traits also scale-up to canopy and whole-plant properties of shrubs and trees. For example,

species with low SLA and long leaf lifespan (LL) accumulate greater total foliage mass per unit ground area than species with higher SLA and shorter LL (Reich *et al.*, 1992; Gower *et al.*, 1993; Read *et al.*, 2006), and have also been shown to have lower rates of height growth (Reich *et al.*, 1992). In this study, SLA was the focal trait representing the leaf economics spectrum.

Seed mass varies by 5–6 orders of magnitude among species (Leishman *et al.*, 2000). The probability of successful seedling establishment in the face of environmental hazards increases with seed mass (Westoby *et al.*, 2002). However, since species that produce larger seeds produce fewer seeds per unit of reproductive effort (Jakobsson and Eriksson, 2000; Aarssen and Jordan, 2001; Henery and Westoby, 2001), the probability of dispersal to a safe site where establishment is possible decreases with increasing seed mass. This trade-off underpins the ‘seed size–seed output’ strategy dimension (Moles and Westoby, 2004). Here, the trait chiefly representing this dimension was seed size (volume), but fruit size (volume) was also recorded.

Leaf size also varies by 5–6 orders of magnitude among species. Species with larger leaves tend also to have thicker twigs, forming a ‘leaf size–twig size’ trait-dimension among species (Westoby *et al.*, 2002). Here, the position of species along this dimension was represented by their average leaf size (area of individual leaves or leaflets). Species with larger leaves and twigs tend also to have less frequent branching and to bear larger fruits than species with smaller leaves/twigs; this set of relationships has become known as ‘Corner’s Rules’ (Corner, 1949; Ackerly and Donoghue, 1998; Cornelissen, 1999; Westoby and Wright, 2003). Still, the adaptive significance of interspecific variation in leaf size is not well understood (Westoby *et al.*, 2002). In theory, larger leaves have thicker boundary layers and thus overheat more easily than smaller leaves, leading to higher respiration and transpiration costs (Givnish, 1978). While this may help explain why community-mean leaf size tends to decrease with increasing site aridity (Givnish, 1978), 1000-fold variation in leaf size is commonly seen among sets of co-occurring species (Fonseca *et al.*, 2000), suggesting that there must be additional costs and benefits associated with variation in leaf size. For example, in Australian evergreens both the degree of self-shading (Falster and Westoby, 2003) and stem support costs per unit leaf mass (Pickup *et al.*, 2005) decrease with increasing leaf size, while herbivory levels have been shown to increase (Moles and Westoby, 2000).

Typical maximum height of adult plants was the fifth trait that we recorded. Maximum height ranges from 1 cm to 100 m, four orders of magnitude, and can be considered as a strategy dimension in its own right (Weiher *et al.*, 1999; Westoby *et al.*, 2002). Taller species or individuals have an advantage over shorter plants in that they are able to intercept more light. At the same time, the accrued cost of investment in stems increases with increasing height, as does the continuing cost of maintaining stem tissues (respiration); further, taller individuals suffer from

TABLE 1. Location, climate attributes and additional details about data collection at the seven Neotropical forests

Site	Latitude, longitude	MAT (°C)	Annual rainfall (mm)	Months with rain <100 mm
BCI	9°10'N, 79°85'W (Barro Colorado Island, Panama)	26.2	2632	4
Fort Sherman	9°17'N, 79°58'W (Fort Sherman canopy crane, Panama)	26.2	3057	3
La Chonta	15°45'S, 62°60'W (La Chonta, Bolivia)	24.8	1517	7
La Selva	18°34–36'N, 95°04–09'W (La Selva Biological Research Station, Costa Rica)	26.1	4323	0
Los Tuxtlas	18°N, 93°30'W (Los Tuxtlas Tropical Rainforest Reserve, Mexico)	24.6	4725	0
PNM	8°59'N, 79°33'W (Parque Natural Metropolitano canopy crane, Panama)	25.8	1778	4
Yasuní/Manu	0°26'–1°08'S, 75°25'–76°40'W (Yasuní National Park, Ecuador)	26.1	3110	0
	11°19'–13°11'S, 71°10'–72°22'W (Manu National Park, Peru)	24.5	2603	2

Climate. Data for mean annual temperature (MAT) and annual rainfall were averaged or summed (rainfall) across all months of the year. Sources of climate data: BCI, site-specific data, 1929–2004; Fort Sherman, site-specific data, 1997–2004; La Chonta, data from nearest weather station (approx. 60 km away), rainfall 1970–1992, temperature 1981–1992; La Selva, site-specific data, rainfall 1962–2002, temperature 1982–2003; Los Tuxtlas, data from nearby Coyame weather station, 1953–1981 (Ibarra-Manríquez and Sinaca, 1987); PNM, site-specific data, 1995–2004; Yasuní/Manu: data estimated separately for the Ecuador and Peru sites from an interpolated 1961–1990 global dataset (New *et al.*, 1999).

Species selection. Only species with stems >1 cm dbh were sampled at sites in Panama; plot sizes, BCI 50 ha, Fort Sherman 6 ha, PNM 1 ha. Leaf data from La Chonta are mostly for understory saplings. At La Selva, only woody species (lianas and trees) growing in the shade were sampled.

an increased risk of breakage (Niklas, 1992; Givnish, 1995; Ryan and Yoder, 1997; Becker *et al.*, 2000). Trade-offs such as these mean that species with a wide range of maximum heights often co-occur. Maximum plant height also tends to be positively correlated with seed size among species, but for reasons that are as yet unclear (Moles *et al.*, 2004, 2005).

The final trait requiring introduction is wood density. Wood density (WD) is associated with several, somewhat inter-related aspects of ecological strategy. Firstly, sapling and adult mortality rates of Neotropical forest trees decrease with increasing WD (Zimmerman *et al.*, 1994; Muller-Landau, 2004), presumably because higher WD confers greater resistance of stems to pathogen attack and to mechanical damage (Turner, 2001). Secondly, species with higher WD tend to have slower stem-diameter and volumetric growth rates than lower WD species (Enquist *et al.*, 1999; Roderick, 2000), this relationship largely underpinning a successional continuum in tropical forests from fast-growing, light-demanding species to slow-growing, shade-tolerant species (Lawton, 1984; Poorter and Arets, 2003; Muller-Landau, 2004; King *et al.*, 2005). Finally, WD is also linked to several hydraulic properties of plants. Species with low WD tend to have highly conductive sapwood and store considerable water in their stems, while those with higher WD tend to be more resistant to xylem cavitation, and their leaves show larger daily fluctuations in leaf water potential (Stratton *et al.*, 2000; Meinzer, 2003; Ackerly, 2004; Bucci *et al.*, 2004; Santiago *et al.*, 2004; Hacke *et al.*, 2005).

In this study we compiled trait data for woody species from seven Neotropical forests, the traits being SLA, seed and fruit size, leaf size, plant maximum height and wood density. Our expectations were as follows.

- (1) Due to the physical constraint that fruit size constrains the maximum possible size of seeds, seed and fruit size would show a 'triangular' relationship (small-fruited species would have small seeds only, whereas large-fruited species would have a wide range of seed sizes).
- (2) Leaf size and fruit size would be positively correlated (Corner's Rules).
- (3) SLA and wood density would be negatively correlated, reflecting the continuum from fast-growing pioneer species with low WD to slow-growing climax species with high WD.
- (4) Taller species would have larger seeds (Moles *et al.*, 2004, 2005).
- (5) Otherwise, we expected the traits to be essentially unrelated, indicating orthogonality of the ecological strategy dimensions they represented.

MATERIALS AND METHODS

Dataset

Trait data were compiled for woody species (trees, shrubs, lianas) from seven rainforests spanning most of the Neotropical rainforest zone (sites ranged from 18°N to 15°S; Table 1). Some 'sites' consisted of a restricted geographical area; e.g., 1, 6 and 50 ha plots in Panama at Parque Natural Metropolitano (PNM), Fort Sherman and Barro Colorado Island (BCI), respectively. Others consisted of a large region of more or less continuous forest (e.g., Yasuní/Manu in Ecuador/Peru). Originally the Yasuní and Manu datasets were separate but they were combined because a large proportion of data for these sites came

from published floras and over 200 species were recorded in both forests. The seven forests differ considerably in mean annual rainfall (1517 to 4725 mm y⁻¹) and in the number of months with mean rainfall <100 mm (0 to 7), but differ little in mean annual temperature (24.5 to 26.2 °C). Further information on the sites can be found in relevant publications (Croat, 1978; Bongers *et al.*, 1988; Bongers and Popma, 1990; McDade and Hartshorn, 1994; Wright and Colley, 1994; Leigh *et al.*, 1996; Pitman *et al.*, 2001; Condit *et al.*, 2004).

Sources of plant trait data included published studies (Augsburger, 1986; Bongers and Popma, 1988, 1990; Kitajima, 1992; Dalling *et al.*, 1998; Ibarra-Manríquez *et al.*, 2001; Pitman *et al.*, 2001), unpublished field-collected data from the authors, and information from relevant floras, monographs and other publications, e.g. Croat (1978). In general, mean trait values were calculated from several individuals of each species at each site. However, in a number of cases seed volumes were based on samples from single individuals. The dataset comprised information on 2134 species, representing 607 genera, 101 families and 36 orders. Family- and genus-level taxonomic delineation followed current information available from the Angiosperm Phylogeny Group (<http://www.mobot.org/MOBOT/research/APweb/>; accessed December 2004). Three hundred and forty-five species occurred at more than one site. Approximately 80% of the species were trees; the remainder were lianas (11%), shrubs (6%) and hemi-epiphytes (1%). Coverage for each trait varied widely (Table 2), ranging from 453 records for SLA to 1498 for leaf size; similarly, not every trait was measured at each site (Table 2).

In some cases the protocols for measuring the traits varied among sites; however, all efforts were made to standardize data so that they could be analysed together. At most sites seed and fruit volume (mm³) were calculated from linear dimensions (following removal of appendages such as wings), assuming an ellipsoidal shape. A small number of species with seeds or fruits that were clearly not ellipsoidal were not included. At BCI, seed and fruit masses were recorded rather than volumes. Mass (mg) was converted to volume using allometric equations derived from the Los Tuxtlas data, where both volume and mass had been measured:

$$\log(\text{seed volume}) = 1.027 \log(\text{seed mass}) - 0.043;$$

$$r^2 = 0.93, n = 272.$$

$$\log(\text{fruit volume}) = 0.968 \log(\text{fruit mass}) + 0.405;$$

$$r^2 = 0.90, n = 273.$$

Leaf data were in some cases measured for outer canopy ('sun') leaves only (La Chonta; although these were for saplings in this case), for shade leaves only (La Selva), for both (Fort Sherman, Los Tuxtlas, PNM), or were not distinguished on this basis (leaf size data for BCI

TABLE 2. Sample size and range of variation for the six plant traits among woody species (trees, shrubs, lianas) from seven Neotropical forests

Trait	n1	n2	n3	Min.	Max.	Orders of magnitude variation
Plant height (m)	1342	1288	6	1.5	60.3	1.6
Wood density (g cm ⁻³)	991	959	7	0.10	1.11	1.0
Seed size (mm ³)	1237	1236	5	0.003	6.16 × 10 ⁴	7.3
Fruit size (mm ³)	1030	410	3	0.47	3.02 × 10 ⁶	6.8
SLA (mm ² mg ⁻¹)	453	597	6	4.3	69.2	1.2
Leaf size (mm ²)	1497	1228	7	2.6	2.57 × 10 ⁵	5.0

For compound-leaved species, leaf size refers to the average size of individual leaflets. n1: total number of species/site combinations for each trait in the database; n2: number of species for each trait used in species-mean analyses; n3: number of sites for which we had data for each trait.

and Yasuní/Manu). Where both sun and shade values were known, the former were given preference. Leaf size was measured directly in most datasets. Only maximum and minimum values for leaf length were available for the Yasuní/Manu dataset (data from a number of published floras; see Pitman *et al.*, 2001), hence for that site leaf size was estimated using an allometric equation relating mean length (mm) to area (mm²), derived from the BCI dataset:

$$\log(\text{leaf size}) = 2.146 \log(\text{leaf length}) - 0.882;$$

$$r^2 = 0.94, n = 223.$$

The average size both of leaflets and of whole-leaves was known for a number of compound-leaved species. Except where specified, leaf size refers to data for leaflets for these species (generally the terminal leaflet). SLA was measured for leaf discs rather than for whole leaves (or leaflets) for some species at BCI. Whole-leaf SLA (mm² mg⁻¹) was estimated for these species using an allometric equation calculated from species for which both types of data were known:

$$\log(\text{whole-leaf SLA}) = 0.972 \log(\text{leaf disc SLA})$$

$$- 0.0129;$$

$$r^2 = 0.91, n = 101.$$

Data analyses

Five of the six traits showed strongly right-skewed distributions and were therefore log₁₀-transformed prior to analyses. Wood density showed an approximately normal distribution already and was not transformed. Four types of analyses were used for examining trait relationships.

Bivariate trait correlations, across all species and within individual sites

The all-species analysis was based on a dataset of species-mean trait values (i.e., site-specific values were averaged for species occurring at more than one location; sample sizes given in Table 2). Relationship strength was quantified using correlation r^2 and P values; relationship slopes were described by their standardized major axes (SMAs). SMA analyses are appropriate when the purpose of line-fitting is to summarize the relationship between two variables, as in many allometric studies (Sokal and Rohlf, 1995). An SMA line is the slope of the first principal axis in a PCA analysis based on standardized data, fitted through the centroid of the data. SMA routines were run in a DOS-based computer package, (S)MATR (Falster *et al.*, 2003). Next we quantified the strength of bivariate trait correlations at each individual site. These analyses are complementary to the first analysis in two ways. (1) They assess how consistent the relationships are among sites, giving a sense of the degree of generality of each trait relationship; and (2) if the site-specific relationships are generally strong but the correlation seen across all species is weak, it indicates that the site-specific relationships must be offset from one another, either in their slope or intercepts (or both).

Evolutionary divergence analyses

We also tested whether (inferred) evolutionary divergences in each trait were correlated with those in the other traits. Cross-species (above) and evolutionary divergence correlation analyses ask different questions, i.e. they are complementary methods rather than alternative statistical techniques for the same question (Westoby, 1999). In cross-species analyses each species contributes a single data point; in correlated divergence analyses each independent *divergence* (or radiation, or contrast) contributes a data point. Hence, these are also known as ‘phylogenetically independent contrast’ or PIC analyses (Felsenstein, 1985; Harvey and Pagel, 1991).

A phylogenetic tree describing the hypothesized evolutionary relationships between species was constructed using Phylomatic software (Webb and Donoghue, 2005). Phylomatic starts with a backbone family-level tree of the angiosperms, based on a synthesis of recent phylogenetic analyses (Stevens, 2004). Given a species list for a particular study, the appropriate families are selected and the remainder pruned from the tree. Genera are generally pasted on as polytomies within families, and species as polytomies within genera. The phylogenies used for this study were based on the Phylomatic conservative tree C20040402. Analyses were run using the ‘Analysis of Traits’ (v. 3.0) module in Phylocom v.3.22 (Webb *et al.*, 2004). Independent contrasts (divergences) were calculated as the difference between the trait values for the two nodes or species descending from the contrast-node; internal node values were themselves calculated using a weighted averaging procedure based on a Brownian motion model of trait evolution (Felsenstein, 1985). The direction of subtraction in calculating contrasts is

unimportant, providing all traits are treated in the same manner. For polytomies, daughter nodes were ranked by trait value, and split at the median into two groups (high and low). If there was an odd number of daughter nodes the median daughter node value was assigned to the lower group if its value was lower than the mean across all daughter nodes, or to the upper group if its value was higher than the mean. A harmonic mean branch length was calculated for each group, then the contrast size was calculated as for a dichotomous node (Pagel, 1992). A correlation coefficient was then calculated between the set of divergences for each pair of traits. In a bivariate plot of divergences in one trait against divergences in another, a data point indicating a positive divergence in both traits would have indicated negative divergences in each trait had the subtractions been performed the other way around. Due to this symmetry, analyses of contrast data have no intercept term: they are ‘forced’ through the origin (Garland *et al.*, 1992). Accordingly, significance testing is done as for standard Pearson correlation analyses, but using $N - 1$ degrees of freedom (where N is the number of internal nodes providing contrasts) rather than $N - 2$, as would be done for a model with an intercept term (Sokal and Rohlf, 1995).

Summarizing multivariate trait covariation

Multidimensional variation among the six traits was summarized using principal components analysis (PCA) of the trait correlation matrix calculated from species-mean trait values. Two analyses were run: one on a data subset consisting of 122 species for which all six traits were known; another on the entire dataset in an analysis where missing cells in the trait matrix were allowed (SPSS for Windows v. 11.0; SPSS Inc., Chicago, Illinois). Although a number of components were extracted in both analyses, we discuss only those with eigenvalues > 1 , these being most informative (Kaiser, 1960).

Preliminary investigation of properties of sun leaves versus shade leaves

SLA and leaf size were measured separately for outer-canopy (‘sun’) and shaded leaves at three sites (PNM, Fort Sherman and Los Tuxtlas), for 96 species in total. We ran additional analyses to those described above in order to assess the likelihood that these differences in sampling protocol would have affected the results and conclusions from the study. These analyses are described in detail in Appendix 1 [Supplementary Information]. For comparing SLA or leaf size with the other measured traits, the results indicated that no systematic bias in terms of relationship slope should have been introduced by the different leaf-sampling protocols at different sites. However, shifts in SMA intercepts may have resulted, weakening our ability to interpret any such patterns in terms of other variables such as site climate. Consequently, we do not present analyses comparing SMA of trait relationships fitted to individual sites.

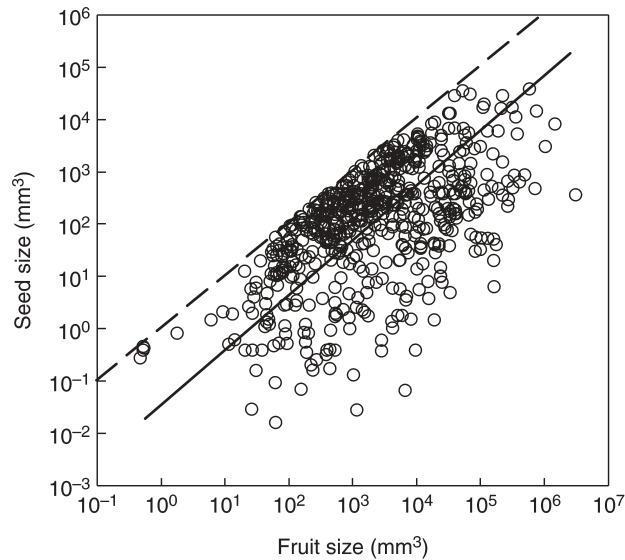


FIG. 1. Relationship between seed size and fruit size among 622 woody species from Neotropical forests. Each data point represents the mean value for a species. Correlation statistics are given in Table 3. Standardized major axis (SMA) slope (and 95 % confidence interval): 1.05 (0.99, 1.12). The dashed line indicates the 1 : 1 physical constraint that seed size cannot be larger than fruit size.

RESULTS

Positive correlations among seed size, fruit size and plant height

The most tightly related trait pair was seed size and fruit size, being positively related in both the species-based ($r^2 = 0.35$; Fig. 1) and PIC analyses ($r^2 = 0.42$), and within each of the three sites at which both traits were measured ($r^2 = 0.28$ to 0.43 ; Appendix 2, **Supplementary Information**). Taller species tended to have larger seeds and larger fruits, both across all species and within individual sites, although these relationships had relatively little explanatory power. Across all species, five to six orders of magnitude in seed or fruit size were observed at any given height (Fig. 2). Evolutionary divergences in plant height were also positively correlated with those in seed and fruit size (Table 3).

Negative correlations between leaf size and wood density

Leaf size and wood density (WD) were negatively correlated in all three types of analyses. Whether leaf size of compound-leaved species was taken as that of the leaflets or of the whole leaves, these relationships tended to be considerably tighter when only simple-leaved species were analysed (Table 3; Appendix 2, **Supplementary Information**). Among simple-leaved species, wood density explained 20 % of variation in leaf size (Fig. 3). The traits were also negatively correlated at five of six sites, with r^2 values ranging from 0.16 to 0.30. Even at the sixth site wood density explained 23 % of variation in leaf size, but with only seven species sampled this was not statistically significant ($P = 0.275$).

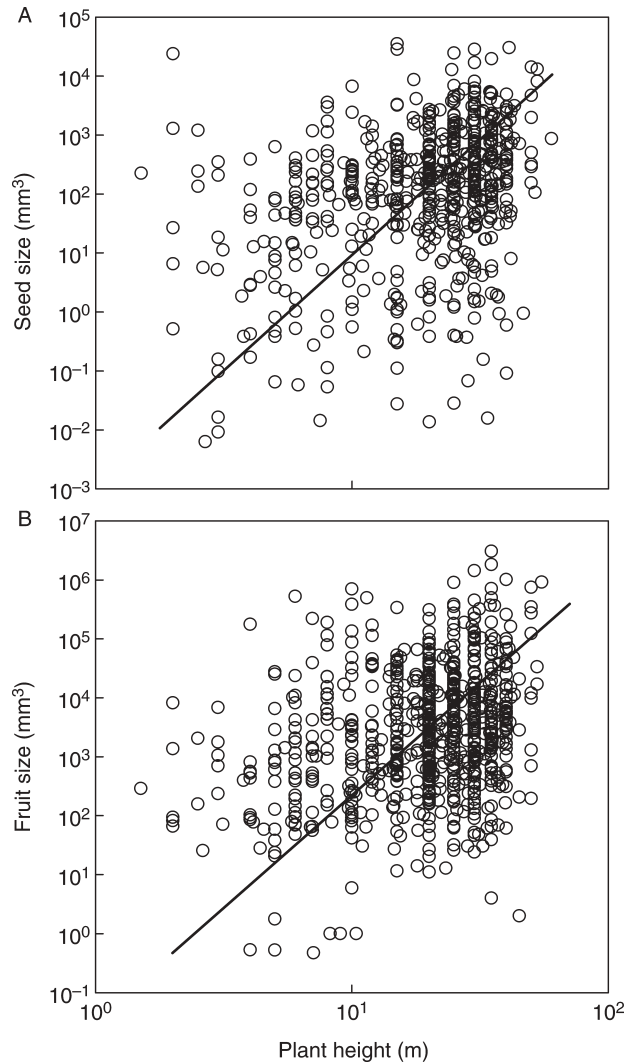


FIG. 2. Relationships between species-mean (A) seed size and plant height, and (B) fruit size and plant height. Correlations statistics are given in Table 3. SMA slopes (and 95 % confidence interval): (A) 3.92 (3.64, 4.22), (B) 3.82 (3.58, 4.08).

Leaf size and WD were unrelated among compound-leaved species, both across all species (Fig. 3) and within individual sites (not shown), whether leaf size was taken to mean leaflet size or the size of whole leaves. The lack of a relationship between wood density and leaflet size was influenced strongly by several species from the Fabaceae that have very small leaflets (pinnae) in combination with wood densities in the middle of the observed range (Fig. 3B). With these species removed, leaflet size and wood density were then negatively correlated, albeit considerably more weakly than leaf size and wood density were among simple-leaved species (details in Fig. 3 caption).

Larger-leaved species tended to have larger fruits

In all three types of analyses there was a weak positive relationship between fruit size and leaf size (Table 3;

TABLE 3. Pairwise cross-species and PIC relationships between the six plant traits for woody species from the seven Neotropical forests

		Plant height	Wood density	Seed size	Fruit size	SLA	Leaf size
Plant height	r^2		0.002	+0.12	+0.09	−0.08	−0.01
	n	—	483	636	822	239	973
	P		0.313	<0.001	<0.001	<0.001	0.019
Wood density	r^2	<0.001		+0.04	0.01	−0.003	−0.08
	n	167	—	394	352	191	438
	P	0.949		<0.001	0.107	0.418	<0.001
Seed size	r^2	+0.04	0.02		+0.35	−0.04	−0.01
	n	214	143	—	622	242	532
	P	0.002	0.109		<0.001	0.001	0.088
Fruit size	r^2	+0.06	0.001	+0.42		−0.08	+0.02
	n	259	127	222	—	215	718
	P	<0.001	0.712	<0.001		<0.001	<0.001
SLA	r^2	0.01	0.02	0.02	−0.04		0.002
	n	97	78	103	89	—	391
	P	0.281	0.196	0.129	0.047		0.419
Leaf size	r^2	0.01	−0.02	0.01	+0.06	0.01	
	n	260	156	190	225	148	—
	P	0.152	0.048	0.126	<0.001	0.178	

Correlation data are given for species-based analyses above the diagonal and for PIC analyses below the diagonal. The sign of the correlation r value is indicated for relationships with $P < 0.10$; relationships for which $P < 0.003$ are shown in bold (Bonferroni correction for 15 comparisons: $0.05/15 = 0.003$). All traits except wood density were \log_{10} -transformed prior to analysis. Relationships between wood density and leaf size were considerable stronger when only simple-leaved species were considered. Species-based analysis: $r^2 = 0.20$, $n = 309$, $P < 0.001$; PIC analysis: $r^2 = 0.12$, $n = 116$, $P < 0.001$.

Appendix 2, **Supplementary Information**). Still, almost any fruit size was observed at any given leaf size, and vice versa (Fig. 4A). There was even less patterning of seed size with respect to leaf size (Fig. 4B), although the cross-species correlation was marginally significant (Table 3). Little difference was made by considering the leaf size of compound-leaved species as that of the whole leaf rather than that of the leaflets (not shown).

SLA varied independently from the other plant traits

In general, SLA showed no relationship with either wood density or leaf size (Table 3; Appendix 2, **Supplementary Information**). Still, at one site (La Chonta) species with higher density wood had lower SLA, and at two sites SLA was correlated with leaf size (positively at BCI, negatively at La Selva). Whereas SLA was weakly negatively related to plant height and seed size across all species, no relationship was evident in either case when evolutionary divergences were considered (Table 3). Considering individual sites, taller species tended to have leaves of higher SLA at La Chonta and leaves of lower SLA at Los Tuxtlas, but no relationship was seen at the other sites (Appendix 2, **Supplementary Information**). SLA and fruit size were weakly and negative related in the species-based and PIC analyses (Table 3), and at one of the two individual sites (Los Tuxtlas) for which we had data for both traits.

Other trait-pairs were unrelated

All other trait-pairs were essentially unrelated, the exception being wood density and seed size. These traits

were weakly positively correlated across species ($r^2 = 0.04$; $P < 0.001$) and at two of five sites (Appendix 2, **Supplementary Information**), but unrelated in the PIC analysis.

Multivariate analyses confirmed the pairwise patterns

All six traits were known for 122 species. Principal components analysis of these data largely confirmed the results from the pairwise analyses. The first principal axis extracted from the data explained 33 % of the total trait variation and was most strongly correlated with seed size and fruit size (Table 4). Variation in plant height and, to a lesser extent, SLA (negatively) were also associated with this axis. The second axis explained a further 24 % of variation, reflecting the negative relationship between leaf size and wood density. Weak correlations between axis 2 and the other traits indicated that covariation between leaf size and wood density was largely independent (orthogonal) from variation in the other traits. A second analysis involving all species confirmed these findings: each axis explaining a similar amount of variation as in the first analysis, and the same strong pattern of trait correlations was evident, especially with the first two extracted principal axes (Appendix 3; **Supplementary Information**).

DISCUSSION

Orthogonality among key traits and trait dimensions

Five of the six plant traits are focal traits in particular ecologically important plant strategy dimensions: leaf economics (SLA), seed size/seed output (seed and fruit size), leaf size/twig size (leaf size), and typical maximum plant

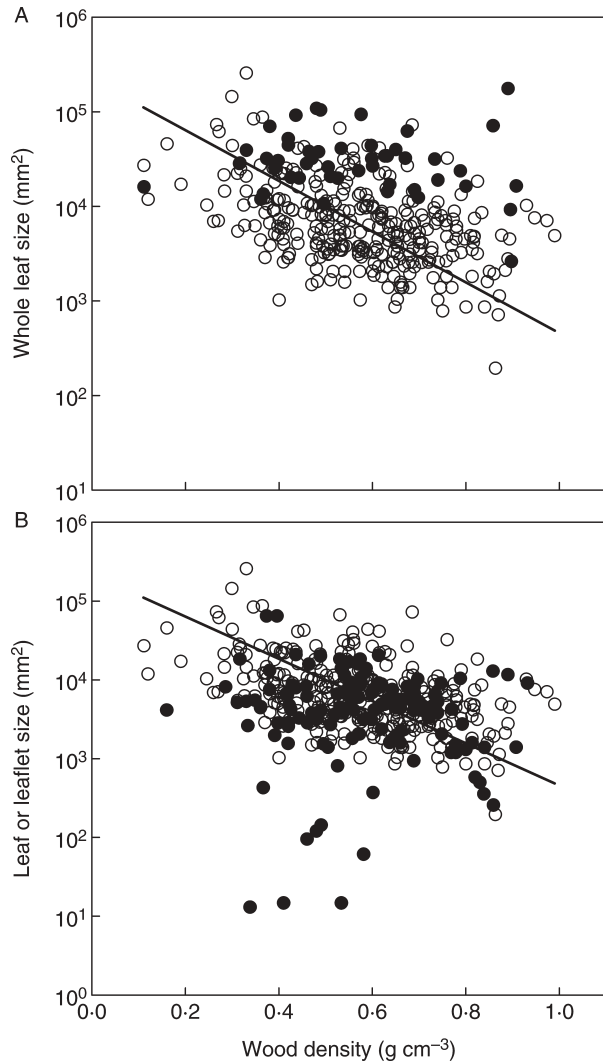


FIG. 3. Relationships between species-mean leaf size and wood density. (A) Whole-leaf size versus wood density, with open circles indicating simple-leaved species and filled circles indicating compound-leaved species. Only the SMA slope fitted to simple-leaved species is shown (slope -2.68 , 95 % CI -2.97 to -2.43); correlation statistics are given in the notes associated with Table 3. No relationship was found among compound-leaved species ($P = 0.250$, $n = 49$). (B) Leaf or leaflet size versus wood density, with symbols and fitted slope as in (A). No relationship was found among compound-leaved species ($P = 0.726$, $n = 129$); however, with the seven smallest-leaflet species removed, leaflet size and wood density were then negatively correlated ($r^2 = 0.06$, $P = 0.005$). These species were *Albizia niopoides*, *Hydrochorea corymbosa*, *Macrolobium acaciifolium*, *Parkia multijuga*, *P. nitida*, *P. velutina*, and *Schizolobium parahyba* (all in the Fabaceae).

height. The sixth trait, wood density, is associated with several, somewhat inter-related trait dimensions. Taken together, our results suggested that the leaf economics, seed size/seed output and leaf size/twig size dimensions are essentially orthogonal among woody species in the neotropics. Demonstrating orthogonality among strategy dimensions is of considerable importance as it indicates that the dimensions convey essentially different information (Ackerly, 2004). Plant height showed little relationship to

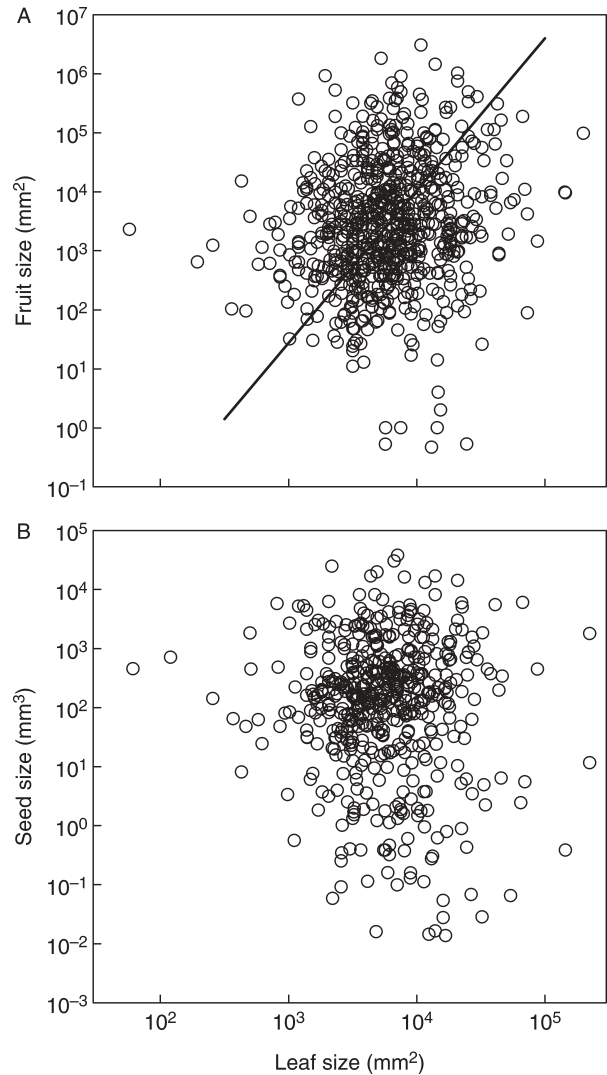


FIG. 4. Relationships between species-mean (A) fruit size and leaf size, and (B) seed size and leaf size. Leaf size for compound-leaved species was taken as the mean size of individual leaflets. Correlation statistics are given in Table 3. (A) SMA slope (and 95 % confidence interval) = 2.58 (2.40 , 2.78); (B) No slope was calculated as the relationship was statistically non-significant.

any other traits except seed and fruit size. Still, around 90% of height variation was not associated with seed or fruit size, suggesting that the plant height dimension could perhaps also be considered as largely orthogonal from the other strategy dimensions. The results from cross-species and evolutionary divergence analyses were highly congruent, indicating that our findings were not unduly influenced by taxonomic biases in the dataset. Our dataset was large, both in terms of the number of species represented (2134) and in its taxonomic breadth (607 genera from 101 families), giving added weight to the results.

Wood density (WD) was largely unrelated to the other traits (except for leaf size, discussed below). We had expected a negative relationship between WD and SLA, reflecting the continuum from fast-growing,

TABLE 4. Principal components analysis of trait data for 122 species for which all six traits were known

	Axis 1	Axis 2	Axis 3	Axis 4	Total %
Seed size	0.63 (+)	0.03	0.17 (+)	0.01	84
Fruit size	0.63 (+)	0.05 (+)	0.14 (+)	0.01	84
Plant height	0.39 (+)	0.02	0.22 (–)	0.27 (+)	89
SLA	0.28 (–)	<0.01	0.44 (+)	0.23 (+)	95
Wood density	0.03	0.66 (–)	0.01	0.05 (–)	75
Leaf size	<0.01	0.65 (+)	0.01	0.15 (–)	81
Eigenvalue	1.95	1.42	0.98	0.72	

The first component (axis) explained 33 % of total trait variation, the second a further 24 %, the third 16 %, the fourth 12 % (total, 85 %). The proportion of variation (r^2) in each trait explained by each axis is indicated, as well as the sign of the correlation coefficient (trait loading), where significant ($P \leq 0.05$). For each trait the total proportion of variation explained by the analysis is given in the rightmost column. Eigenvalues < 1 indicate axes that explain less variance than each individual variable contributes. All variables except wood density were \log_{10} -transformed, and the PCA was run on standardized data (i.e. the correlation rather than the covariance matrix).

light-demanding species (low WD, high SLA) to slow-growing, shade-tolerant species (high WD, low SLA). Indeed, in previous interspecific studies of Panamanian trees, WD was negatively correlated with photosynthetic capacity (Santiago *et al.*, 2004), and height growth rate negatively correlated with leaf lifespan, LL (Coley, 1988) – photosynthetic capacity and LL being key traits in the leaf economics spectrum (Reich *et al.*, 1997; Wright *et al.*, 2004). However, besides SLA and WD being negatively correlated at La Chonta, our analyses suggested that WD is largely unrelated to the leaf economics spectrum among woody species from Neotropical forests.

Interpreting the significant relationships among the measured traits

Despite the general conclusion of orthogonality among the strategy dimensions, several quite consistent (though mostly weak) trait relationships did emerge (Fig. 5). That is, positive relationships were found between seed and fruit size, between leaf and fruit size, and between plant height and each of seed and fruit size, while a generally negative relationship was found between wood density and leaf size. Below we discuss possible underlying reasons for these relationships.

Fruit size constrains seed size

A seed cannot be bigger than the fruit in which it is found, nor can a seed be larger than the entire fruit–seed complex if a seed is borne outside the fruit, as in *Anacardium excelsum* (cashew; Anacardiaceae). This physical constraint (shown as a dashed line in Fig. 1) led to the expectation of a ‘triangular’ relationship, i.e., small-fruited species should have small seeds only,

whereas large-fruited species could have a wide range of seed sizes. However, this was not what we observed: except for the very smallest fruits (for which seed and fruit size were almost identical), three to four orders of magnitude variation in seed size was seen at any given fruit size. Furthermore, no species had very large fruits in combination with very small seeds. It is unclear how to interpret these departures from the expected pattern. Perhaps there is some maximum number of seeds per fruit beyond which there is no longer a pay-off to packing in more, smaller seeds?

Leaf size in relation to seed and fruit size: Corner’s Rules were weak rules at best.

‘Corner’s Rules’ describe the tendency for species with thick twigs to have large appendages (leaves, fruit) and wide branching angles. Previous studies have not detected a tight relationship between fruit and leaf size so much as showing that particular combinations of fruit and leaf size were absent. Cornelissen (1999) reported a triangular relationship such that small-leaved species had small seeds (and fruit) only, whereas large-leaved species were observed with a wide range of seed (or fruit) size. By contrast, Westoby and Wright (2003) found a positive correlation but not a triangular relationship between leaf size and seed size across Australian arid and sclerophyll species. Here also there was no evidence of a triangular trait relationships among these traits. While fruit and leaf size were indeed positively correlated, both the large leaf/small fruit and small leaf/large fruit corners of graph space were essentially empty (Fig. 4A) while, if anything, the most empty corner of seed size–leaf size graph space was the lower left (small seeds and small leaves). In other words, Corner’s Rules held only weakly at best among these species, for unknown reasons.

Why do taller species tend to have larger seeds and fruit?

A tendency for larger species or growth forms to have larger fruits and seeds has been recognized many times previously (Leishman *et al.*, 2000; Moles *et al.*, 2004). In the most comprehensive study to date, seed size and maximum plant height were positively correlated across 2113 species from a wide range of habitats, including deserts, grasslands, shrublands and both temperate and tropical forests ($r^2 = 0.35$; Moles *et al.* 2004). The strength of this global relationship was considerably greater than that found here. However, when just the tropical forest species from that study are considered the traits were correlated with similar strength to those among the species in this study ($r^2 = 0.09$).

It is unclear why larger species tend to have larger fruits and seeds (Leishman *et al.*, 2000; Moles *et al.*, 2004). While, logically, there must be a physical constraint whereby very small plants cannot support very large fruits or seeds, it seems unlikely that observed fruit and seed sizes are close enough to any physical limit for this factor to be very important (Thompson and Rabinowitz, 1989; Leishman *et al.*, 2000). Presumably, diaspore dispersal

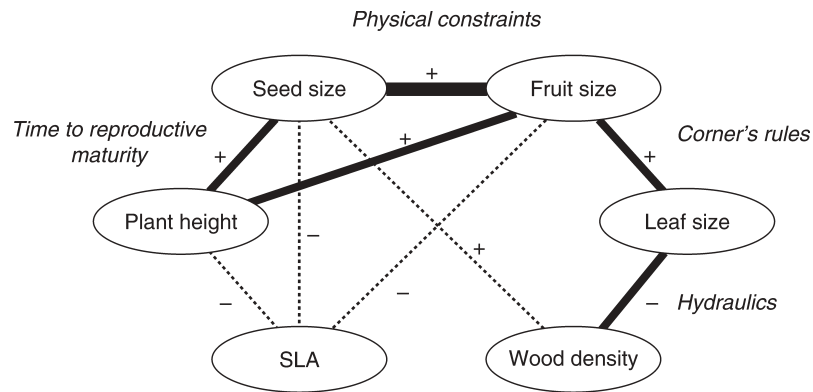


FIG. 5. Summary of relationships among the six plant traits. The strength and consistency of the relationship among any pair of traits is indicated by the thickness of the line connecting them, dotted lines indicating the weakest and most inconsistent relationships. The main hypothesized factor underlying the relationship is indicated (see Discussion), as well as the sign (positive or negative) of the relationship.

distance increases with plant height, at least for wind-assisted diaspores or for those without specialized dispersal adaptations. While this may contribute to observed relationships between plant height and seed or fruit size, it does not provide a general explanation: these relationships are actually just as strong among species with animal-dispersed diaspores as among those with wind-assisted or unassisted dispersal (Leishman *et al.*, 2000). One promising recent explanation is based on the time taken to reach reproductive maturity (Moles *et al.*, 2004). The argument is as follows: species that are large as adults have a long juvenile period; to survive a long juvenile period requires high juvenile survivorship; high juvenile survivorship is associated with large seed size; hence there is a link between seed size and plant size. Moles *et al.* (2004) point out that this is similar to the positive relationship seen in mammals between adult body size and offspring mass at the time of independence (Charnov, 1993), but a full test of these ideas would require quantification of the relationship between seed mass and survival from seed production to reproductive maturity.

Wood density and leaf size: linked via hydraulics of water transport?

Wood density and leaf size were negatively associated across all species, within individual sites, and when considered in terms of evolutionary divergences. Indeed, this was the strongest and most consistent relationship observed, after that between seed and fruit size. Several other studies, from a range of vegetation types, have recently reported a negative correlation between WD and leaf size (Ackerly, 2004; Cavender-Bares *et al.*, 2004; Pickup *et al.*, 2005; Rossetto and Kooyman, 2005), suggesting that this trait relationship may be quite generally true. No explanation has yet been offered for the relationship, but one possibility is that it relates to the hydraulics of water supply. The line of argument is as follows. (1) On average, species with lower WD have higher hydraulic conductivity per unit sapwood area (K_s) as a result of having a higher proportion of stem cross-section taken up by vessel lumen; this being due to having larger-diameter vessels, on average, or to

having similar average vessel size, but more vessels per unit sapwood area (Stratton *et al.*, 2000; Ackerly, 2004; Bucci *et al.*, 2004; Kocacinar and Sage, 2004; Santiago *et al.*, 2004). (2) Within a given habitat, species with higher K_s should (all else being equal) be able to transport more water and thus deploy a larger total leaf area per stem (Mencuccini, 2003; Ackerly, 2004; Cavender-Bares *et al.*, 2004). (3) Interspecific variation in total leaf area per shoot is driven more strongly by variation in individual leaf size than by variation in leaf number per shoot (Falster and Westoby, 2003; Westoby and Wright, 2003; Ackerly, 2004). Thus, the negative WD–leaf size relationship arises via the pairwise correlations between each of these traits with total leaf area per stem. Nonetheless, 20-fold or more variation in leaf size was seen at any given wood density among the species in this study (Fig. 3), indicating that this prospective causal pathway, even if true, is by no means hard-wired.

Are multivariate trait relationships in the Neotropics similar to elsewhere?

In previous sections we have shown that leaf size and WD are correlated among species from other habitats in a similar way to among the species in this study, and the same was true for plant height with respect to seed and fruit size. But how does the overall pattern of multivariate trait associations – or trait orthogonality – compare to elsewhere? Several of the traits used here were also included in a study that used principal components analysis to investigate trait relationships among 640 species from Argentina, England, Iran and Spain (Diaz *et al.*, 2004). In that study, as found here, SLA was essentially unrelated to plant height, seed size and plant 'woodiness' (treated as an ordinal variable), and plant height was positively associated with seed size. However, unlike here, both height and SLA were positively associated with leaf size; furthermore, plant woodiness was positively associated with each of plant height, seed size and leaf size. Still, when considering only the 113 laminar-leaved trees and shrubs in their dataset, leaf size and woodiness were in fact negatively correlated, as found here and elsewhere,

albeit only very weakly (Spearman's $\rho = -0.17$, $P = 0.08$; S. Diaz, pers. comm.). At this stage there have been too few multi-species, multi-trait studies to ascertain the extent to which differences in trait relationships between the Diaz *et al.* (2004) study and our own reflect peculiarities of the vegetation types studied, or whether the similarities reflect globally general trait relationships.

CONCLUSIONS

To understand the life-history trade-offs that have shaped plant evolution we need to understand the basis of relationships among ecologically important plant traits, and among correlated sets of such traits (strategy dimensions). Here, relationships among several ecologically important traits (and thus trait dimensions) were investigated across a large number of woody species from the Neotropics. The leaf economics, seed size–seed output, and leaf size–twig size strategy dimensions were shown to be essentially orthogonal. Wood density, a trait implicated in several strategy dimensions, was generally unrelated to the other traits (or trait dimensions), except for leaf size. The plant height dimension was largely orthogonal to the other trait dimensions, but less clearly so. In particular, taller species tended to have larger seeds and fruit, as shown previously in a variety of vegetation types. Seed and fruit size were tightly related, most likely reflecting a simple physical constraint. Wood density and leaf size were negatively associated, our tentative explanation for this relationship invoking a link via plant hydraulics. The overall pattern of trait relationships was similar in the cross-species and evolutionary divergence analyses, indicating that the observed results were not strongly affected by taxonomic biases in the dataset.

This study concerned woody species from Neotropical forests. Limited evidence suggests that patterns of trait relationships may vary somewhat according to the types of species and site-types that are studied. As additional multi-species, regional and global datasets of plant traits accumulate, these sorts of results will be able to be placed into world-wide context, and thus contribute to a better understanding ecological trait variation among the plants of the world.

SUPPLEMENTARY INFORMATION

Three Appendices are available online as Supplementary Information (<http://aob.oxfordjournals.org/>). Appendix 1: preliminary investigation of properties of sun leaves versus shade leaves; Appendix 2: Details of pairwise trait relationships among woody species (trees, shrubs, lianas) from seven Neotropical forests; and Appendix 3: principal components analysis of trait data for 2134 woody species from the neotropics.

ACKNOWLEDGMENTS

This work was conducted as part of the 'Life-history variation and community structure in Neotropical rainforest communities: Ecological and phylogenetic influences'

Working Group supported by the National Center for Ecological Analysis and Syntheses, a Center funded by NSF (Grant #DEB-94-21535), UCSB, and the State of California. Wright and Westoby acknowledge support from the Australian Research Council. Vriesendorp's contribution to this paper was supported by NSF (DEB 0075472 to R. Kobe). Many thanks to Steve Paton (STRI) and the Organization for Tropical Studies for access to climate data for the Panamanian sites and La Selva, respectively. We also thank the many people who helped create the datasets used in this paper, particularly Osvaldo Calderon in Panama and Fernando Cornejo in Peru, and Sandra Diaz for providing us with unpublished results from Diaz *et al.* (2004).

LITERATURE CITED

- Aarssen LW, Jordan CY. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience* 8: 471–477.
- Ackerly DD. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* 74: 25–44.
- Ackerly DD, Donoghue MJ. 1998. Leaf size, sapling allometry, and Corner's Rules – phylogeny and correlated evolution in maples (*Acer*). *American Naturalist* 152: 767–791.
- Augsburger CK. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353–363.
- Becker P, Meinzer FC, Wullschlegel SD. 2000. Hydraulic limitation of tree height: a critique. *Functional Ecology* 14: 4–11.
- Bongers F, Popma J. 1988. Is exposure-related variation in leaf characteristics of tropical rain forest species adaptive? In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA eds. *Plant form and vegetation structure*. The Hague: SPB Academic Publishing, 191–200.
- Bongers F, Popma J. 1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. *Botanical Gazette* 151: 354–365.
- Bongers F, Popma J, Del Castillo JM, Carabias J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55–80.
- Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC, Bustamante M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* 24: 891–899.
- Cavender-Bares J, Kitajima K, Bazzaz FA. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635–662.
- Charnov EL. 1993. *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford: Oxford University Press.
- Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531–536.
- Condit RS, Aguilar S, Hernandez A, Perez R, Lao S, Angehr G, Hubbell SP, Foster RB. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* 20: 51–72.
- Cornelissen JHC. 1999. A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118: 248–255.
- Corner E. 1949. The Durian theory, or the origin of the modern tree. *Annals of Botany* 13: 368–414.
- Croat TB. 1978. *Flora of Barro Colorado Island*. Stanford, CA: Stanford University Press.
- Dalling JW, Hubbell SP, Silveira K. 1998. Seed dispersal, seedling establishment and gap partitioning among pioneer trees. *Journal of Ecology* 86: 674–689.
- Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, *et al.* 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295–304.

- Enquist BJ, West GB, Charnov EL, Brown JH. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**: 907–911.
- Falster DS, Westoby M. 2003. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist* **158**: 509–525.
- Falster DS, Warton DI, Wright IJ. 2003. (S)MATR: standardised major axis tests and routines. <http://www.bio.mq.edu.au/ecology/SMATR/>
- Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.
- Fonseca CR, Overton JM, Collins B, Westoby M. 2000. Shifts in trait combinations along rainfall and phosphorus gradients. *Journal of Ecology* **88**: 964–977.
- Garland TJ, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18–32.
- Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.
- Givnish TJ. 1978. Ecological aspects of plant morphology: leaf form in relation to environment. In: Sattler R ed. *Theoretical plant morphology*. Leiden, The Netherlands: Leiden University Press, 83–142.
- Givnish TJ. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner B ed. *Plant stems: physiology and functional morphology*. San Diego, CA: Academic Press, 3–49.
- Gower ST, Reich PB, Son Y. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiology* **12**: 327–345.
- Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**: 259–281.
- Hacke UG, Sperry JS, Pittermann J. 2005. Efficiency versus safety tradeoffs for water conduction in angiosperm vessels versus gymnosperm tracheids. In: Holbrook NM, Zwieniecki MA eds. *Vascular transport in plants*. Oxford: Elsevier/Academic Press, 333–353.
- Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Henery ML, Westoby M. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* **92**: 479–490.
- Ibarra-Manríquez G, Martínez-Ramos M, Oyama K. 2001. Seedling functional types in a lowland rain forest in Mexico. *American Journal of Botany* **88**: 1801–1812.
- Ibarra-Manríquez G, Sinaca S. 1987. *Listados florísticos de México VII*. Estación de Biología Tropical Los Tuxtlas, Veracruz, Mexico: Instituto de Biología, Universidad Nacional Autónoma de México.
- Jakobsson A, Eriksson O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* **88**: 494–502.
- Kaiser HF. 1960. The application of electronic computers to factor analysis. *Educational and Psychological Measurement* **20**: 141–151.
- King DA, Davies SJ, Nur Supardi MN, Tan S. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology* **19**: 445–453.
- Kitajima K. 1992. *The importance of cotyledon functional morphology and patterns of seed reserve utilization for the physiological ecology of neotropical tree seedlings*. PhD Thesis, University of Illinois, Urbana-Champaign.
- Kocacinar F, Sage RF. 2004. Photosynthetic pathway alters hydraulic structure and function in woody plants. *Oecologia* **139**: 214–223.
- Lawton RO. 1984. Ecological constraints on wood density in a tropical montane rain forest. *American Journal of Botany* **71**: 261–267.
- Leigh J, Egbert G, Rand S, Windsor DM, eds 1996. *The ecology of a tropical forest: seasonal rhythms and long-term changes*, 2nd edn. Washington, DC: Smithsonian Institution Press.
- Leishman MR, Wright IJ, Moles AT, Westoby M. 2000. The evolutionary ecology of seed size. In: Fenner M ed. *Seeds: the ecology of regeneration in plant communities*. Wallingford, UK: CAB International, 31–57.
- McDade LA, Hartshorn GS. 1994. La Selva Biological Station. In: McDade LA, Bawa KS, Hespeneheide HA, Hartshorn GS, eds. *La Selva: ecology and natural history of a neotropical rain forest*. Chicago: University of Chicago Press, 6–14.
- Meinzer FC. 2003. Functional convergence in plant responses to the environment. *Oecologia* **134**: 1–11.
- Mencuccini M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell and Environment* **26**: 163–182.
- Moles A, Westoby M. 2000. Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos* **90**: 517–526.
- Moles AT, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* **92**: 372–383.
- Moles AT, Falster DS, Leishman MR, Westoby M. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology* **92**: 384–396.
- Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M. 2005. A brief history of seed size. *Science* **307**: 576–580.
- Muller-Landau HC. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **36**: 20–32.
- New M, Hulme M, Jones P. 1999. Representing twentieth-century space-time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate* **12**: 829–856.
- Niklas K. 1992. *Plant biomechanics: an engineering approach to plant form and function*. Chicago: University of Chicago Press.
- Pagel MD. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* **156**: 431–442.
- Perez-Harguindeguy N, Diaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil* **218**: 21–30.
- Pickup M, Westoby M, Basden A. 2005. Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology* **19**: 88–97.
- Pitman NCA, Terborgh JW, Silman MR, Nunez VP, Neill DA, Ceron CE, Palacios WA, Aulestia M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**: 2101–2117.
- Poorter L, Arets EJMM. 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. *Plant Ecology* **166**: 295–306.
- Read C, Wright IJ, Westoby M. 2006. Scaling up from leaf to canopy-aggregate properties in sclerophyll shrub species. *Austral Ecology* **31**: 310–316.
- Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA* **94**: 13730–13734.
- Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span – a test across biomes and functional groups. *Oecologia* **114**: 471–482.
- Roderick ML. 2000. On the measurement of growth with applications to the modelling and analysis of plant growth. *Functional Ecology* **14**: 244–251.
- Rossetto M, Kooyman RM. 2005. The tension between dispersal and persistence regulates the current distribution of rare palaeo-endemic rain forest flora: a case study. *Journal of Ecology* **93**: 906–917.
- Ryan MG, Yoder BJ. 1997. Hydraulic limits to tree height and tree growth: what keeps trees from growing beyond a certain height? *Bioscience* **47**: 235–242.
- Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* **140**: 543–550.
- Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd edn. New York: W.H. Freeman and Company.

- Stevens PF. 2004.** *Angiosperm phylogeny website*, Version 5, May 2004. <http://www.mobot.org/MOBOT/research/APweb/>
- Stratton L, Goldstein G, Meinzer FC. 2000.** Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell and Environment* **23**: 99–106.
- Thompson K, Rabinowitz D. 1989.** Do big plants have big seeds? *American Naturalist* **133**: 722–728.
- Turner IM. 2001.** *The ecology of trees in the tropical rain forest* Cambridge: Cambridge University Press.
- Webb CO, Ackerly DD, Kembel S. 2004.** *Phylocom. Software for the analysis of community phylogenetic structure and character evolution.* <http://www.phylodiversity.net/phylocom/>
- Webb CO, Donoghue MJ. 2005.** Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* **5**: 181–183.
- Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999.** Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**: 609–620.
- Westoby M. 1999.** Generalization in functional plant ecology: the species sampling problem, plant ecology strategies schemes, and phylogeny. In: Pugnaire FI, Valladares F eds. *Handbook of functional plant ecology* New York: Marcel Dekker, 847–872.
- Westoby M, Wright IJ. 2003.** The spectrum of twig-size variation and its correlates among perennial species in fire-prone sclerophyll vegetation. *Oecologia* **135**: 621–628.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, et al. 2004.** The world-wide leaf economics spectrum. *Nature*, **428**: 821–827.
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, et al. 2005.** Assessing the generality of global leaf trait relationships. *New Phytologist* **166**: 485–496.
- Wright SJ, Colley M. 1994.** Introduction to tropical forests and the Parque Natural Metropolitano. In: Wright IJ, Colley M eds. *Assessing the canopy: assessment of biological diversity and microclimate of the tropical canopy. Phase 1.* Nairobi, Kenya: United Nations Environment Program, Smithsonian Tropical Research Institute and Parque Natural Metropolitano, 1–4.
- Zimmerman JK, Everhami EM, Waide RB, Lodge DJ, Taylor CM, Brokaw NVL. 1994.** Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* **82**: 911–922.

APPENDIX 1

Preliminary investigation of properties of sun leaves versus shade leaves

Specific leaf area (SLA) and leaf size were measured separately for outer-canopy ('sun') and shaded leaves at three sites (PNM, Fort Sherman and Los Tuxtlas), for 96 species in total. We ran additional analyses to those described in the main text in order to determine whether (or what size of) systematic bias was likely to be introduced to our analyses by using data collected using different protocols (i.e. sun only, shade only, and mixed sun/shade leaves collected at different sites). For these analyses, the (\log_{10} -transformed) trait data were compared using the standardized major axis (SMA) analogue of standard analysis of covariance (Warton and Weber, 2002). That is, a SMA slope was fitted for the species at each individual site, and these site-specific slopes then tested for heterogeneity. Where non-heterogeneity is demonstrated a common SMA slope can be estimated and elevation (intercept) differences among the individual slopes can be tested for. SMA routines were run in a DOS-based computer package, (S)MATR (Falster *et al.*, 2003); further details of the methods can be found in the (S)MATR documentation (available from <http://www.bio.mq.edu.au/ecology/SMATR/>). In these analyses, a common fitted slope with 95 % CIs overlapping 1 would indicate directly proportional scaling between the \log_{10} -transformed variables, i.e. that any mean difference between properties of sun and shade leaves was invariant with respect to variation in that property (SLA or leaf size). To show that no mean difference existed between sun and shade leaves, a y-intercept not significantly different to 0 would also be required.

SMAs fitted to each site for SLA_{sun} (y) on SLA_{shade} (x) did not differ significantly in slope ($P = 0.333$), with a common fitted slope (β) not significantly different from 1 ($\beta = 0.96$; 95 % CI: 0.82, 1.12). However, the SMA intercept of each individual slope differed significantly from 0, and intercepts also differed among sites ($P < 0.001$). On average, SLA_{sun} was 33 % lower than SLA_{shade} at Los Tuxtlas and 59 % lower than SLA_{shade} at both PNM and Fort Sherman. SMAs fitted to each site for leaf size_{sun} on leaf size_{shade} did not differ significantly in slope ($P = 0.233$), with a common fitted slope of 1.02 (95 % CI: 0.91, 1.14). In this case the SMAs fitted to each site did not differ in intercept ($P = 0.394$), but were significantly offset from a $y = x$ slope such that, on average, sun leaves were 28 % smaller in area than shade leaves.

For comparing SLA or leaf size with the other measured traits, these results indicated that no systematic bias in terms of relationship-slope should have been introduced by the different leaf-sampling protocols at different sites. However, shifts in SMA intercepts may have resulted, weakening our ability to interpret any such patterns in terms of other variables, such as site climate. Consequently, in the main text we do not present analyses comparing SMA trait relationships fitted to individual sites.

Appendix 2

Details of pairwise trait relationships among woody species (trees, shrubs, lianas) from 7 neotropical forests

	Site*	Wood density				Seed size				Fruit size				SLA				Leaf size				Leaf size (S only) [†]			
		r^2	P	n	+/-	r^2	P	n	+/-	r^2	P	n	+/-	r^2	P	n	+/-	r^2	P	n	+/-	r^2	P	n	+/-
Plant height	BCI	0.02	0.071	138	(-)	0.08	0.001	153	+	0.17	<0.001	129	+	0.001	0.890	28		0.02	0.038	221	+	0.05	0.005	163	+
	FS	0.05	0.674	6										0.07	0.667	5		0.01	0.855	6		0.06	0.684	5	
	LC	0.01	0.397	59		0.002	0.769	51						0.22	0.004	36	+	<0.001	0.997	37		<0.001	0.997	37	
	LS																								
	LT	0.02	0.166	104		0.13	<0.001	198	+	0.15	<0.001	196	+	0.37	<0.001	69	-	0.04	0.096	66		0.01	0.638	47	
	PNM																								
	YM	0.004	0.268	308		0.06	<0.001	295	+	0.03	<0.001	552	+					0.01	0.003	748	-	0.003	0.192	551	
Wood density	BCI					0.01	0.382	103		0.02	0.231	87		0.01	0.579	24		0.15	<0.001	108	-	0.24	<0.001	70	-
	FS													0.08	0.167	26		0.15	0.033	31	-	0.25	0.015	23	-
	LC					0.07	0.058	51	(+)					0.21	0.005	36	-	0.25	0.002	37	-	0.25	0.002	37	-
	LS					0.01	0.897	6						0.002	0.694	78		0.05	0.030	96	-	0.15	0.001	73	-
	LT					0.13	<0.001	101	+	0.01	0.470	101		0.05	0.117	49		0.36	<0.001	49	-	0.30	0.001	34	-

	PNM													0.00	0.930	14		0.23	0.164	10		0.23	0.275	7	
	YM					0.04	0.004	210	+	0.01	0.243	212						0.03	0.002	292	-	0.16	<0.001	201	-
Seed size	BCI									0.43	<0.001	193	+	0.05	0.286	23		<0.001	0.905	131		<0.001	0.956	100	
	FS																								
	LC													0.04	0.295	30		0.002	0.796	32		0.002	0.796	32	
	LS													<0.001	0.986	17		0.08	0.244	19		0.03	0.514	16	
	LT									0.34	<0.001	251	+	0.15	0.001	69	-	0.07	0.038	66	-	0.06	0.083	48	(-)
	PNM																								
	YM									0.28	<0.001	212	+					0.004	0.280	274		0.002	0.556	209	
Fruit size	BCI													0.01	0.756	19		0.05	0.020	107	+	0.06	0.032	84	+
	FS																								
	LC																								
	LS																								
	LT													0.18	<0.001	69	-	0.02	0.308	66		0.02	0.363	48	
	PNM																								
	YM																	0.02	<0.001	531	+	0.03	<0.001	449	+

SLA	BCI																	0.16	0.040	26	+	0.17	0.104	17	
	FS																	<0.001	0.962	55		0.001	0.825	41	
	LC																	0.00	0.938	22		<0.001	0.938	22	
	LS																	0.17	<0.001	217	–	0.17	<0.001	215	–
	LT																	0.03	0.189	67		0.01	0.536	48	
	PNM																	0.01	0.701	27		0.02	0.591	15	
	YM																								

* Site codes: BCI, Barro Colorado Island (Panama); FS, Fort Sherman canopy crane (Panama); LC, La Chonta (Bolivia); LS, La Selva (Costa Rica); LT, Los Tuxtlas (Mexico); PNM, Parque Natural Metropolitano canopy crane (Panama); YM, Yasuní (Ecuador) + Manu (Peru).

† For compound-leaved species, ‘leaf size’ refers to the average size of individual leaflets. Only simple-leaved species were included in analyses concerning ‘leaf size (S only)’. All traits except wood density were log₁₀-transformed prior to analysis. The sign of the correlation *r* value is indicated for statistically significant relationships ($P \leq 0.05$), and included in parentheses for marginally significant cases ($0.05 \leq P \leq 0.10$).

APPENDIX 3

Principal components analysis of trait data for 2134 woody species from the Neotropics

	Axis 1	Axis 2	Axis 3	Axis 4	Total %	Analysis N
Seed size	0.65 (+)	<0.01	0.11 (+)	0.03	80	1288
Fruit size	0.62 (+)	0.06 (+)	0.12 (+)	<0.01	80	959
Plant height	0.41 (+)	<0.01	0.22 (–)	0.18 (+)	81	1236
SLA	0.30 (–)	<0.03	0.30 (+)	0.31 (+)	95	410
Wood density	0.09 (+)	0.51 (–)	0.06 (+)	0.19 (–)	85	597
Leaf size	<0.01	0.69 (+)	0.07 (+)	0.06 (–)	82	1228
Eigenvalue	2.07	1.30	0.89	0.78		

The first component (axis) explained 35 % of total trait variation, the second a further 22 %, the third 15 %, the fourth 13 % (total, 85 %). The proportion of variation (r^2) in each trait explained by each axis is indicated, as well as the sign of the correlation coefficient (trait loading), where significant ($P \leq 0.05$). For each trait the total proportion of variation explained by the analysis is given in the rightmost column. Eigenvalues <1 indicate axes that explain less variance than each individual variable contributes. All variables except wood density were \log_{10} -transformed, and the PCA was run on standardized data (i.e. the correlation rather than the covariance matrix).

LITERATURE CITED

Falster DS, Warton DI, Wright IJ. 2003. *(S)MATR: standardised major axis tests and routines*. <http://www.bio.mq.edu.au/ecology/SMATR/>

Warton DI, Weber NC. 2002. Common slope tests for bivariate errors-in-variables models. *Biometrical Journal* **44**: 161–174.