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REVIEW AND SYNTHESIS

Global patterns of leaf mechanical properties

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Abstract

Leaf mechanical properties strongly influence leaf lifespan, plant–herbivore interactions, litter decomposition and nutrient cycling, but global patterns in their interspecific variation and underlying mechanisms remain poorly understood. We synthesize data across the three major measurement methods, permitting the first global analyses of leaf mechanics and associated traits, for 2819 species from 90 sites worldwide. Key measures of leaf mechanical resistance varied *c.* 500–800-fold among species. Contrary to a long-standing hypothesis, tropical leaves were not mechanically more resistant than temperate leaves. Leaf mechanical resistance was modestly related to rainfall and local light environment. By partitioning leaf mechanical resistance into three different components we discovered that toughness per density contributed a surprisingly large fraction to variation in mechanical resistance, larger than the fractions contributed by lamina thickness and tissue density. Higher toughness per density was associated with long leaf lifespan especially in forest understory. Seldom appreciated in the past, toughness per density is a key factor in leaf mechanical resistance, which itself influences plant–animal interactions and ecosystem functions across the globe.

Keywords

Biomechanics, fibre, global-trend, leaf traits, meta-analysis, toughness.

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INTRODUCTION

Leaves are the primary organ of photosynthesis, responsible for most terrestrial carbon assimilation (Beer *et al.* 2010). Leaves of many species are thin, flat structures, ideal for light interception (Givnish 1988) but susceptible to herbivores, wind and other sources of physical damage (Niklas 1992; Read & Stokes 2006). Mechanical resistance is thus essential to protect leaves from herbivores and other risks of injury (e.g. Feeny 1970; Coley 1983; Grubb 1986; Turner 1994;

Choong 1996; Wright & Vincent 1996; Pérez-Harguindeguy *et al.* 2003; Lucas 2004; Fine *et al.* 2006; Sanson 2006; Clissold 2007; Kitajima & Poorter 2010), and has been considered a key trait involved in plant ecological strategies (Coley 1983; Reich *et al.* 1991; Wright & Westoby 2002). The mechanical resistance of leaves also has important consequences for ecosystem function through species-specific effects on leaf litter decomposition and nutrient cycling (Cornelissen & Thompson 1997; Pérez-Harguindeguy *et al.* 2000; Díaz *et al.* 2004). Despite these important roles in ecological processes we

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know relatively little about which factors influence mechanical resistance across a range of species, and to what extent habitat conditions such as temperature, precipitation and light are associated with leaf mechanical resistance. We addressed these gaps in knowledge by analysing a newly compiled, global dataset across wide latitudinal ranges on multiple continents.

Leaf mechanical resistance can be expressed per unit fracture length or per unit fracture surface area, these quantities being known as 'structural resistance' and 'material resistance', respectively. Structural resistance depends both on leaf thickness and material resistance. In turn, material resistance depends both on tissue density and toughness per unit density. For example, thicker leaves are more structurally resistant than thinner leaves when leaves are made from the same material. Higher structural resistance can also be achieved via tougher material or denser tissue, without changing thickness. To understand the mechanisms underlying variation in leaf structural resistances, we propose a framework to partition the variation of leaf structural resistance into three underlying components: lamina thickness T, tissue density ρ and toughness per unit tissue density γ (Fig. 1d; see Material and Methods for more detail). Applying this framework to many species, we look for general mechanisms underlying variation in leaf structural resistance.

From the three underlying components of leaf structural resistance, thickness and tissue density together determine leaf mass per area (LMA; e.g. for flat leaves, by definition, LMA = $T \times \rho$). LMA is a key trait underlying the 'leaf economic spectrum'. This spectrum captures about three-quarters of the interspecific variation in several key traits concerning carbon fixation and nutrient use (Wright *et al.* 2004). At one end of the spectrum, 'fast-return' species are characterized by having low LMA, high nitrogen and phosphorus concentrations, high respiration rates and maximum photosynthetic rates, and short leaf lifespan (LL) – meaning that their fast photosynthetic returns are not sustained for long periods. At the other extreme, 'slow return' species have the opposite set of traits (Chabot & Hicks 1982; Reich *et al.* 1991, 1997; Wright *et al.* 2004). Although this relationship has been frequently found in regional studies as well as in global analyses, the mechanisms that coordinate LL with carbon metabolism and nutrient profiles are unclear. LMA is reasonably well correlated with LL (e.g. $R^2 = 0.42$; Wright *et al.* 2004), but it is not known whether LL is influenced by LMA *per se*, or instead by leaf structural resistance associated with higher LMA (Shipley *et al.* 2006; Poorter *et al.* 2009; Kitajima & Poorter 2010). Thus, an analysis of leaf structural resistance should provide improved mechanistic understanding of the relationship between LMA and LL.

Plant communities established in different climates have long been considered to show different levels of leaf structural resistance. Sclerophylly (meaning 'hard leaved') is common in plants from Mediterranean climates that have strong seasonal drought (Schimper 1903; Read & Sanson 2003). However, because sclerophyllous species are also common on infertile soils (Loveless 1961; Beadle 1966; Grubb 1986; Edwards *et al.* 2000; Read *et al.* 2005, 2009) and in tropical forests (Turner *et al.* 1993), moisture regime cannot be the sole driver of structural resistance (Turner 1994). Nonetheless, the relationship between leaf structural resistance and water availability has yet to be quantified at broad geographic scales.

Another long-standing hypothesis is that, on average, leaves of tropical species are more mechanically resistant than those of temperate species – due to an evolutionary response to higher herbivore pressures in the tropics (Coley & Aide 1991; Coley &
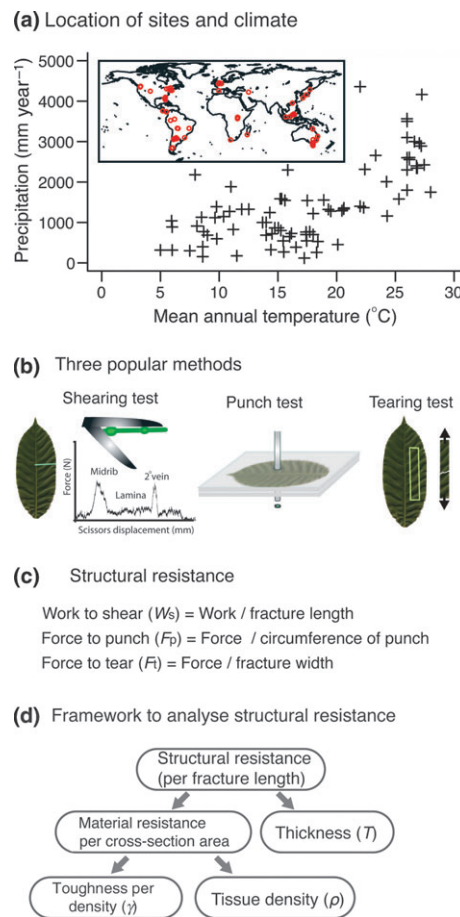

Figure 1 Synthesis of leaf biomechanics and framework for the analysis. (a) Mean annual temperature and mean annual precipitations for the 90 sites. Locations of the sites are shown in the inset. (b) Three commonly used tests in leaf biomechanics studies. Shearing tests measure the work (force × displacement) to traverse a leaf. Punch tests measure the maximum force to punch out the leaf lamina. Tearing tests measure the maximum force to tear a leaf strip. (c) To make data comparable across studies, we first normalized the data; total work (unit: J) or maximum force (unit: N) were expressed per unit fracture length, defined here as work to shear (W_s), force to punch (F_p) and force to tear (F_t) respectively. These we call 'structural resistance'. (d) A framework to analyse this structural resistance. First, it was partitioned into 'leaf thickness (T)' and 'material resistance'. Then material resistance, which is expressed on a cross-section area basis, was further partitioned into 'tissue density (ρ)' and 'toughness (or strength) per unit tissue density (γ)'. This framework can be applied equally to the three tests. See the main text for detail.

Barone 1996; Pennings & Silliman 2005; Schemske *et al.* 2009). Some studies have indeed supported this view (Coley & Aide 1991; Siska *et al.* 2002), but there have been others in which no such trend was found (Hallam & Read 2006; Read & Stokes 2006). In common, all of these analyses concerned species from fewer than 10 sites. Here, we compile data from many more species and sites, facilitating a robust test of this hypothesis.

Independent of broad geographic trends in leaf traits, there can be wide variation in leaf mechanical resistance among co-occurring species (Turner 1994; Read & Stokes 2006). Part of this variation may be associated with local light environment. Leaves developed in shade ('shade leaves', including shade specialists and juveniles of canopy trees in forest understory) often have lower LMA, thus they are expected to have lower structural resistance than leaves that have

developed in higher light (sun leaves). However, evidence is accumulating that shade leaves may achieve longer lifespans at a given LMA than do sun leaves (Coley & Aide 1991; Westoby *et al.* 2002; Lusk *et al.* 2008), in apparent conflict with the positive LMA–LL relationship underlying the leaf economics spectrum (Wright *et al.* 2004). Recent case studies suggest that, even though shade leaves are thin, they also tend to be tougher per unit dry mass (Onoda *et al.* 2008; Lusk *et al.* 2010). Examination of leaf mechanical properties may thus explain this anomalous trend in the LMA–LL relationship.

For this study, we compiled a global dataset of 2819 species-at-site observations from 90 sites covering a wide range of ecosystems including tropical rainforests, temperate forests, grasslands and deserts (Fig. 1a). Using this dataset, we quantify: (1) the range of variation in leaf mechanical resistance across the globe, (2) the relative contributions of underlying components to variation in leaf structural resistance, (3) whether tropical leaves are indeed more mechanically resistant than temperate leaves, (4) to what extent climate variables explain global patterns of leaf mechanical resistance and (5) whether leaf mechanical resistance is a better predictor of LL compared to LMA.

MATERIAL AND METHODS

Data compilation

Leaf mechanical trait data were compiled from both published and unpublished sources. A dataset was considered suitable provided it contained data for at least four species. The total dataset represented 90 sites from a wide range of ecosystems (Fig. 1a, Appendix S1) and contained 2819 species-at-site combinations, consisting of 2004 species, with 490 species occurring at two or more sites. Sun, gap and shade leaves were considered separately, where available. The data set is available in TRY database according to the intellectual property guidelines of TRY (http://www.try-db.org/).

Most datasets were site-based, meaning that we could reasonably attach climate data to the trait data. Literature data from growth chamber experiments were also compiled but these were excluded from climate-related analyses, as were data from species that had obviously been transplanted from other regions (e.g. some plants in botanical gardens). Climate data (MAT, mean annual temperature and MAP, mean annual precipitation) were taken from the original literature or data providers. For a small portion of studies (< 20%), climate data were extracted from the CRU CL 2.0 dataset – a set of global climate grids with 10 min spatial resolution (New *et al.* 1999).

The methods that have been most frequently used to measure leaf mechanical resistance can be classified into three major types of tests: (1) Shearing tests, also called scissoring, cutting and guillotine tests (Atkins & Mai 1979; Lucas & Pereira 1990; Wright & Illius 1995; Darvell *et al.* 1996; Henry *et al.* 1996; Aranwela *et al.* 1999; Wright & Cannon 2001), (2) Punch tests, including punch-and-die and penetrometer tests (Williams 1954; Cherrett 1968; Feeny 1970; Coley 1983; Choong *et al.* 1992; Aranwela *et al.* 1999; Onoda *et al.* 2008) and (3) Tearing tests, also called tensile tests (Vincent 1992; Hendry & Grime 1993; Aranwela *et al.* 1999; Cornelissen *et al.* 2003). We examined details of measuring methods, units of leaf mechanical properties and conditions of leaf samples to facilitate our data comparison in a biologically meaningful way (see Supporting information for detail). Here, we briefly review methods of the three main test-types and describe how data were normalized in each test (see also Fig. 1).

Shearing test

Shearing tests measure how much work is required to cut across a leaf with a single blade (against an anvil) or with a pair of blades (i.e. instrumented scissors). For all shearing tests, force and displacement are simultaneously recorded, and the total work required to cut a specimen is given by the area under the force–displacement curve. Work can be expressed per unit fracture length or per unit cross-section area. Here, work per unit fracture length is defined as 'work to shear' (W_s, J m^{-1}) and work per unit cross-section area ($= W_s$/lamina thickness) is defined as 'specific work to shear' (W_{ss}, J m^{-2}) (Aranwela *et al.* 1999; Read & Sanson 2003). Specific work to shear is also known as 'fracture toughness' (Atkins & Mai 1979; Lucas & Pereira 1990). The midrib is normally avoided when making shearing tests, except sometimes in the case of small leaves, for which it is difficult to distinguish the midrib from the rest of the lamina (Wright & Cannon 2001).

Five types of cutting devices were used in the studies from which we sourced shearing test data. Among them, 'a portable fracture tester' (scissor test) (Darvell *et al.* 1996) was the most common, accounting for 83% of available data. To estimate how sensitive reported data were to differences in machine configuration (Henry *et al.* 1996), a set of standard materials was cut with each machine, and data were compared (see Supporting information for more detail). We found that the five machines produced similar values for these standard materials (Table S1), therefore no further cross-calibration of source data was made.

Punch test

Penetrometer or punch-and-die tests measure the maximum load required for the punch rod to penetrate a leaf. In most cases, measurements were made on leaf laminas (excluding midribs), except for leaves so small that the midrib could not be avoided (which, typically, have little thickening about the midrib anyway). There was variation in the punch diameter (0.5–9.5 mm) and shape (flat-end, blunt or pointed) among studies. Here, we restricted our analyses to studies that specified punch size and used a flat-end punch, so that data could be normalized. As test specimens typically fracture at the rim of punch where force is most concentrated, fracture length can be calculated from the circumference of the punch (Gere & Goodno 2009). Maximum force can then be expressed per fracture length along the lamina surface ('force to punch', F_p, kN m^{-1}) and per cross-section area of lamina ('specific force to punch', F_{ps}, MN m^{-2}), as for shearing tests. Note that our normalization (per unit circumference of punch rod) differs from the traditional form of expression for punch strength (i.e. per unit punch area) because data calculated in the latter way are very sensitive to the size of the punch diameter (Aranwela *et al.* 1999; see Supporting information for more detail), hence our method avoided this problem.

Tearing test

Tensile tests measure the breaking force required to tear a strip of leaf lamina; hence these are also known as 'tearing' tests. Tests are commonly made from the central part of the leaf, in parallel to its main axis and avoiding the midrib, unless the midrib was not obvious (e.g. monocots) or could not be avoided (very small leaves)

(Cornelissen *et al.* 2003; Díaz *et al.* 2004). The maximum force per unit width of leaf specimen was defined as the 'force to tear' (F_t, kN m^{-1}), and the maximum force per unit cross-section area (=F_t divided by lamina thickness) was defined as 'specific force to tear' (F_{ts}, MN m^{-2}). Strictly speaking, F_{ts} is equivalent to the property known as 'tensile strength' in engineering (Gere & Goodno 2009), however, in the past this term has been used for both what we call here F_t and F_{ts} (Hendry & Grime 1993; Cornelissen *et al.* 2003; Díaz *et al.* 2004). Therefore, to avoid confusion, we use F_t and F_{ts} instead of the term 'tensile strength'.

Mechanical terms

Shearing tests measured the energy while punch and tearing tests often measured the maximum force required to fracture a leaf. Therefore, the units for shearing tests are different from those for punch and tearing tests. However, in common, work to shear (W_s), force to punch (F_p) and force to tear (F_t) are parameters normalized per unit fracture length, reflecting the degree to which a leaf can resist external forces, per unit fracture length. For practical reasons we refer to these parameters collectively as 'structural resistance'. Similarly, specific work to shear (W_{ss}), specific force to punch (F_{ps}) and specific force to tear (F_{ts}) are parameters normalized per unit cross-sectional area, and we refer to these collectively as 'material resistance'. We use 'mechanical resistance' as a more general term including both 'structural resistance' and 'material resistance'.

Other leaf traits

Where available, data for lamina thickness, LMA, chemically extracted fibre content and LL were also extracted from source datasets. Lamina thickness was generally measured with a micrometre or thickness gauge. LMA was measured either on whole leaves or on leaf discs. Whole-leaf LMA and leaf disc LMA were strongly correlated in the subset of our database where both measurements were available ($LMA_{leaf\ discs} = 0.899 \times LMA_{whole}^{1.003}$, $R^2 = 0.920$, $n = 364$) and this relationship was used to standardize whole-leaf LMA to leaf disc LMA. Tissue density was calculated as LMA divided by lamina thickness. In all cases chemical fibre content was measured using the van Soest method (Van Soest 1994). This technique extracts fibre with neutral detergent or acid detergent, giving neutral detergent fibre (NDF) and acid detergent fibre (ADF), respectively. NDF roughly represents cellulose, hemicellulose, lignin and cutin, and ADF represents cellulose, lignin and cutin (Van Soest 1994). Leaf lifespan was measured by long-term field observations/phenological data. The number of biomechanics studies which included LL data was limited, therefore additional data were obtained from studies not involving leaf biomechanics (Wright *et al.* 2004), provided that the species name was exactly matched between the studies, and that the light environment category (sun, gap or shade) was the same.

Data analysis

Leaf trait values were log$_{10}$-transformed before analysis, both because these variables are most naturally interpreted on a proportional scale and because log-transformation approximately normalized the data (which were right-skewed). Site rainfall was also log-transformed, whereas MAT was left untransformed because its distribution was approximately symmetric without transformation.

Structural resistance (W_s, F_p and F_t) can be understood as the product of three components – lamina thickness (T), tissue density (ρ) and toughness (or strength) per unit tissue density (γ) (Fig. 1d).

$$W_s = T \cdot \rho \cdot \gamma$$
$$F_p = T \cdot \rho \cdot \gamma* \quad\quad\quad (1)$$
$$F_t = T \cdot \rho \cdot \gamma*,$$

where γ (or $\gamma*$) is calculated from measurements of W_s (or F_p, F_t), T and ρ. Toughness per density is equivalent to the property called 'specific toughness' in engineering (Atkins & Mai 1985), but we call it γ to avoid confusion. For the punch and tearing tests, $\gamma*$ (strength per density) is used instead of γ as these methods measure the force rather than the work required to fracture. When log-transformed, eqn (1) has the structure:

$$Y = X_1 + X_2 + X_3, \quad\quad\quad (2)$$

where Y is log(structural resistance), X_1 is log(T), X_2 is log(ρ) and X_3 is log(γ). The sum of covariances between Y and X_i ($i = 1, 2, 3$) equals the variance of Y as follows:

$$Var(Y) = Cov(Y, Y) = Cov(Y, X_1) + Cov(Y, X_2) + Cov(Y, X_3).$$
$$(3)$$

Thus, the relative contribution of each component to structural resistance can be determined from its covariance [$Cov(Y, X_i)$] taken as a proportion of the variance of structural resistance [$Var(Y)$]. This type of variance partitioning has previously been used in key factor analysis (Smith 1973) and calculation of growth response coefficients (Poorter & van der Werf 1988). Note that eqn (3) differs from a standard regression model in two ways: first, the relationship is exact, with no error term; and second, the regression coefficients in the model are all known (and equal to one). This means that usual methods of analysis (such as multiple regression or path analysis) are not appropriate.

We note that since γ is a calculated quantity (e.g. $\gamma = W_s/T/\rho$) – rather than being measured directly – any measurement error is 'absorbed' by this term, potentially inflating the proportion of variance in structural resistance that is explained by γ. There were differences in machine devices, blade sharpness and handling protocols across studies, and the extent of these effects can be assessed by comparing results calculated across studies with results calculated separately within individual studies. Within individual studies, a single device and one protocol were used to measure leaf traits, so error variances associated with measuring methods should be minor.

Standardized major axis (SMA) slopes (Warton *et al.* 2006) were fitted to bivariate trait relationships because our aim was to describe the best-fit lines, or central axes, of these 'scaling' relationships. We note that the R^2 of an SMA relationship is identical to that of an ordinary least squares regression. Effects of climate variables (MAT and MAP) were quantified using bivariate regression as well as multiple regression analyses. Climate-related analyses were also run using monthly maximum/minimum temperature and precipitation from the CRU CL 2.0 data set, but since the correlation coefficients were no better than when using MAP and MAT we do not report these results. To partition variance of leaf traits into cross-site and within-site factors, linear mixed-effects models with a normally distributed random effect for site location were used (30, 37 and 41 sites for shear, punch and tear tests). We examined residual vs.

fitted plots from multiple regression analyses and mixed-effects models and did not observe any clear trends that led to us rejecting our assumption of linear effects (Figure S1). All analyses were run using the R software package (v2.9.0; R Foundation for Statistical Computing, Vienna, Austria).

For angiosperm species (98% of all species in our dataset), phylogenetically independent contrasts (PICs; Felsenstein 1985) were used to test whether correlations among traits in the 'cross-species' comparisons were driven by coordinated evolutionary trait-shifts in a convergent manner across the phylogeny. These tests used the 'aot' (analysis of traits) option within the program Phylocom (Webb *et al.* 2008). A phylogenetic tree was constructed for all of the angiosperms in our dataset from the updated APG II with a program, Phylomatic (http://www.phylodiversity.net/phylomatic/trees/R20040402.new). Species averages were calculated for each trait. Phylocom calculates Pearson's correlations between pairs of PIC, taking into account the branch lengths in the phylogeny (Webb *et al.* 2008). Phylocom handles polytomies with a method introduced by Pagel (1992) to obtain a single degree of freedom contrast at each polytomy. In this method, one trait was designated as X variable, whereas all other traits to be correlated with X were designated as Y variables. The nodes arising from a polytomy were then ranked based on the values of trait X. The species were then split into two groups at the median. This maximized the difference in means for trait X, and the other traits fell out according to their distribution between the two groups.

RESULTS

Leaf structural resistance and its underlying components

We found 481, 548 and 820-fold variation in leaf structural resistance for shear, punch and tearing tests across 1171, 970 and 928 species-at-site combinations, respectively. Within-species variation was typically less than sixfold with a few exceptions up to 35-fold. The overall variation was slightly larger for tearing data (F_t) compared to other

measures (W_s and F_p). This was partly due to the fact that tearing data included many forbs and monocots as well as woody eudicot species (hereafter woody species), while shear and punch data included mostly woody species. Monocots had on average 3.3 and 7.0 times higher force to tear than did woody and forb species, respectively (Table 1), indicating that monocot leaves with parallel veins are generally more resistant to tearing than woody and forb leaves.

The ranges of variation in leaf structural resistance (481–820-fold) were much wider than the range for T and LMA, which varied 58 and 42-fold respectively for the same leaves (Table 1). Leaf structural resistance was positively correlated with LMA across species (Fig. 2). In the shear test, LMA explained 50% of variation in W_s. The predictive power of LMA was lower in punch and tearing tests ($R^2 = 0.31$ and 0.22 respectively). The low R^2 in the tearing test was partly due to the mixture of different growth forms since each growth form has its own F_t–LMA relationship. F_t was more tightly correlated with LMA within growth forms ($R^2 = 0.242$–0.519; Fig. 2c) than across all species. The scaling coefficients of the all-species SMA slopes were significantly steeper than 1 in all cases (95% CIs: 1.52–1.66, 1.78–1.99 and 1.46–1.64 for shear, punch and tear tests, respectively). This indicates that leaves with higher LMA tended to be disproportionally more resistant against external forces such that a 10-fold increase in LMA corresponded with a 35–87-fold increase in structural resistance.

Thicker leaves tended to have greater structural resistance (W_s, F_p and F_t) ($R^2 = 0.06$–0.29; Fig. 3a–c). However, for any given T there was still substantial variation in structural resistance. Material resistance (W_{ss}, F_{ps} and F_{ts}), which was standardized to thickness, was modestly correlated with tissue density ($R^2 = 0.14$–0.20; Fig. 3d–f). The remaining variation could be attributed to toughness (or strength) per tissue density. Monocot species had higher strength per density than other growth forms (Fig. 3f, 3.6–4.2 times). Forbs and woody species had similar strength per density (Table 1), but tissue density of forbs was much lower than that of woody species (c. 60%), which contributed to their lower force to tear. When the data were expressed as phylogenetic divergences, there were similar positive

Table 1 Median, lower and upper 95% confidence intervals and number of species-at-site observation for leaf traits

|	All	Woody (sun leaf)	Woody (shade leaf)	Forb	Monocot
Work to shear (W_s, J m^{-1})	0.0874 (0.022, 0.539, 1197)	0.127 (0.029, 0.724, 591)	0.0664 (0.021, 0.171, 486)	0.0574 (0.033, 0.338, 15)	0.175 (0.018, 1.083, 16)
Force to punch (F_p, kN m^{-1})	0.321 (0.034, 1.619, 972)	0.331 (0.052, 1.758, 560)	0.35 (0.022, 1.179, 208)	0.231 (0.029, 0.754, 40)	0.557 (0.064, 2.056, 7)
Force to tear (F_t, kN m^{-1})	0.87 (0.17, 15.34, 928)	0.957 (0.20, 13.73, 289)	0.7 (0.40, 1.48, 35)	0.59 (0.14, 3.28, 361)	2.72 (0.54, 35.1, 201)
Specific work to shear (W_{ss}, J m^{-2})	452 (110, 1606, 1335)	513 (111, 1995, 651)	432 (192, 943, 520)	212 (6.3, 801.4, 26)	543 (176, 2684, 38)
Specific force to punch (F_{ps}, MN m^{-2})	1.58 (0.26, 6.10, 633)	1.33 (0.25, 6.10, 398)	2.35 (0.35, 5.58, 177)	0.561 (0.19, 1.31, 15)	0.354 (0.35, 0.35, 1)
Specific force to tear (F_{ts}, MN m^{-2})	3.31 (0.5, 47.2, 1021)	2.86 (0.56, 15.53, 339)	3.31 (1.7, 10.0, 35)	2.29 (0.43, 10.58, 365)	12.5 (1.9, 92.6, 240)
Leaf mass per area (LMA, g m^{-2})	65.3 (24, 215, 2105)	90.7 (37, 251, 965)	50.9 (26, 93, 510)	43.1 (16, 138, 348)	48.7 (22, 215, 132)
Lamina thickness (T, mm)	0.22 (0.11, 0.74, 2229)	0.259 (0.13, 0.86, 935)	0.187 (0.11, 0.32, 584)	0.247 (0.12, 0.95, 372)	0.21 (0.088, 1.505, 209)
Tissue density (ρ, g cm^{-3})	0.288 (0.093, 0.595, 1809)	0.360 (0.16, 0.68, 783)	0.278 (0.14, 0.44, 470)	0.178 (0.062, 0.429, 347)	0.222 (0.066, 0.472, 130)
W_{ss}/ρ (mJ g^{-1} m)	1.23 (0.37, 4.82, 873)	1.3 (0.28, 5.39, 445)	1.2 (0.54, 3.02, 372)	1.37 (0.8, 4.7, 11)	1.16 (0.64, 1.67, 6)
F_{ps}/ρ (N g^{-1} m)	4.51 (0.73, 16.06, 837)	4.13 (0.68, 12.93, 539)	8.22 (0.9, 19.2, 174)	3.94 (1.3, 9.8, 10)	3.43 (2.6, 6.1, 3)
F_{ts}/ρ (N g^{-1} m)	12.7 (3.4, 103.6, 823)	8.33 (3.1, 65.5, 280)	11.7 (7.7, 29.9, 35)	12.9 (3.2, 48.9, 340)	44.1 (13, 150, 128)
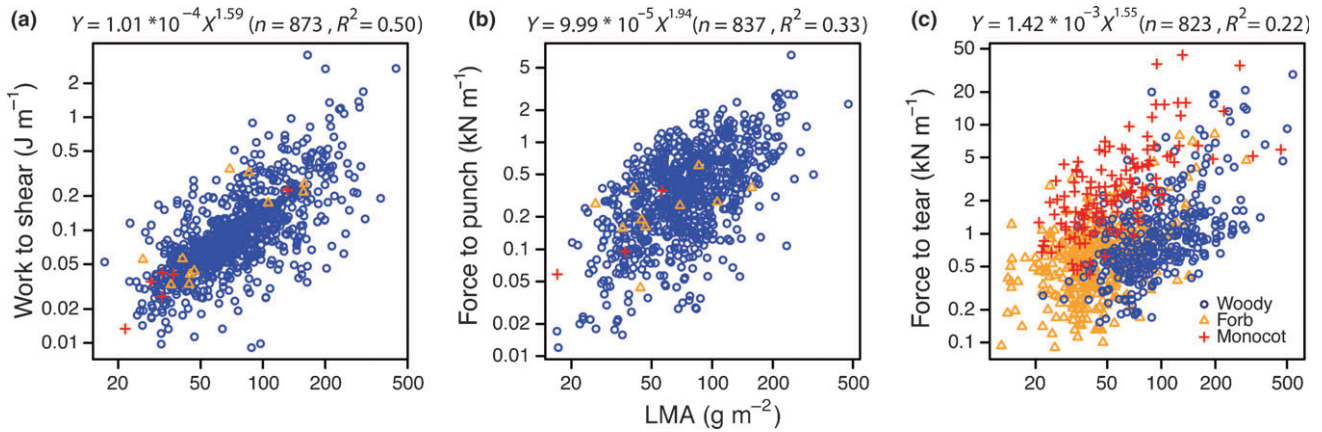
Figure 2 Relationships between leaf structural resistances and leaf mass per area (LMA). (a–c) Work to shear (W_s), force to punch (F_p) and force to tear (F_t) plotted against LMA.
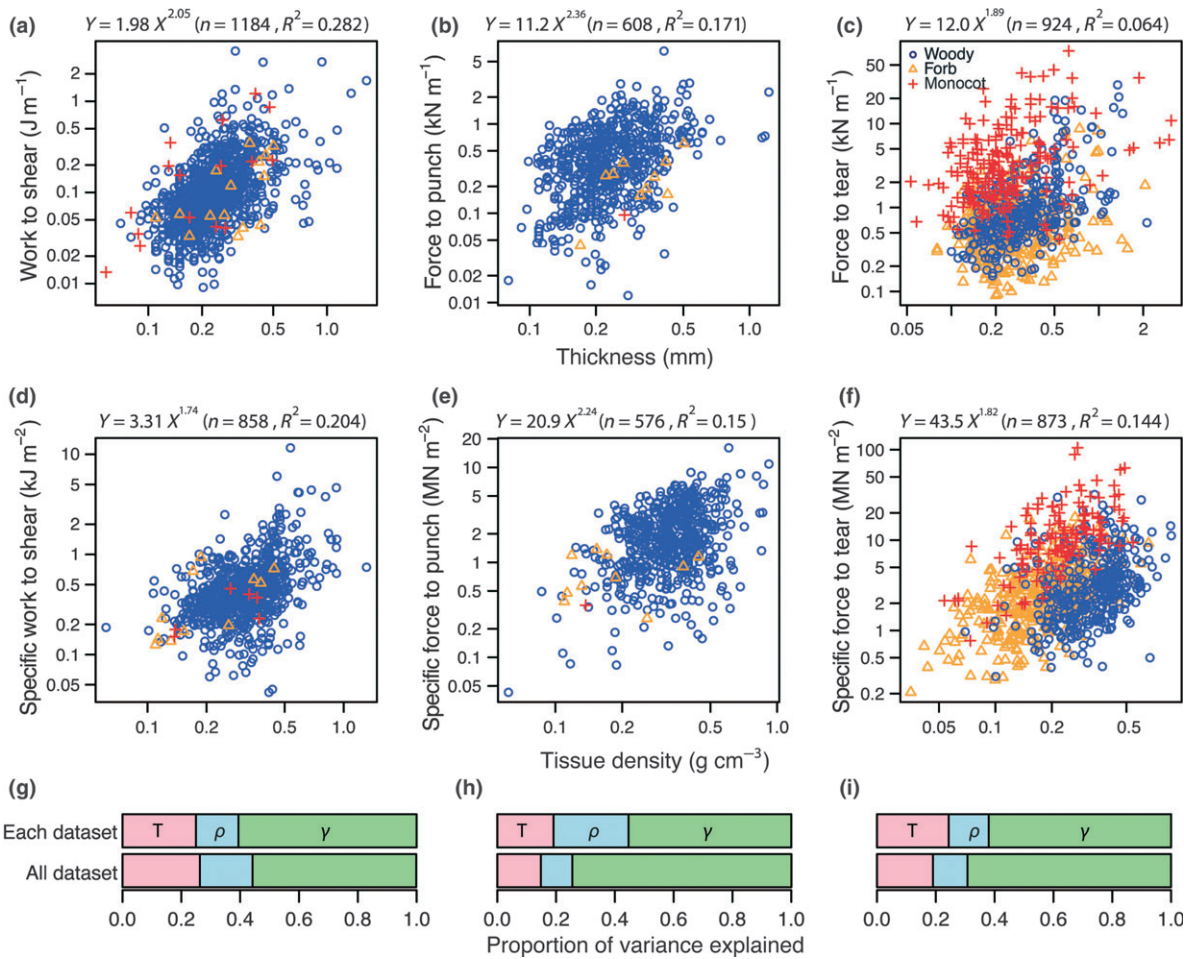

Figure 3 Analyses of leaf mechanical properties. (a–c) Work to shear (W_s), force to punch (F_p) and force to tear (F_t) plotted against lamina thickness (T). (d–f) Specific work to shear (= W_s/T), specific force to punch (F_p/T) and specific force to tear (F_t/T) plotted against tissue density. All correlations were significant ($P < 0.001$, either all observations or woody species). (g–i) Proportions of variance in structural resistance explained by lamina thickness (pink, T), tissue density (blue, ρ) and toughness (or strength) per density (green, γ) (see eqns 1 and 3). The pairs of bars represent proportions calculated with species-level observations pooled across studies (lower bar) or as averages of proportions obtained for each study separately (upper bar) (see also Table S3).

correlations among these traits as seen in cross-species analyses, suggesting that these trait associations have evolved repeatedly in many different clades of plants (Table S2).

Lamina thickness contributed 26% of the total variance in work to shear (W_s) among species, tissue density contributed 18%, and toughness per density (γ) 56% (Fig. 3g). Variation associated with

differences in shearing devices would inflate the proportion of variance in work to shear (W_s) attributed to γ (see Materials and Methods). However, the proportion of variance in W_s attributed to γ was, in fact, robust to pooling across studies – as indicated by very similar results between pooled data and means of individual studies (Fig. 3g). This was consistent with the similar values of W_s obtained for standard materials in different laboratories using different devices (Table S1). Punch and tearing tests showed broadly similar patterns to the shearing test: F_p and F_t could be partitioned between components in a similar manner to W_s (Fig. 3h,i). Contributions of γ^* (strength per density) in punch and tear tests in pooled data were slightly larger than those calculated as means of individual studies, suggesting that some variations in the punch and tear data were related to methodological differences among studies. Nevertheless, even within individual studies, on average 55–59% of variation in leaf structural resistance was still due to variation in γ^*.

Leaf mechanical resistance and climate

Despite the long-standing view of the importance of anti-herbivore defense in the tropics (Schemske *et al.* 2009), species from lower latitudes on average had lower structural resistance than species from higher latitudes in the shearing and punch tests (Fig. 4a,d; $P < 0.001$). In tearing tests, the overall latitudinal trend was the opposite, but this trend was obtained from a limited number of sites in low latitudes in combination with many forbs and monocots (especially graminoids) at higher latitudes (Fig. 4g). Among woody species there was no trend between latitude and tear resistance ($P > 0.05$). The predictive power of temperature was modest ($R^2 = 0$–0.14), and in any case, the trend was opposite from what had been predicted (Fig. 4b,e,h).

Species from low rainfall sites showed higher structural resistance across all three tests. For example, as precipitation decreased over a fivefold range (2000–400 mm), structural resistance increased on average by 1.9–2.4 times (Fig. 4c,f,i). These trends were little affected by phylogeny (Table S2). As MAT and MAP are correlated for the sites in our dataset ($R^2 = 0.63$; as cold, high-latitude environments typically have low rainfall), a multiple regression analysis was employed to tease out these two factors. While the MAT effect became non-significant, the MAP effect was consistent with the simple regression, as structural resistance was significantly correlated with MAP. To partition the variance of leaf structural resistance into across-site and within-site components, the data were further analysed with a linear mixed model, with species nested within sites. In this analysis, 41–72% of variance in leaf structural resistance occurred within sites and 28–59% of variance occurred across sites. In regard to cross-site variation, MAT and MAP together explained up to 16% of total variance, and the rest (22–52%) was partitioned among other unknown cross-site factors (Table 2).

The underlying components of structural resistance were analysed in relation to MAP (Fig. 5), MAT and latitude (Figures S2 and S3). LMA did not correlate with MAP across all species ($R^2 < 0.001$, $P > 0.05$, $n = 2099$), but the relationship was negative when
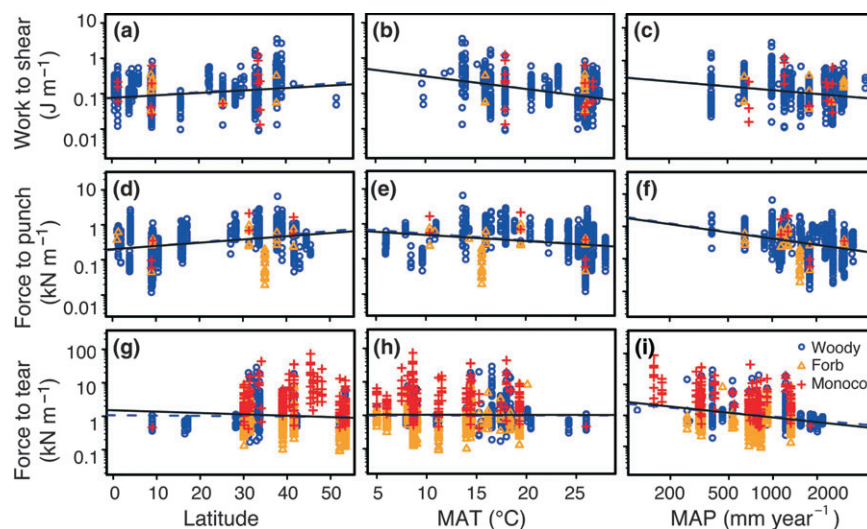

Figure 4 Structural resistance across latitudes and climate variables. Work to shear (a–c), force to punch (d–f) and force to tear (g–i) are plotted against latitude, mean annual temperature (MAT) and mean annual precipitation (MAP). A solid regression line indicates significant correlations ($P < 0.05$). Dashed regression line represents only woody species as a comparison to the overall trend.

Table 2 Proportion of variance explained (R^2) by MAP, MAT, other cross-site factors (cross-site random effect term) and within-site variation to leaf structural resistance

	R^2					
	MAP (MAT)	MAT (MAP)	Other cross-sites factors	Within site	Number of observations	Number of sites
Work to shear	0.040 (0.137)	0.125 (0.028)	0.216	0.619	1153	30
Force to punch	0.061 (0.047)	0.006 (0.020)	0.522	0.410	904	37
Force to tear	0.057 (0.000)	0.005 (0.062)	0.218	0.719	880	41

MAP, mean annual precipitation; MAT, mean annual temperature.
Leaf traits and MAP were log-transformed prior to analysis. Sums of squares (R^2) were calculated by comparison of R^2 across different models. Relative change in R^2 is reported on the addition of each additional term in the model, moving from left-to-right across the table. As change in R^2 is sensitive to the order of terms, we calculated R^2 with two scenarios (1) MAP first and MAT second, (2) MAT first and MAP second. The latter results are shown in the parenthesis.
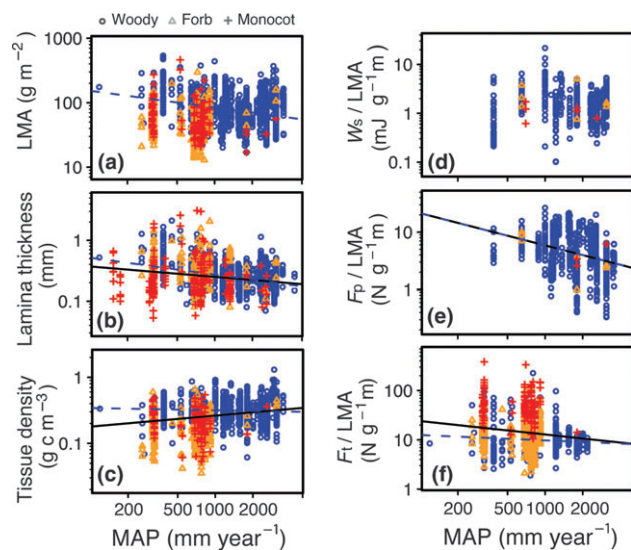
Figure 5 The underlying components of structural resistance across mean annual precipitation (MAP). A solid regression line indicates significant correlations ($P < 0.05$). Dashed regression line represents only woody species as a comparison to the overall trend.

considering woody species only ($R^2 = 0.089$, $P < 0.001$, $n = 1611$; Fig. 5a). A negative correlation was also found in the PIC analysis ($R^2 = 0.030$, $P < 0.001$; Table S1). Across all species, lamina thickness was negatively and tissue density was positively correlated with MAP (Fig. 5b,c). A similar trend was found among woody species for lamina thickness ($R^2 = 0.152$, $P < 0.001$), but tissue density was largely independent from MAP ($R^2 = 0.003$, $P = 0.035$). Toughness (strength) per density was negatively related to MAP in punch and tearing tests but no such correlation was found in shearing tests (Fig. 5d,e,f).

Local light availability

In this study, leaf data were classified into sun (sampled from top canopy or in other well-lit microsites), gap (sampled from forest gaps) and shade leaves (sampled from shade specialists and juveniles of canopy trees in forest understory). In woody species, sun leaves had LMA almost twice as high as shade leaves (medians 90.7 vs. 50.9 g m^{-2}) and hence had significantly higher work to shear (0.127 and 0.066 J m^{-1}) than did shade leaves. Lamina thickness and tissue density of sun leaves were also respectively 1.39 and 1.29 times higher than those of shade leaves. On average, 12.7% of within-site variance in work to shear was explained by local light environment categories in the datasets that documented both sun and shade leaves. Interestingly, shade leaves had significantly higher work to shear for a given LMA than did sun leaves (Fig. 6a; significant upward shift in SMA slope, $P < 0.001$), indicating that shade leaves were more resistant for a given mass. Shade leaves also had higher fibre content for a given LMA (Fig. 6b); i.e. they had higher fibre concentration per unit mass. LMA was a good predictor of LL for both sun and shade leaves, however, local light environment shifted the relationship (Fig. 6c), with shade leaves achieving longer lifespans at a given LMA. Due to higher work to shear at a given LMA in shade leaves, the relationship between work to shear and LL brought shade-leaf data into closer alignment with sun-leaf data (Fig. 6d).

DISCUSSION

Our synthesis of leaf mechanical traits from 90 sites around the world showed that, regardless of measuring methods, structural resistance (data normalized per unit fracture length) varied by 2–3 orders of magnitude (480–820-fold) among species. This variation was far larger than the variation in LMA (42-fold) and lamina thickness (58-fold), from the same leaves. The variation in structural resistance was also larger than the global variation in photosynthesis per unit leaf mass (138-fold across 770 species) and nitrogen concentration per unit mass
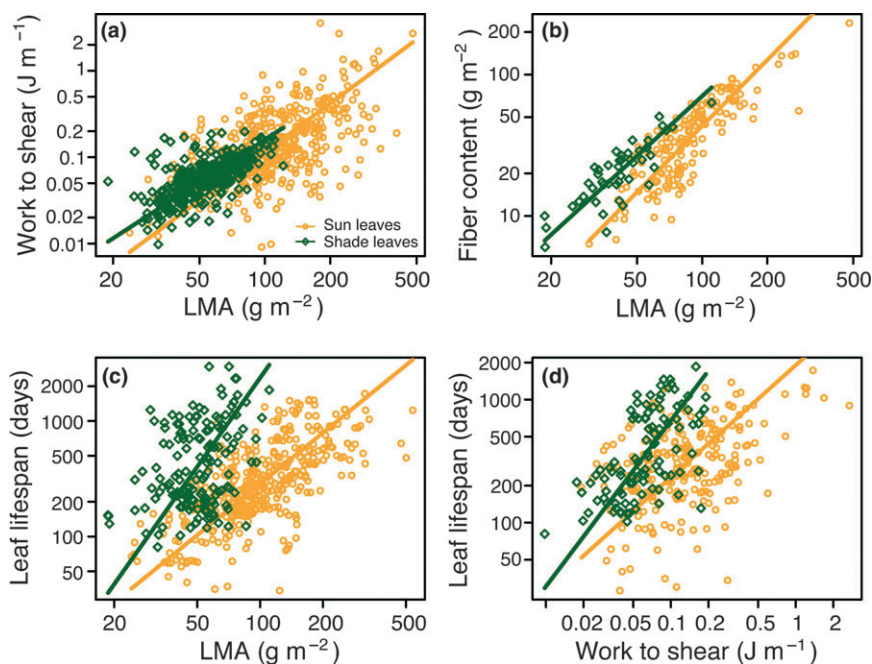

Figure 6 Leaf structural resistance, leaf mass per area (LMA) and leaf life span of sun and shade leaves. (a) Relationship between work to shear and LMA. Shade leaves showed higher work to shear at a given LMA than sun leaves (significant upward shift in the elevation of the SMA slope, $P < 0.001$). (b) Relationship between acid detergent fibre (including cellulose, lignin and cutin) and LMA. (c) Relationship between leaf lifespan and LMA. (d) Relationship between leaf lifespan and work to shear.

(26-fold across 2,061 species) reported by Wright et al. (2004). Studies at regional and community scales have found that leaf structural resistance (normally involving < 20-fold variation within a study) correlates positively with LL (e.g. Reich et al. 1991; Wright & Westoby 2002), and negatively with rates of herbivory (e.g. Coley 1983; Choong 1996), individual growth (e.g. Kitajima & Poorter 2010) and leaf litter decomposition (e.g. Cornelissen & Thompson 1997; Pérez-Harguindeguy et al. 2000). The wide variation of leaf mechanical properties across the globe thus should be a sensitive indicator of many different ecological processes.

The three tests (shear, punch and tear) differed in the mode of fracture (Wright & Vincent 1996) and what was measured (i.e. work or force), yet the ranges of variation and their associations to leaf thickness and tissue density were generally similar (Fig. 2; Table 1). These results increase confidence in the trends found in this study and also suggest that any of the three methods could be used as a general indicator of leaf mechanical resistance at the regional or global scale. Still, there is an interesting difference in values between force to tear and force to punch, which have the same units. Force to tear tended to be larger than force to punch whether considered across all data or just for woody species (Fig. 2b,c; Table 1) – implying that leaf laminas may be more resistant to 'tear-apart' forces aligned parallel to their surface than to shearing forces aligned perpendicular to their surface.

Partitioning of structural resistance

As expected (Reich et al. 1991; Wright et al. 2004; Read & Stokes 2006), leaf structural resistances were positively correlated with LMA (Fig. 2). However, there was also substantial variation in structural resistance that could not be attributed to LMA. Toughness per density (γ) accounted for 56% of interspecific variation in leaf structural resistance (i.e. W_s) (Fig. 3g). The wide variation of γ implies that leaves could potentially increase their resistance by as much as 10-fold (Fig. 1; Table 1) without incurring greater dry mass cost per area (i.e. higher LMA). If so, then which factors are responsible for the large variation in γ? Studies on leaf biomechanics and anatomy suggest that veins and vascular bundles can be 20–30 times tougher than other lamina tissues (Lucas et al. 1991; Choong et al. 1992). Detailed anatomical data were rarely available for our meta-analysis, but the proportion of NDF in leaf drymass varied by sixfold across species in our limited dataset (13.7–76.8%, median 47.3, n = 302). There were indeed moderate correlations between NDF concentration and γ (Figure S4; R^2 < 0.53), indicating that high fibre content was partly responsible for higher γ. Nevertheless, there was also substantial variation in γ for a given fibre content. Specific properties of cell walls and other anatomical details such as vein networks and epidermis/cuticle properties could also be important (Lucas 2004; Read & Stokes 2006; Sanson 2006; Peeters et al. 2007; Onoda et al. 2008). Presumably, the chemical composition and anatomy required for high γ trades off strongly with traits that enhance photosynthetic productivity. For example, greater allocation to fibre could reduce allocation to photosynthetic proteins (Onoda et al. 2004; Takashima et al. 2004), thicker and tougher cell walls may be associated with lower CO_2 conductance (Evans et al. 2009), and bundle-sheath extensions may block lateral CO_2 diffusion within leaves (Terashima 1992). The large variation in γ in our global synthesis suggests that the costs and benefits of structural tissue should be subjected to a much more detailed quantitative analysis.

While there was substantial variation in structural resistance within each growth form, monocot species had on average 3–7 times higher tear resistance (F_t) than woody and forb species. Among monocots, graminoid and palm leaves were especially resistant (see also Dominy et al. 2008). The higher F_t in monocots was mainly attributed to their higher γ^* (3.6–4.2 times higher; Table 1) rather than having thicker laminas or denser tissues. NDF concentration was on average 1.4 times higher in monocots than in woody species (median 60.7 vs. 43.3% for 58 and 241 species respectively). Asuming that fibre tissues were 20–30 times tougher than the other tissues, the amount of NDF was not enough on its own to explain the difference in γ^*. This result may highlight the importance of the spatial arrangement of veins and vascular bundles (Lucas et al. 1991; Roth-Nebelsick et al. 2001). Most monocot leaves in the data set have parallel venation, giving increased resistance along the leaf blade for a given fibre mass. This high resistance in monocot leaves is presumably related not just to defense but also to the fact that many monocot leaves are self-supporting, rather than being borne on woody stems.

Tropical vs. temperate species

Contrary to the long-standing hypothesis that tropical species are better mechanically defended than temperate species as an evolutionary response to greater herbivore pressure in tropical habitats (Coley & Aide 1991; Coley & Barone 1996; Pennings & Silliman 2005; Schemske et al. 2009), our analysis, which covered > 10-fold more species and sites than previous studies, found no indication that tropical plant species had higher structural resistance than species from higher latitudes (Fig. 4a–c). Similarly, LMA and γ (traits underlying structural resistance) were no higher in the tropics than in temperate regions. If herbivory pressure is indeed higher in the tropics (Coley & Aide 1991; Coley & Barone 1996; but see Adams & Zhang 2009), our results in turn may suggest the importance of other defensive strategies such as chemical defenses (Levin 1976; Levin & York 1978; Coley & Aide 1991; Hallam & Read 2006) and delayed greening (Kursar & Coley 1992) in tropical plant species. Compared to leaf mechanical properties, which are a general defense against both herbivores and abiotic stresses, chemical defense is more specific, and its quality and abundance are notably diverse (Coley & Barone 1996; De Luca & St Pierre 2000). A great diversity of chemical defenses may be particularly important for tropical plant species under pressure from a wide range of herbivores (Coley & Barone 1996), although this diversity is still poorly understood at broad geographic scales.

Leaf structural resistance across rainfall gradients

Among the climate variables we tested, mean annual rainfall (MAP) was most consistently associated with leaf structural resistances. Leaves tended to be more structurally resistant at lower MAP (Fig. 5). This result is consistent with the classical view that sclerophylly is related to water deficit (Schimper 1903). However, the result that MAP explains only 4–6% of global variation of leaf structural resistance, suggests that water deficit was only one factor in the evolution of sclerophylly. Variation in structural resistance may also be related to soil fertility, other environmental stresses and herbivory pressure (Grubb 1986; Turner 1994; Read et al. 2005).

The overall trend of higher structural resistances with lower MAP was associated with thicker leaf laminas and higher γ but lower tissue

density. The trend of thicker laminas with decreasing MAP was very general, being observed both across and within growth forms, as well as in phylogenetic analyses (Table S2; Niinemets 2001). Thicker leaves may have a strong selective advantage for plants in dry environments as it reduces the surface–volume ratio and can improve the rate of carbon assimilation per unit water loss (Givnish 1979; Wright *et al.* 2003). On the other hand, the positive correlation between tissue density and MAP may not be such a general trend as it was observed only among growth forms and not within individual growth forms. In arid sites, ephemeral herbs, graminoids and succulent species were abundant and they had lower tissue density with often higher water content than leaves of woody plants (Table 1; Vendramini *et al.* 2002). These growth forms (especially ephemeral herbs and graminoids) have ecological strategies that permit very fast growth rates when water (and other resources) is abundant (Whittaker 1975). The contrasting trends of lamina thickness and tissue density with MAP in our all-species analyses resulted in a flat distribution of LMA with respect to MAP (Fig. 5a; Table S1). This lack of a MAP signal in regard to LMA was also seen in a previous global analysis of leaf traits (2370 species; Wright *et al.* 2004) with relatively little overlap with the current dataset. That said, LMA did in fact increase with decreases in precipitation when woody species were considered on their own, and in analyses that took into account phylogenetic relatedness.

The trend in punch and tearing tests of higher toughness per density (γ) at low MAP sites may be associated with drought tolerance. For example, vascular bundles may be more lignified to prevent vessel implosion at very low water potential. However, the negative association of γ and MAP was weak within growth form. A high abundance of high γ monocot species (especially graminoids) was partly responsible for the negative correlation between γ and MAP across all species.

Sun and shade leaves

Previously, LMA has been shown to be a strong predictor of LL in analyses concerning outer-canopy leaves, for species across the world (Wright *et al.* 2004). A strong correlation between LMA and LL was also found for both sun and shade leaves in this study, but there was a clear shift between the two groups (Fig. 6c) such that the LMA of shade leaves was less than half of that of sun leaves, at a given LL (e.g. 52 vs. 137 g m^{-2}, for a LL of 500 days). To our knowledge, this is the first study to show this type of shift so clearly, across a broad range of species. When structural resistance was instead used as a predictor of LL, sun and shade species were more closely aligned, suggesting that structural resistance may be more directly associated with LL than LMA, across light environments (Fig. 6d). Higher γ and fibre concentration in shade leaves are likely to be responsible for their higher structural resistance at a given LMA. Moreover, high γ in shade leaves should decrease attractiveness to herbivores: they would require more time and energy to ingest and digest leaves to gain a given amount of nutrient and energy (Lusk *et al.* 2010). These results suggest that structural resistance and toughness per density are both important for achieving long LL. For example, higher structural resistance presumably confers greater defense against potential damage from the wind or from leaf chewing herbivores; whereas, on the other hand, higher toughness per density can impede herbivores through affecting the crucial balance between feeding cost and nutritional benefit. Tougher tissue with longer LL may have a strong selective advantage in the shade

because the cost of replacing such leaves is especially high relative to their potential photosynthetic income (Coley & Aide 1991).

CONCLUDING REMARKS

This first analysis of the 'global leaf mechanics spectrum' has revealed that, regardless of test methods, leaf mechanical resistance against external forces spanned 2–3 orders of magnitude, greatly exceeding worldwide variation in LMA, lamina thickness and photosynthetic rates. Leaf mechanical resistance was modestly related to climate, most clearly so to rainfall, and it was influenced by local light environments. Still, 41–72% of variation in mechanical resistance occurred among coexisting species. Presumably, prevailing herbivore pressures must have had an important influence on the evolution of leaf mechanical resistance. When partitioning structural resistance into three different components, toughness per density contributed a surprisingly large share to variation in structural resistance, larger than the shares contributed by lamina thickness and tissue density. Using LMA as a surrogate for leaf structural resistance thus potentially overlooks important variation in tissue properties. More importantly, our results suggest that there are large variations in the amount, qualities and geometry of leaf mechanical tissues across species, which may link to physiological and evolutionary trade-offs underlying diversity of leaf traits. From this study we conclude that toughness per density and fibre content are critically important in determining LL and, likely influence plant–herbivore interactions. A more fully developed physiological and ecological understanding of the factors underlying leaf mechanical resistance will lead to deeper insights into the ecology and evolution of leaf traits in relation to macro- and micro-scale environmental variation.

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SUPPORTING INFORMATION

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

Data S1 Supplementary information of method.
Appendix S1 Data source.
Figure S1 Residual vs. fitted plots in leaf traits–climate relationship.
Figure S2 Leaf morphological traits across latitude and climates.
Figure S3 Leaf toughness per density across latitude and climates.
Figure S4 Relationship between leaf toughness per density and fibre content.
Table S1 Comparison of different shearing devices.
Table S2 Correlation test between leaf traits and climate variables.
Table S3 Partitioning of variance in structural resistance for individual studies.

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