Biogeosciences Discuss., 8, 5083–5158, 2011
www.biogeosciences-discuss.net/8/5083/2011/
doi:10.5194/bgd-8-5083-2011

Biogeosciences
Discussions

Coordination of physiological and structural traits in Amazon forest trees

S. Patiño[1,2], N. M. Fyllas[2], T. R. Baker[2], R. Paiva[3], C. A. Quesada[2,3,4], A. J. B. Santos[3,4,†], M. Schwarz[1], H. ter Steege[5], O. L. Phillips[2], and J. Lloyd[2,6]

[1]Max-Planck-Institut für Biogeochemie, Postfach 100164, 07701, Jena, Germany
[2]School of Geography, University of Leeds, LS2 9JT UK
[3]Institito Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil
[4]Departamento de Ecologia, Universidade de Brasília, DF, Brazil
[5]Dept. of Plant Ecology and Biodiversity, Utrecht University, The Netherlands
[6]James Cook University, Cairns, Qld 4871, Australia
[†]deceased

Received: 5 May 2011 – Accepted: 6 May 2011 – Published: 25 May 2011

Correspondence to: J. Lloyd (j.lloyd@leeds.ac.uk)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Many plant traits covary in a non-random manner reflecting interdependencies associated with ”ecological strategy” dimensions. To understand how plants modulate their structural investments to best maintain and utilise their physiological capabilities, data on leaf and leaflet size and the ratio of leaf area to sapwood area (Φ_{LS}) obtained for 1040 tree species located in 53 tropical forest plots across the Amazon Basin were incorporated into an analysis utilising existing data on species maximum height (H_{max}), seed size, leaf mass per unit area (M_{A}), foliar nutrients and δ^{13}C and branch xylem density (ρ_{x}).

Utilising a common principal components approach allowing eigenvalues to vary between two soil fertility dependent species groups, five genetically controlled trait dimensions were identified. The first involves primarily cations, foliar carbon and M_{A} and is associated with differences in foliar construction costs. The second relates to the classic “leaf economic spectrum”, but with increased individual leaf areas and a higher Φ_{LS} newly identified components. The third relates primarily to increasing H_{max} and hence variations in light acquisition strategy involving greater M_{A}, reductions in Φ_{LS} and less negative δ^{13}C. Although these first three dimensions were more important for species from high fertility sites the final two dimensions were more important for low fertility species and were associated with variations linked to reproductive and shade tolerance strategies.

Environmental conditions also influenced structural traits with ρ_{x} decreasing with increased soil fertility and decreasing with increased temperatures. This soil fertility response appears to be synchronised with increases in foliar nutrient concentrations and reductions in foliar [C]. Leaf and leaflet area and Φ_{LS} were less responsive to the environment than ρ_{x}.

Thus although genetically determined foliar traits such as those associated with leaf construction costs coordinate independently of structural characteristics, others tend to covary with leaf size, Φ_{LS}, S tolerance strategies. Several traits such as M_{A} and [C]

are important components of more than one dimension with their ambiguous nature reflecting different underlying causes of variation. Environmental effects on structural and physiological characteristics are also coordinated but in a different way to the gamut of linkages associated with genotypic differences.

1 Introduction

Plant functional traits are widely used at both the ecology-evolution and ecology-biogeochemistry modelling interface. Sets of functional characters can serve as the basis of identifying important evolutionary adaptations that improve the success of different taxa at different environments as well as for obtaining a mechanistic basis of plant and ecosystem functioning. Over the last decade significant advances have been made in terms of our understanding of plant trait inter-relationships and associated trade-offs (Reich et al., 1997; Westoby et al., 2002), especially in terms of the so called "leaf economic spectrum" (Wright et al., 2004) with well documented systematic and co-ordinated changes in leaf nitrogen and phosphorus concentrations, leaf mass per unit area, M_A and leaf lifetimes.

Attention has also been paid to the relationships between physiological and structural characteristics of leaves and other plant traits. For example, it has been reported that leaf size declines with wood density, ρ_w (Pickup et al., 2005; Wright et al., 2006, 2007; Malhado et al., 2009). It has been suggested that this is because the ratio of leaf area to sapwood area (Φ_LS) should also decline with increasing wood density due to hydraulic constraints (Wright et al. 2007). Nevertheless, although Φ_LS may decline with ρ_w for trees in some ecosystems that are clearly water-limited (Ackerly, 2004; Cavender-Bares et al., 2004), Φ_LS sometimes actually increases with ρ_w (Wright et al., 2006; Meinzer et al., 2008). The latter study also found that associated with these higher Φ_LS and high wood density stems were lower stem hydraulic conductances, more negative midday leaf water potentials, and more negative bulk leaf osmotic potentials at zero turgor. Thus, leaves of some high wood density species may be characterised by adaptations allowing them to function at more severe water deficits than is the case for low wood density species.

The Panama study of Meinzer et al. (2008) also found that higher ρ_w species tended to have higher M_A. Although similar positive correlations between M_A and ρ_w have also been reported for other ecosystems (e.g. for sclerophyllous forest: Ishida et al., 2008) when examining the bivariate relationship between ρ_w and M_A across a range of tropical forest sites, Wright et al. (2007) observed no significant relationship. Likewise, when examining variation in leaf and stem traits for 17 dipterocarp species growing in a common garden in southern China, Zhang and Cao (2009) also found no significant correlation between ρ_w and M_A.

Variations in M_A may also be related to a suite of additional plant physiological characteristics (Poorter et al., 2009), varying negatively with dry-weight foliar nitrogen and phosphorus concentrations (Wright et al., 2004; Fyllas et al., 2009) as well as tending to increase with increasing tree height (Thomas and Bazzaz, 1999; Kenzo et al., 2006; Lloyd et al., 2010). Potential tree height, H_{max}, has also been related to a number of wood traits (Chave et al., 2009) with taller plants tending to have bigger conduits in their trunks, but fewer conduits overall (Preston et al., 2006), this reflecting longer path lengths to the transpiring tissue and therefore a need for wider vessels to maintain a high hydraulic conductance, K_P (Coomes et al., 2007). Although lumen fraction and/or hydraulic conductivity are also sometimes negatively correlated with wood density (e.g. Santiago et al., 2004a; Russo et al., 2010), this providing one explanation for smaller shade tolerant trees tending to have higher ρ_w (e.g. Falster and Westoby 2005; Keeling et al., 2008), ρ_w is not necessarily well correlated with H_{max}, perhaps because of differences between species in the density of fibre tissue in the wood matrix (Poorter et al., 2009; Russo et al., 2010). Indeed, although many recent papers have suggested that low-density wood will also tend to be that with a higher hydraulic conductivity (Stratton et al., 2000; Meinzer, 2003, Bucci et al., 2003; Santiago et al., 2004a; Swenson and Enquist, 2007), in a survey across 584 angiosperm species, Zanne et al. (2010) found no relationship between ρ_w and non-lumen vessel fraction. Nevertheless, there are many methodological issues surrounding the accurate measurements of wood density and with many published estimates of ρ_w and its twig-level analogue (ρ_x) of a dubious accuracy (Williamson and Weimann, 2010).

Although often assumed simply to be a fixed genetically defined trait (e.g. Swenson and Enquist, 2007; Zanne et al., 2010), considerable intra-species variation in ρ_x or ρ_w can occur, even within the one stand. For example, Osunkoya et al. (2007) reported coefficients of variation of as much as 0.25 for species within a tropical rain forest stand on Borneo. For many species, ρ_w is also documented to vary with location (Gonzalez and Fisher, 1998; Muller-Landau, 2004; Parolin and Ferreira, 2004; Roque, 2004; Nogueira et al., 2007) and when investigating the basis for ρ_x for over 1000 trees across the Amazon Basin, Patiño et al. (2009) found plot location was more important than species identity in accounting for the observed variations. For individual species, some of this site specific variability in ρ_w and/or ρ_x may be due to variations in soil fertility (Quesada et al., 2010). For example, in response to an increase in P availability Lovelock et al. (2004) found an increase in xylem vessel lumen fraction (and thus a likely decline in ρ_w) for dwarf *Rhizophora mangle* (mangrove) trees growing in the field. This was also associated with increased stem hydraulic conductivities and improved leaf phosphorus status and associated higher CO_2 assimilation and transpiration rates. Small but significant increases in ρ_w with increasing soil water deficit have also been reported for the Asian rain forest tree *Castanopsis acuminatissima* (Schuldt et al., 2010).

Within a given stand, taller and generally more light-demanding rain forest species also tend to have larger leaves, this being associated with shallower crown and a more efficient light capture (Poorter et al., 2006; Poorter and Rozendaal, 2008). Leaf-size may also be influenced by other factors. For example, Australian rain forests growing on oligotrophic soils typically have a greater abundance of smaller leaved species than for nearby forests found on more mesotrophic soil types (Webb, 1968).

Seed size may also relate to the above plant functional traits. For example, one of “Corner’s rules” describes a tendency for species with thick twigs to have large appendages (leaves and fruit). The range of viable seed size also tends to increase with plant height (Moles et al., 2005; Grubb et al., 2005). Forests on the more fertile soils of western Amazonia tend to have smaller average seed masses than their less fertile counterparts on the Guyana Shield and elsewhere (ter Steege et al., 2006), this perhaps being related to several advantages attributable to large seeded species under nutrient-poor conditions, viz. greater initial nutrient stores, greater initial root zone expansion, and increased mychorrizal infection, all of which would be expected to increase the probability of seedling survival (Foster, 1986). An additional factor related to soil fertility may be that forests on the richer soil of the western Amazon tend to have higher tree turnover rates as opposed to the less fertile eastern Amazon forest. This may be primarily a consequence of differences in soil physical properties (Quesada et al., 2009) with more opportunities for gap-based regeneration in the west favouring smaller seeded species.

This paper presents new data on leaf and leaflet size and Φ_{LS} for 661 species located in 52 plots across the Amazon Basin. The trees sampled form a subset of those also examined for variations in branch xylem density (Patiño et al., 2009), and for foliar nutrients, M_{A} and δ^{13}C (Fyllas et al., 2009). We investigate relationships between all these parameters as well as with genetic variations in $H_{\max}$ (Baker et al., 2009) and seed mass (ter Steege and Hammond, 2001; ter Steege et al., 2006). Specifically, we were interested to assess the degree to which the observed variations in the studied structural and physiological traits were coordinated with each other, especially with their genetic versus environmental components considered separately. For the environmental effects, we were also interested to quantify the extent to which the observed integrated structural and physiological responses were modulated by soil fertility and climate.

2 Materials and methods

2.1 Study sites

In the analysis here, RAINFOR sample plots have been aggregated as discussed in Fyllas et al. (2009), with further plot details available in Patiño et al. (2009) and Quesada et al. (2010). As in Fyllas et al. (2009) plots were classified into two soil fertility groups based on the measured total reserve bases (Quesada et al., 2010). Ten plots in Fyllas et al. (2009) have not been included due to insufficient structural trait data having been collected.

2.2 Structural traits

For most trees sampled in Patiño et al. (2009) and Fyllas et al. (2009), and from the same terminal branches for which data has already been presented in those studies, all leaves from the branch had also been counted. From that branch, a sub-sample of 10–20 leaves was randomly chosen to estimate individual leaf area, L_A, and leaflet area, ℓ_A (when a species had compound leaves), and to estimate the total leaf area of the branch. All age and size leaves or leaflets were selected for this analysis except for very young leaves or those which were obviously senescent. The chosen leaves were usually scanned fresh on the same day of collection. When this was not possible the same day, they were stored for a maximum of two days in sealed plastic bags to avoid desiccation and any consequent reduction of the leaf area. Scans were analysed using "Win Folia Basic 2001a" (Regent Instruments Inc., 4040 rue Blain Quebec, QC., G2B 5C3 Canada) to obtain L_A and ℓ_A.

The distal (sapwood + pith) and pith diameters for each branch were also measured with a digital caliper (Mitutoyo Corporation, Japan) with sapwood area, A_S, then estimated by subtracting pith area from the total branch area with $\Phi_\mathrm{LS}=n\bar{L}_\mathrm{A}/A_\mathrm{S}$ where n is the number of leaves distal to the piece of branch sampled and $\bar{L}_\mathrm{A}$ is the average area of the individual leaves sub-sampled for the estimation of L_A and/or ℓ_A.

Branch xylem density data for the same samples were obtained as described in Patiño et al. (2009) with species maximum height taken from the database developed by Baker et al. (2009) and seed mass (S – taken as a genus dependent variable and already on a $\log_{10}$ ordinal scale) from ter Steege et al. (2006).

2.3 Related foliar traits

Foliar traits used here are as described/measured in Fyllas et al. (2009) and Lloyd et al. (2010) and include leaf mass per unit area (M_A) and foliar [N], [C], [P], [Ca], [K] and [Mg] expressed on dry-weight basis. Foliar $^{13}C/^{12}C$ discrimination, Δ, was estimated from measurements of foliar $\delta^{13}C$ (Fyllas et al., 2009) using an assumed value for the isotopic composition of source air equal to –8.0 ‰ (Farquhar et al., 1989) and subsequently transformed to a diffusional limitation index, $\oslash$, according to

$$\oslash = 1 - \sqrt{\frac{(\Delta - 4.4)/25.6 - 0.2}{0.8}} \quad (1)$$

which utilises the well known relationship between Δ and the ratio of internal to ambient CO_2 concentrations, c_i/c_a (Farquhar et al., 1989). Equation (1) assumes that at current day c_a, photosynthesis can be considered a roughly linear function of c_i and with a maximum practical c_i/c_a (indicating minimal diffusional limitation) of 0.8. Here we have taken a value of 4.4 ‰ for the fractionation against $^{13}CO_2$ during diffusion into the leaf and 30.0 ‰ for the fractionation against $^{13}CO_2$ during photosynthetic fixation (Farquhar et al., 1989). Increasing $\oslash$ values are associated with lower c_i/c_a, and thus, other things being equal, a higher water use efficiency, W, this being the ratio of carbon gained to water lost during photosynthetic CO_2 assimilation. Equation (1) relies on a simplified expression for Δ which ignores difference between gas- and liquid-phase fractionations within the leaf (Farquhar et al. 1989), but this should not seriously compromise its utility in the current context.

2.4 Climate and soils

The soil and climate predictors table used was the same as in Fyllas et al. (2009), using a set of measured soil properties (Quesada et al., 2010) with precipitation variables and temperature from the "WorldClim" dataset (http://www.worldclim.org). Estimates of mean annual solar radiation are from New et al. (2002). As in Fyllas et al. (2009) we separate soils into two fertility classes based on the total sum of reserve bases, these being estimated as described in Quesada et al. (2010).

2.5 Statistical analysis

This paper implements a similar set of statistical analyses to that described in detail in Fyllas et al. (2009). Preliminary tests included analysis of normality (Shapiro-Wilk) and homogeneity of variance (Fligner-Killeen) for each of the structural traits of interest. The foliar related structural traits (L_A, ℓ_A and Φ_{LS}) presented a right skewed distribution and thus were all $\log_{10}$ transformed. As ρ_x, H_{max} and S (the latter already provided as size classes on a $\log_{10}$ scale) were more or less symmetrically distributed around their mean we did not apply this transformation for these variables, even though the Shapiro test failed to identify strict normality. The nonparametric Kruskal-Wallis test (Hollander and Wolfe, 1999) was used to explore for differences between fertility groups as well as for differences between families, genera within a family and species within a genus. All analyses were performed with the R statistical platform (R Development Core Team, 2010).

2.5.1 Partitioning of variance and estimation of genetic and environmental effects

A multilevel model was initially fitted for all traits except H_{max} and S according to

$$\Theta = \mu + p + f/g/s + \epsilon, \tag{2}$$

where μ is the overall mean value of each trait, Θ; p is the plot effect, i.e. the effect of the location that each individual is found, and $f/g/s$ represents the genetic structure of the data, i.e. that each individual belongs to a species (s), nested in a genus (g), nested in a family (f), and ϵ is the error term. All parameters were estimated by the Residual Maximum Likelihood (REML) method with the `lme4` library available within R (Bates and Sarkor, 2007). Fyllas et al. (2009) have already discussed further details of the above formulations and the advantage in being able to partition the variance from the family to the species level, also taking into account the location (thus the environmental contribution to trait variation) where the trait was measured. The Supplement (II) of that paper also provides an empirical validation of the approach used. Again we were interested in exploring the genetic (estimated as the sum of family ± genus ± species random effects) and environmental terms, using bivariate relationships as well as multiple nonparametric regressions of plot effect contributions on a set of environmental predictors. For $H_{\max}$ and S no multilevel model was fitted or environmental effect assumed, the available data being considered to express directly the genetic potential of each species. It is also worth noting that our estimates of S are resolved at the genus level only (ter Steege and Hammond, 2001) and is only on a $\log_{10}$ categorical scale. This introduces potential errors into the analyses where S is involved because all other traits have been resolved at the species level. We therefore note that, even though a small portion of the observed variation in S generally occurs at the species level (Casper et al., 1992), bivariate and multivariate analyses involving this trait as presented here may carry somewhat more “noise” than would otherwise be the case.

2.5.2 Bivariate relationships

Relationships were initially assessed with the Pearson’s correlation coefficient (r) with subsequent Standardized Major Axis (SMA) line fits where significant correlations were identified. In this study, SMA line fits are applied to the raw dataset (including all measured traits and thus intraspecific variation), to the genetic component of trait variation (i.e. each species is represented by a single data point) as well as to the plot level effects (i.e. each plot is contributing a single data point). In each case, we initially fitted separate lines for each fertility group, and when a common SMA slope was identified we tested for differences in elevation and/or slope between fertility groups, using the `smartr` library available within R (Warton et al., 2006).

We explored the plot level effect of each structural trait, through non-parametric correlation analysis on selected soil and environmental predictors, with the soil variables reduced to three principal axes to avoid multicollinearity (Fyllas et al., 2009). The climatic variables of mean annual temperature, total annual precipitation, dry season precipitation and mean annual radiation were also examined. As extensively discussed in Fyllas et al. (2009) we dealt with spatial autocorrelation issues by fitting appropriate simultaneous autoregressive models (SAR) which include a spatial error term (Lichstein et al., 2002) to help interpret the significance of full and partial Kendall's τ coefficients as a measure of association between plot-level trait effects and environmental predictors.

2.5.3 Multivariate analyses

Inferred genetic effects were analysed jointly for species found on fertile versus infertile soils (excluding those found on both soil types) by calculating separate variance-covariance matrices for the two species groups and then using the common principal components (CPC) model of Flury (1988) as implemented by Phillips and Arnold (1999). Within this model, it is assumed that the two populations of species have the same eigenvectors (principal components; denoted here as U) but that the relative loading of the various U as expressed through their eigenvalues (λ) may potentially vary between the two populations. Flury's model provides a hierarchy of tests corresponding to a range of possible relationships between matrices including equality, proportionality, common principal components, partial common principal components or unrelated (Flury, 1988; Phillips and Arnold, 1999). CPC can thus be seen as a method for summarizing the variation in two or more matrices. Nevertheless, caution needs to be applied when using CPC to address the more complex goal of diagnosing and understanding the nature of the changes that underlie the difference between the matrices. This is because CPC tends to spread any differences over many of the vectors it extracts and often over all of them (Houle et al., 2002).

As the CPC model does not strictly apply to correlation matrices (Flury, 1988), we standardised each variable before calculating the input variance-covariance matrix by dividing each variable by its observed range (across both high and low fertility soils) as first proposed by Gower (1966) but, due to the presence of the occasional outlier, taking the effective range as the 0.1 to 0.9 quantiles. Standard errors of the U and λ for the CPC models were estimated assuming asymptotic normality as described in Flury (1988).

All other multivariate analyses (e.g. PCA of the derived environmental effects) were implemented with the `ade4` package available within the R statistical platform with the environmental effect PCA undertaken on the correlation matrix.

3 Results

3.1 Statistical distribution of measured traits

The structural traits distributions along with those for M_{A} and $\oslash$ for the complete dataset divided to low and high fertility groups are shown in Fig. 1 with overall mean values, range and variances for each plot for all traits also provided in the Supplement (Table S1). The three leaf related traits introduced here (L_{A}, ℓ_{A} and Φ_{LS}) did not differ significantly between low and high fertility sites (Fig. 1). On the other hand, ρ_{x} and S showed significant differences between the two fertility groups, with their distributions shifted to the left for fertile sites, i.e. higher ρ_{x} and S were found for species found on infertile soils. This is similar to the shifted distributions identified for most leaf mineral concentrations across fertility gradients (Fyllas et al., 2009) but in the opposite direction, i.e. with higher structural carbon and lower mineral investment in more fertile environments.

3.2 Partitioning of the variance

The variation apportioned to different taxonomic levels varies for each of the traits examined (Fig. 2). When leaf size was expressed per leaflet, most of the variation was attributed at the species level (0.31) with the overall genetic component (i.e. family ± genus ± species) adding up to a very high (0.62) proportion. When leaf size was expressed at the leaf level, most of the variation was attributed at the family level (0.29) with a very high overall genetic component (0.71). In contrast to L_{A} and ℓ_{A}, plot level contributions to the total variance were substantial for the other structural traits: being around 0.30 for ρ_{x} and 0.27 for Φ_{LS}. These are not necessarily higher than their respective genetic components, but underline the importance of the site growing conditions in influencing structural traits such as ρ_{x} and Φ_{LS}. This must have direct implications for different physiological processes, as for $\oslash$ for which the environmental component was the dominant source of variation.

3.3 Bivariate relationships: raw data

These are not considered in any detail here, but for the interested reader data are summarised in the Supplement, Table S2A.

3.4 Bivariate relationships: genetic components

Considering data from both low and high fertility sites together, Table 1 lists correlations and SMA slopes for the derived genetic components with this same information shown in more detail (including confidence intervals) in the Supplement (Table S2A) and with low and high fertility species separated for OLS and SMA regression analyses in Table S2B. Within Table 1, the SMA slopes reflect the relationship $y \leftrightarrow x$, with the x as the column headers and the y being the row labels. Figures 3 through 6 illustrate the more important relationships involving the sampled structural traits. Due to considerations associated with multiple testing, we focus only on relationships significant at $p \leq 0.001$

though, where interesting and/or informative, statistically less significant relationships are also considered.

3.4.1 Maximum tree height

Generally only poor correlations were observed for H_{max}, these being significant only for $\log_{10}(M_{\mathrm{A}})$ ($p \leq 0.001$) and $\log_{10}(S)$ ($p \leq 0.01$). The $M_{\mathrm{A}} \leftrightarrow H_{\mathrm{max}}$ and $S \leftrightarrow H_{\mathrm{max}}$ relationships are shown in Fig. 3. Here, due to differences in the SMA slope and/or intercept between the species associated with the two soil fertility classes (see Supplement, Table S2B) we have fitted separate lines for species found on low and high fertility soils. This shows that for species associated with low fertility soils, both M_{A} and S tend to be slightly higher at a given H_{max} than their lower fertility counterparts. Especially for $S \leftrightarrow H_{\mathrm{max}}$ the variation is considerable, particularly at low H_{max}, with S varying three orders of magnitude for H_{max} between 10 and 30 m.

3.4.2 Branch xylem density

As detailed in Table 1, the derived genetic component of ρ_{x} was negatively correlated with $\log_{10}$ [P], $\log_{10}$[Ca], $\log_{10}$, [K] $\log_{10}$, (ℓ_{A}) and positively associated with $\log_{10}(S)$ ($p \leq 0.001$), with weaker but significant positive correlation being observed with $\log_{10}(M_{\mathrm{A}})$ and with a negative correlation with $\log_{10}$[Mg] ($p \leq 0.01$) and even less significant, negatively with $\log_{10}(L_{\mathrm{A}})$ ($p \leq 0.05$). Some of these relationships are illustrated in Fig. 4 which shows the relationships between ρ_{x} and both [P] and [K] to be particularly compelling and, as is also the case for M_{A} and S, there was no difference between species associated with low versus high fertility soils. Note that all four panels in Fig. 4 are log-linear plots meaning that a linear change in ρ_{x} causes a proportional change in the other variable. For example, an increase in ρ_{x} from 500 to 600 $\mathrm{kg\,m^{-3}}$ is associated with a reduction in [P] of about 0.3 $\mathrm{mg\,g^{-1}}$ but a further increase from 600 to 700 $\mathrm{kg\,m^{-3}}$ is associated with an additional reduction in [P] of only just over 0.2 $\mathrm{mg\,g^{-1}}$.

3.4.3 Leaf area: sapwood area ratio

Reasonably strong correlations were found between $\log_{10}(\Phi_{LS})$ and $\log_{10}(M_A)$, $\log_{10}$[N] and $\log_{10}(L_A)$ ($p \leq 0.001$) with the relationship between $\log_{10}(\Phi_{LS})$ and $\log_{10}$[P] also significant ($p \leq 0.01$). The relevant biplots are shown in Fig. 5. Because of the log-log nature of the bivariate relationships the slopes can in this case be interpreted as scaling coefficients, the most notable being a value of 1/0.19 = 5.3 for $L_A \leftrightarrow \Phi_{LS}$. This suggests that for each doubling of Φ_{LS} there is a $2^{5.3}$ or 40-fold increase in L_A. Thus, tropical tree species with a higher L_A tend to have relatively fewer leaves per unit stem cross-sectional area (A_L) meaning that Φ_{LS} is a mostly conserved (but still significantly variable) plant trait. The slope for the genetic component $M_A \leftrightarrow \Phi_{LS}$ relationship is 1/−1.27 = −0.79. Thus, as Φ_{LS} increases across species, then M_A declines proportionally less. That is to say, species with a higher Φ_{LS} also tend to carry a greater weight of (generally larger) leaves per unit A_L with those leaves also tending to have higher foliar [N] and [P].

3.4.4 Leaf nutrients and other structural traits

Strong positive correlations ($p \leq 0.001$) were also observed for $\log_{10}(L_A)$ with $\log_{10}$[N] and $\log_{10}$[P] as well as between $\log_{10}$[Ca] and S. These relationships are shown in Fig. 6 for which, from the slopes of Table 1 (6.36 and 5.37 respectively) we can conclude that a 50 % increase in foliar [N] or [P] is associated with approximately 9-fold and 13-fold increases in L_A. Interestingly, both the slope and intercept of these relationships are dependent on the soil fertility with which a species is associated (Supplement Table S2B). Species found on low fertility soils tend to have a higher L_A at any given foliar [N] and/or [P].

For the [Ca] ↔ S pairing the negative slope is also large (−8.3), though in this case with no soil fertility effect detected. Though not shown in Fig. 6, also of note is the positive [C] ↔ S relationship ($p \leq 0.001$) with species with a low seed mass also tending to have a low foliar carbon contents.

3.5 Common Principal Component modelling (genetic components)

Results from the CPC modelling are shown in Table 2, with the full model output, details of the rationale for eigenvector inclusion and assessments of the overall model fit as given in the Supplement Tables S3, S4 and S5 and their accompanying captions. These considerations gave rise to five eigenvectors being selected, listed in Table 2 in order of max $[\lambda_{\text{low},j}, \lambda_{\text{high},j}]$ where $\lambda_{\text{low},j}$ and $\lambda_{\text{high},j}$ are the values for the jth characteristic root for the low and high fertility species respectively.

The first eigenvector, U_1, had somewhat higher λ for high versus low fertility associated species (accounting for 0.24 and 0.27 of the dataset variance respectively) and with high positive coefficients for all three foliar cations and to a lesser extent foliar [P], and negative coefficients for foliar [C] with smaller but still significant coefficients for M_A and S. In terms of cations, carbon and M_A, this first component seems similar to that first described by Poorter and de Jong (1999) and thus we dub it the Poorter-De Jong (PDJ) dimension, Д_{PDJ}.

The second component, U_2, accounts for an additional 0.18 and 0.19 of the dataset variances for low and high fertility species respectively, and is characterised by high positive coefficients for foliar [N] and [P] as well as L_A and, to a lesser extent, Φ_{LS}. Also characterised by modestly negative coefficients for M_A and foliar [Mg]. In terms of [N], [P] and M_A, U_2, seems to reflect some components of what is considered the classic leaf economic spectrum (Reich et al., 1997; Wright et al., 2004). We thus label this the Reich-Wright dimension, Д_{RW}, of tropical tree functional trait coordination.

Although H_{max} would seem to have little influence on either Д_{PDJ} or Д_{RW} it emerges as the dominant term for U_3 along with M_A and, of opposite sign, Φ_{LS}. Also of note here is the relatively high value for the coefficient of the diffusion limitation index, $\oslash$ which is positively associated with both H_{max} and M_A. Interestingly, for this component L_A varies in the opposite direction to Φ_{LS} (albeit with a large standard error) suggesting that there is a tendency towards considerably fewer but also significantly larger leaves in taller statured species. There also being a modest but significant negative contribution of ρ_x to this dimension. We consider U_3, which on its own accounts for 0.08 and 0.10 of the variation in the dataset respectively, to contain several features similar to those described by Falster and Westoby (2005) for climax tropical forest in Australia, and it is thus denoted as $Д_{FW}$.

The first three axes species scores (normalised to ± 100) are plotted against each other in Fig. 8a–c. This shows the required lack of any systematic correlations between the species scores as expected for the output from any good fit of a principle components model. Clearly a wide range of combinations of these three trait dimensions can occur. But with Fig. 8a also showing that it is (generally speaking) only species typically associated with high fertility soils that have scores for both $Д_{PDJ}$ and $Д_{RW}$.

Figure 8d shows the major components of the three major CPCs and their overlap of traits in diagrammatic form. This illustrates that many traits seem to be "shared", especially M_A which is an important factor for all three of $Д_{PDJ}$, $Д_{RW}$ and $Д_{FW}$. Also occurring in ($Д_{PDJ} \cap Д_{RW}$) and of the same sign is [C], but with [P] and [Mg] varying in opposite directions with respect to M_A for these two trait dimensions. Intersecting $Д_{RW}$ and $Д_{FW}$ and in the same direction relative to M_A is Φ_{LS}. Although with a high estimated standard error as part of $Д_{FW}$, we have also included L_A in ($Д_{RW} \cap Д_{FW}$), this also showing that it varies in the opposite direction relative to M_A and Φ_{LS} for $Д_{RW}$ *cf.* $Д_{FW}$.

The fourth component axis is dominated by S and Φ_{LS} with these coefficients of different sign. Associated with the higher S are also lower [Ca] but higher foliar [P] and L_A. With lower values for their coefficients and higher standard errors, also being of different sign, are the M_A and [N] terms. As mentioned in the Discussion, U_4 (accounting for 0.09 and 0.07 of the population variance for low and high fertility species respectively) seems to be dominated by the presence of large seeded members of the Leguminaceae whose importance in the phytogeography of Amazon forest has already been recognised by ter Steege et al. (2006). We therefore denote this dimension as $Д_{TS}$.

The last eigenvector included in our analysis, U_5, differs from the others in having a substantially greater importance for low fertility versus high fertility species (accounting for 0.09 and 0.04 of the population variances respectively). This component is characterised by H_{max} and M_{A} having opposite signs (in contrast to Д_{FW}) and with higher S and $\oslash$ also being associated with a lower H_{max} along with a less substantial but significant coefficient for ρ_{x}. Also of influence in characterising U_5 are greater foliar [C] associated with the higher M_{A} and $\oslash$. Although, U_5 presents some traits combinations as reported previously in the literature, this component, mostly related with species found at low fertility soils, it does not seem to have been recognised before. It is thus here denoted as Д_{PFL}.

Overall the five eigenvectors selected, all of which we believe to be physiologically relevant (see Supplement), accounted for 0.68 of the total variance for both low and high fertility soil species.

3.6 Bivariate relationships: environmental components

Considering data from both low and high fertility sites together, Table 3 lists correlations and SMA slopes for the environmental effects with this information provided in more detail (including confidence intervals) in the Supplement (Table S2A). As for Table 1, the SMA slopes reflect the relationship $y \leftrightarrow x$, with the x as the column headers and the y being the row labels. For the structural traits, the most significant relationships are all negative and appear between ρ_{x} and $\log_{10}$[P], $\log_{10}$[Ca], $\log_{10}$[K] and, to a lesser extent $\log_{10}(\ell_{\mathrm{A}})$. The slopes observed (−0.26 to −0.41) are, however, much less than for the associated slopes for the genetic components as listed in Table 1 (−0.37 to −0.72). This means that a per unit change in ρ_{x} is accompanied by a proportionally lesser change in these elements when environment (as opposed to genotype) was the inferred source of variation. Two of these relationships are illustrated in Fig. 7 which shows the relationships of both [P] and [K] with ρ_{x} to be quite strong and consistent across soil fertility types.

3.7 Principal component analysis of environmental effects

Especially given the strong relationships between ρ_x and the foliar cation environmental components shown above, it was of additional interest to see if coordinated structural/leaf biochemical responses to the environment exist for Amazon forest. We therefore undertook a PCA analysis of the full plot effects correlation matrix (excluding H_{max} and S both of which were considered to be environmentally invariant for any given species) with the results shown in Table 4. This shows that 0.33 of the total variation in the 11 traits examined could be explained by the first PCA axis ($\mathfrak{y}_1$) with ρ_x an important contributor and this also relating positively to foliar [C] and M_A, but negatively with all foliar nutrients examined and also with $\oslash$. The second axis of the PCA on the plot effects correlation matrix ($\mathfrak{y}_2$) is also significant, accounting for 0.25 of the variance, with substantial negative weightings for M_A, foliar [C] and $\oslash$ (and to a lesser extent foliar [P]) being balanced by positive weightings for foliar [Mg] in particular, but also with contributions from Φ_{LS} and ρ_x.

Taken together, the first two axes of the environmental effects PCA account for an impressive 0.58 of the total variance observed. This suggests that the modulation of the trait characteristics of tropical trees as a result of variations in their environment occurs in a highly coordinated manner.

3.8 Relationship between plot effect PCAs and soil/climate

Given the strong coherence in plot effect responses for the various traits as indicated by the PCA analysis of Table 4 we were interested to see if any of the corresponding plot axes scores correlated with previously derived soil and/or climate characteristics of the same sample plots. The most significant relationships are shown in Fig. 9. First, the top panel of Fig. 9 shows $\mathfrak{y}_1$ as a function of the first soil PCA axis of Fyllas et al. (2009), the latter considered a strong integrated measure of soil fertility and denoted ϕ_F. The strong relationship observed suggests a strong integrated response of Amazon tropical forest trees to soil fertility, with most nutrients increasing, and with foliar [C] and ρ_x decreasing as ϕ_F increases. Interestingly, the Kendall's τ for this plot of ψ_1 versus ϕ_F of 0.63 is greater than for any of the original variables examined by Fyllas et al. (2009), the highest of which was 0.56 for foliar [P]. Comparison with Fyllas et al. (2009) also shows that the ψ_2 contains significant weightings of leaf-level variables that, individually, were all strongly correlated with mean annual precipitation (P_A) viz. positive correlations with foliar [C] and M_A and a negative correlation with foliar [Mg]. It is therefore not surprising, as is shown in the middle panel of Fig. 8, that ψ_2 and P_A also show strong association, but with examination of Table 4 also suggesting that for any given species, both Φ_{LS} and ρ_w also decline with increasing precipitation and, somewhat counter intuitively, with $\oslash$ increasing.

Finally, as in Fyllas et al. (2009) we show values for Kendall's partial τ (denoted τ_p) for all traits of interest as well as ψ_1 and ψ_2 as functions of ϕ_f, ϕ_t, T_a, P_a and Q_a in Table 5. Here the calculated value of τ_p and associated probability giving an indication of the effect of each soil/environmental parameter after accounting for the effect of the other four. Taking into account to the potential confounding effects of spatial autocorrelation (Fyllas et al., 2009) we only consider relationships with $p \leq 0.01$ or better. As for the (full) Kendall's τ shown in Fig. 9, Table 5 suggests the ϕ to be superior predictors than the individual variables, the only exception being T_a. In that case, [N], [K] and ρ_w all show relationships not present when regressing the plot effect PCs as dependent variables.

4 Discussion

The extent to which variations in key plant functional traits are coordinated, especially with species considered the prime source of variability, has been a key focus of plant ecophysiological research over the recent decade with several important papers investigating relationships between leaf physiology, nutrients and structure and/or wood traits at the global scale (Wright et al., 2004; Chave et al., 2009; Zanne et al., 2010). Although tropical forests tree communities have been one area of focus for such plant

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

functional trait studies, work to date has generally been limited to only one or two sample sites per study (Thomas and Bazzaz, 1999; Santiago et al., 2004a; Kenzo et al., 2006; Sterck et al., 2006; Santiago and Wright, 2007; Poorter, 2008; Zhang and Cao, 2009; Baraloto et al., 2010). Moreover, where geographically or edaphically diverse plots have been examined they have often been analysed as if environment and/or soil has had no important effect on the absolute values of the various traits examined or their interrelationships (e.g., Wright et al., 2006; Baraloto et al., 2010) or limited in terms of the number of study sites and/or traits examined (e.g., Wright et al., 2007). Our study contrasts in that it has involved the integrated measurement of 11 physiological and structural traits for 1021 forest trees sampled from 53 sites of widely varying soil fertility across the Amazon Basin, with a statistical analysis specifically designed to disentangle the effects of environment/soil versus genotype on traits observed and their associations.

Some of the data used here have been presented previously (Fyllas et al., 2009; Patiño et al., 2009), with the current analysis integrating those data with structural traits introduced as part of this study (viz. L_A, ℓ_A, Φ_{LS}, S and H_{max}) as well as with foliar $^{13}C/^{12}C$ ratios as reinterpreted through the diffusional limitation index, $\oslash$, as defined by Eq. (1). We first consider the bivariate relationships between the structural components introduced as part of this study as well as relationships between these structural traits and the others already presented (Fyllas et al., 2009; Patiño et al., 2009) and then the extent to which variations of these traits integrate and coordinate in response to variations in genotype and/or environment,

4.1 Bivariate relationships for the genetic component of trait variation

4.1.1 Maximum tree height, branch xylem density and leaf mass per unit area

These three structural traits have often been associated with each other with significant positive $\rho_x \leftrightarrow M_A$ correlations such as for our genetic component in Fig. 4 also reported by Bucci et al. (2004), Ishida et al. (2008) and Meinzer et al. (2008). These studies have interpreted this relationship in terms of higher density wood species having lower hydraulic conductances leading to a requirement for more robust leaves capable of sustaining more severe soil water deficits. This notion is supported by more negative osmotic potentials being reported for the leaves of higher M_A and ρ_x species (Bucci et al., 2004; Ishida et al., 2008; Meinzer et al., 2008). On the other hand, it is also the case that M_A tends to increase with actual or potential (maximum) tree height (Falster and Westoby, 2005; Kenzo et al., 2008; Lloyd et al., 2010) but that ρ_w and H_max are sometimes negatively (as opposed to positively) correlated (Falster and Westoby, 2005; van Gelder et al., 2006).

One reason for this apparent contradiction may be that wood density and xylem vessel traits do not necessarily represent the same axis of ecophysiological variation (Preston et al., 2006; Martinéz-Cabrera et al., 2009; Poorter et al., 2010; Baraloto et al., 2010). This is because, in contrast to conifers, angiosperm vessel traits can vary significantly (especially in terms of diameter distributions and density) allowing for large changes in stem hydraulic conductance (K_S) for only small changes in ρ_w (Roderick and Berry, 2001). Moreover, wood density can also be affected by many other characteristics such as fibre density, extent and structure of ray parenchyma and (not unrelated to the above) wood air, solid and water fractions (Preston et al., 2006; Chave et al., 2009; Poorter et al., 2010; Zanne et al., 2010). Thus, although ρ_x and K_S may be well correlated in some cases (e.g., Santiago et al., 2004a) this may not be a strict functional linkage. Noting that for individual species ρ_w and ρ_x are likely to be closely correlated, at least for individual sites (Van Gelder et al., 2006; Sarmiento et al., 2011) and that high-density wood is associated with disturbance related advantages other than resistance to high wind (Anten and Schieving, 2010) – for example pathogen attacks (Augspurger, 1984) or a greater resistance to damage caused by falling canopy debris (Putz et al., 1983; King, 1986; Chao et al., 2008), we can thus simply interpret Fig. 4a–c as indicating that tropical tree species with traits associated with a higher photosynthetic productivity such as a high foliar [P] (Domingues et al., 2010), also tend to invest less towards wood defensive strategies.

The absence of a direct causal link underlying the relationships of Fig. 4a–c is also suggested by the CPC analysis of Table 3 where there is no contribution of ρ_x for the second component identified, Д_{RW}. On the other hand, a decline in ρ_x does constitute one component of integrated tropical tree responses to improved soil fertility (Tables 4 and 5, Fig. 9). Similar reductions in ρ_w with improved soil nutrient status, especially in terms of phosphorus have been reported before (Omolodun et al., 1991; Raymond and Muneri, 2000) and for *Eucalyptus* at least, seems to be associated with less secondary thickening of stem fibre cell walls with some evidence of an increased xylem conduit area (Thomas et al., 2005). By similar reasoning then, those results would argue that a lower ρ_w accompanying improved foliar nutrient status on more fertile soils could simply represent a growth response to the most likely greater rate of carbon supply on such soils. This is as opposed to the lower ρ_w observed being necessarily associated with a higher K_S as might be postulated to be required to sustain the higher photosynthetic rates likely accompanying higher values of $ɥ_1$ (Santiago et al., 2004a; Table 4).

Our observation of significant within-species variation in ρ_x as illustrated in more detail by Patiño et al. (2009) and also observed for ρ_w by Omolodun et al. (1991), Hernández and Restrepo (1995), Gonzalez and Fisher (1998), Weber and Montes (2008) and Sungpalee et al. (2009), shows important intraspecific variation in xylem and/or wood density even within the one plot (as also evidenced by the "residual" term for ρ_x in Fig. 1) as well as being affected by soil fertility as mentioned above. Thus, although we do not dispute that xylem traits and ρ_w/ρ_x may not necessarily be closely or mechanistically linked (as discussed above), studies which simply compare xylem trait "species values" as measured in one study or studies with values of ρ_w/ρ_x for the same species but gathered from a completely independent source (Russo et al., 2010; Zanne et al., 2010) are effectively comparing bananas with wombats. Thus, also not employing robust regression techniques more applicable to such analyses (McKean et al., 2009) they must under-estimate the actual significance of any relationship, be it functional or not. Moreover, there is no reason why it should necessarily be the case that wood economic spectrum should be strictly orthogonal to any leaf economics spectrum (Baraloto et al., 2010), especially as that study, as similar to our own data (Table 1) found reasonably strong relationships between ρ_x and all three of foliar [N], [P] and [K].

So, is the presence of large diameter xylem vessels with an associated high K_S associated with a greater H_{max} (e.g., Poorter et al., 2010; Zach et al., 2010) functionally related to the tendency of mature forests species of a greater H_{max} to also have a lower ρ_w (Falster and Westoby, 2005; van Gelder et al., 2006; Poorter et al., 2009)? Or does it more simply reflect that the fast-growing and light-demanding species characteristic of "dynamic" tropical forests also tend to have a lower ρ_w – this presumably allowing a faster height and diameter growth rate? On the basis of the discussion above, we suggest the latter, also noting that ρ_w is actually generally better correlated with juvenile light-exposure than H_{max} (van Gelder et al., 2006; Poorter et al., 2009).

If that argument is correct, then any associations between ρ_x and H_{max} are likely to be site specific: depending for example on the disturbance regime and the relative frequencies of regeneration in gaps versus shade (Sheil and Burslem, 2003). Indeed, although the current study found no significant relationship between H_{max} and the genetic component of ρ_x when simply pooling all species together ($p \geq 0.1$; Table 1), an implementation of a multilevel modelling approach similar to that applied by Lloyd et al. (2010) found a significant (random) plot component modulating the ρ_x and H_{max} relationship (χ^2 test, $p \leq 0.001$) associated with a negative relationship between the within-plot ρ_x vs. H_{max} slope and the associated stand level turnover rate (Fig. 10). For forests with high tree turnover rates (k), such as are typically found on eutric soils and/or limitations to root growth and function (Phillips et al., 2004; Quesada et al., 2009), ρ_x tends to decrease with H_{max}, but with the opposite observed for less dynamic forests (lower k) on deeper and less fertile soils. This points to important differences in species partitioning in respect to within-canopy light climate between the two forest types. We suggest that although for more dynamic forests with a high k, the classic paradigm of fast growing "pioneer" type species dominating the upper-canopy may apply (with higher wood density more shade-tolerant species lower down), for slower growing forests with a characteristic low k, that it does not apply. Rather, it is trees of a high ρ_{w} (and by virtue of this presumably slower height and volume growth rates) that eventually achieve canopy dominance on deep but infertile soils where stand-level growth rates and k are similarly low.

We suspect that that this observation may be due, at least in part, to the different distributions and roles of members of the dominant Amazon tree family, Fabaceae, across Amazonia. Members of this family tend to have a higher wood density than average (Malhado et al., 2010; Powers and Tifin, 2010) but different members of this family play different roles in the more fertile dynamic forests of western Amazonia (where they are often relatively small statured genera such as is the case for most *Inga* species) as opposed to the less dynamic forests of (north) eastern and central Amazon where they are more generally common as emergents such as *Hymenaea* and *Swartzia* (Fyllas et al., 2011) and, overall, represented disproportionately by the very high ρ_{w} Caesaplinoid sub-family. This difference can also be seen in the data presented by Malhado et al. (2010) and this perhaps being attributable to the the two different forest regions having been exposed to different geomorphological and edaphic conditions over extended periods of time (Hammond, 2005); this leading to (other things being equal) the forests of the western region of the Amazon Basin to be relatively short (Feldpausch et al., 2011) and also relatively dynamic (Phillips et al., 2004; Quesada et al., 2009).

The positive relationship between M_{A} and H_{max} of Fig. 3a and as also evident in the data of Falster and Westoby (2005) can also be inferred from the positive M_{A} vs. tree height relationships as reported by Thomas and Bazzaz (1999), Kenzo et al. (2006) and Lloyd et al. (2010). This is also seen within Д_{FW} in the CPC analysis of Table 3, with the leaves of (potentially) taller trees being thicker (Kenzo et al., 2006; Rozendaal et al., 2006) with a greater mesophyll thickness associated with a higher photosynthetic capacity per unit area (Kenzo et al., 2006). This increase in M_{A} with tree height being mostly associated with a greater mesophyll thickness should allow for a more efficient use of the higher rates of insolation towards the canopy top through higher photosynthetic capacities per unit leaf area (Rijkers et al., 2000). Along with more negative osmotic potentials, the greater leaf densities associated with a higher M_A and H_{max} should also help sustain leaves of such taller trees in the face of the more severe water deficits expected for sun exposed leaves higher up in the canopy (Cavaleri et al., 2010; Lloyd et al., 2010).

4.1.2 Leaf size and Φ_{LS}

Species with intrinsically higher foliar nutrient concentrations also tend to be found on more fertile soils (Fyllas et al., 2009), and so the positive correlation between the genetic components of leaf size variation, foliar [N] and foliar [P] observed here (Fig. 6) is consistent with the observation that Australian tropical forest tree species associated with poorer soils tend to have smaller leaves than those associated with more eutric conditions (Webb, 1968), as was also found for south-eastern Australian woodland species once precipitation effects were also taken into account (McDonald et al., 2003). Such a relationships has also been observed for pre-montane subtropical forest species in Argentina (Easdale and Healey, 2009) and has been suggested to be a widespread phenomenon (Givnish, 1987) perhaps being explainable by low N and/or P leaves typically having lower gas exchange rates than those of a higher fertility status (Domingues et al., 2010); with associated lower latent heat loss rates due to lower stomatal conductances. This would give rise to a greater rate of sensible heat loss being required to avoid over-heating during times of high insolation being achieved through the higher boundary layer conductance of smaller leaf sizes (Yates et al., 2010). Alternatively and consistent with the general notion of plants growing on less fertile soils having more conservative growth strategies (Westoby et al., 2002), smaller leaves may be favoured on low nutrient soils despite their relatively higher construction costs. This is because they also have shorter expansion times with an associated reduction in herbivory losses during this susceptible phase of foliar development (Moles and Westoby, 2000). If the “heat budget” explanation were to be correct, then an even better correlation with ℓ_A would be expected for both foliar [N] and [P]. But this was not the case (Table 1) with both foliar [N] and [P] much more closely correlated with L_A.

On the other hand, the relationships between leaf size and expansion time does not appear to differ strongly between simple vs. compound leaves (Moles and Westoby, 2000) suggesting that the herbivory hypothesis may be the more correct.

In apparent contrast to the above result, Malhado et al. (2009) found no strong relationship between soil fertility and average leaf size across a range of Amazonian forests. Their study was, however, based on an ordinal analysis of leaf-sizes based on herbarium samples which, as well as being inherently less accurate, may also have been confounded by the possibility of many of their herbarium samples being collected lower down in the forest canopy (including saplings) where for any given species individual leaf areas may be greater than for sun-exposed leaves as sampled here (Bongers and Popma, 1988; Rozendaal et al., 2006; Markesteijn et al., 2007; Poorter and Rozendaal, 2008). A further consideration may be that many herbarium samples are deliberately taken with flowers and/or fruits present to aid species identification and, as is well known in the horticultural literature for example (e.g., Syvertsen et al., 2003) leaves proximal to developing fruits may be appreciably smaller than those on non-fruiting branches, this also being broadly consistent with the evidence of reproductive/vegetative competition we discuss later in Sect. 4.2.4.

Although not significant across the dataset as a whole, there was a significant negative correlation between L_A and ρ_x for species characteristic of low fertility sites ($r^2 = -0.17, p \leq 0.05$: Supplement, Table S2B) as has also been reported for Australian tree/shrub species by Pickup et al. (2005) and Wright et al. (2007) and for neotropical forest tree species by Swenson and Enquist (2008), Malhado et al. (2009), Baraloto et al. (2010) and, with a much lower correlation ($r^2 = -0.02$) by Wright et al. (2006). Exactly as to why this should be the case is currently unclear. Earlier arguments have revolved around not only ρ_x and K_S being closely linked, but also with the assumption that variations in L_A should to a large extent reflect variations in Φ_{LS} (Wright et al., 2006). But, as discussed in Sect. 4.1.2, wood density and plant hydraulics may not be as closely linked as once thought and, although Φ_{LS} is indeed correlated with L_A (Fig. 6), our data do not actually show any appreciable correlations between Φ_{LS} and

ρ_x (Table 1; Supplement, Table S2B). This suggests that for tropical trees at least, this correlation may be more "casual" than mechanistic. Indeed, both for the dataset as a whole and for the individual fertility groupings, ρ_x was better (negatively) correlated with ℓ_A than L_A (Table 1, Supplement, Table S2B). Given that compound leaves are generally associated with faster diameter increment species (Givnish, 1978; Malhado et al., 2010) as is a generally lower ρ_x (Keeling et al., 2008) this then suggests that the negative correlation between laminar size and wood density may just reflect both traits being associated with faster growth rates. As well as tending to have lower ρ_w (Sect. 4.1.2) such species also tend to exhibit less branching than more shade tolerant species (Poorter et al., 2006; Poorter and Rozendaal, 2006; Takahashi and Mikami, 2008). Presumably (along with wider spacings) this allows for larger leafed upper-canopy species to have greater rates of direct light interception (Falster and Westoby, 2003).

The statistically significant decline in M_A with Φ_{LS} as on our Fig. 6 ($r^2 = -0.24, p \leq 0.01$), is understandable in terms of M_A and Φ_{LS} being important components of the trait dimension Д_{FW} (associated with light capture strategy through H_{max}) as well as also being related (with weaker weightings) through Д_{RW} (discussed further in Sect. 4.2). Such a relationship does not seem to have been detected in other studies with tropical tree species (Meinzer et al., 2008; Zhang and Cao, 2009), perhaps due to sampling a smaller range of genetic variability, although it is notable that working with a range of emergent or upper-canopy dipterocarp species, Zhang and Chao (2009) did find a significant negative relationship between Φ_{LS} and leaf thickness, the latter often being well associated with variations in M_A with tree height for dipterocarp species (Kenzo et al., 2006). Sampling across a range of sites in south-eastern Australia, Pickup et al. (2005) also found a negative relationship between M_A with Φ_{LS} but this relationship was, overall, not significant for species sampled within individual sites. Our own data suggest a stronger linkage of M_A with Φ_{LS} than either L_A or (indeed even of different sign) ℓ_A. This suggests (as is discussed further in Sect. 4.2) that this linkage may be mostly related to plant hydraulics considerations. The positive relationship

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

between ℓ_A and M_A may reflect constraints on the range of possible combinations of leaf(let) size and M_A, with larger laminar areas necessarily requiring a greater (minimum) M_A due to structural constraints (Grubb, 1998).

Not surprisingly, L_A and Φ_{LS} were related, but with a scaling coefficient of only 0.17, meaning that a greater leaf size was to a substantial degree compensated for by reduced numbers of leaves per unit sapwood area A_S. This points to Φ_{LS} being a rather conserved entity as has also been reported by others (e.g., Westoby and Wright, 2003). Φ_{LS} was also correlated with foliar [P] and [N] (Fig. 6), although this correlation was weaker for L_A especially in the case of foliar phosphorus. But for both nitrogen and phosphorus, the slope was still positive and close to 1.0. Thus tropical tree species with larger leaves tend to have not only higher [P] and [N] (and by implication higher gas exchange rates) but also a higher Φ_{LS}. As there is little evidence of greater diffusional limitations on gas exchange for such leaves (as shown by the lack of any significant relationship between Φ_{LS}, [N], [P] or L_A with $\oslash$), this implies that accompanying a higher Φ_{LS} are also increased K_S as also observed by Vander Willigen et al. (2000) for subtropical trees and also by Cavender-Bares and Holbrook (2001) for a range of *Quercus* species.

As would be anticipated on the basis of the very low proportion of the total variability within the dataset attributable to environment (Fig. 2), neither L_A, ℓ_A showed strong variation with environment and/or soil characteristics (Table 5), although Φ_{LS} does contribute slightly to the second environmental response trait PCA, (ψ_2; Table 4), with it's positive coefficient then suggesting a decline in Φ_{LS} with increasing precipitation (Fig. 9). Although this seems counter-intuitive with Φ_{LS} generally declining with reduced soil water availability such as to the average (whole) plant root-to-leaf hydraulic conductivity (Magnani et al., 2002; Addington et al., 2006; Carter and White, 2009), as is explained in Sect. 4.3 it is consistent with intra-specific variation giving rise to population of more "evergreen-like" phenotypes as dry-season lengths decrease.

4.1.3 Seed mass

As has also been reported by others, seed mass showed significant positive correlations with both H_{max} (Fig. 3; Foster and Janson, 1985; Hammond and Brown, 1995; Kelly, 1995; Metcalfe and Grubb, 1995; Grubb and Coomes, 1997), and ρ_w (Fig. 4; ter Steege and Hammond, 2001), although the latter relationship was not detected by Wright et al. (2006), perhaps because of methodological issues (Williamson and Weimann, 2010). Generally speaking, a greater seed size should confer a greater ability for survival and thus tend to be favoured under less favorable environmental conditions such as deep shade or nutrient poor soils (Westoby et al., 2002; ter Steege et al., 2006). This readily provides a basis for indirect correlations between S and wood/stem density to exist as high values of ρ_x or ρ_w are similarly associated with shade and/or dystrophic soil conditions (Sect. 4.1; Kitajima, 1994). More controversial is the basis of the relationship between S and H_{max}. For example, the suggestion of Moles et al. (2005) that, by analogy with Charnov's life history theory for mammals, larger statured species may have larger seeds because they require a longer juvenile period has been contested by Grubb et al. (2005) who maintain that it is simply the range of feasible seed sizes that a species can have that increases with H_{max}. Moreover, for tropical trees at least, there is probably little correlation between juvenile period and H_{max}, with faster-growing low-wood density pioneer type trees attaining greater heights than their smaller statured shade counterparts and in a shorter time (Baker et al., 2009). Indeed, by applying a general scaling model Falster et al. (2008) showed that longer juvenile periods alone are not sufficient to generate a correlation between height and seed size. They suggested that size-asymmetric competition among recruits (i.e. competition for light) may be the main factor having caused evolution towards larger offspring size. In this scheme of things, correlations with adult height comes about because larger adults have a greater total reproductive output, thus generating more intense competition among recruits. That model tested dynamics only with a single species at a time, but it is likely to still apply in more complex species systems such as tropical forests, even though relative size at the onset of maturity is much more variable for tropical trees species than for animal systems (Thomas, 1996; Wright et al., 2005). We also consider it unlikely that simple physical constraints can account for much of the relationships (also seen in Fig. 3) as even small statured species can have reasonably large seeds and/or fruits (for example *Theobromba*, or many members of the genus *Licania*: Prance, 1972). Likewise, wind dispersed species have both small seeds and a tendency to occur in the upper canopy strata where higher wind velocities aiding dispersal are greater (Hughes et al., 1994), one obvious example being the widespread neotropical species *Jacaranda copaia* (Jones et al., 2005).

As was also found by Wright et al. (2006), the study gives little support for one of “Corner’s rules”, viz. that due to their mutual dependence on the available supporting twig mass that leaf size and seed size should be positively correlated (Corner, 1949). There may be two reasons for this. First, as pointed out by Grubb et al. (2005) such biomechanical explanations would only be expected to apply where there is little flexibility in the number of fruits per inflorescence. Second, as for Φ_{LS} (Fig. 5) the ratio of total leaf area to the supporting stem mass is to a large degree independent of L_{A} (Wright et al., 2007). Indeed, if anything, what our data suggest is that reproductive structures compete with leaves for available space as there is a nearly significant correlation between Φ_{LS} and S ($r^2 = -0.09, p = 0.07$) with this negative relationship significant for the low fertility species (Supplement, Table 2). Thus, in contrast to vegetation types from more xeric habits where leaf areas may be substantially constrained by hydraulic considerations, leaf area per unit available stem area or mass may actually be constrained by the requirements for simultaneous allocation of available carbohydrate to reproductive structures for most tropical forest trees. That being consistent with their tropical forest productivity being carbon limited as argued by Lloyd and Farquhar (2008).

Competition between foliage and developing fruit may also be the reason for the negative relationship between seed size and foliar [Ca] shown in Fig. 7, an observation also made for sub-tropical montane tree species by Easdale and Healey (2009). It has long been known that calcium is relatively immobile in plants (e.g., Kirby and

Pilbeam, 1984) with high rates of calcium supply to developing fruit essential for cell wall development and for longer term maintenance of membrane integrity. Sufficient levels of calcium are also required to maintain the integrity of the fruit flesh including resistance to fungal attack even after abscissed from the plant (Bangerth, 1979). Due to its immobility, this calcium accumulation in fruit tissues must occur at the expense of the leaves, and thus Fig. 7 does not necessarily imply that Ca itself may be limiting for either reproductive tissue development or leaf physiological function. Indeed, the SMA slope fit of −8.3 suggests that for each doubling of S foliar [Ca] declines by only about 10 %, a value roughly consistent with the similar [Ca] in both seed and leaf tissue (as evidenced from the seed data of Grubb and Coomes (1997)) and with about 0.1 of total South American tropical forest "soft" litterfall occurring as reproductive organs (Chave et al., 2010). Even though such a result does not, therefore, necessarily imply an direct effect of Ca availability on tree function, it is interesting to note that species growing on extremely cation poor spodosols are characterised by relatively small seed masses as compared to more fertile nearby forests (Grubb and Coomes, 1997) as well as with leaf photosynthetic rates showing an apparent dependence of leaf calcium concentrations (Reich et al., 1995). Moreover, for forests on such nutrient poor soils, carbon allocation to photosynthetic organs is apparently prioritised over that to reproduction (Chave et al., 2010), this being consistent with neotropical forest reproductive structure frequency being highly sensitive to soil fertility as inferred (apparently) from soil nitrogen status (Gentry and Emmons, 1987), being markedly lower for forests growing on less fertile soils. Overall, these observations suggest, as also discussed in Sect. 4.1.2, that foliar and reproductive tissue development may be in direct competition for either carbon or available nutrients where soil fertility is low.

4.2 Integration of structural and physiological traits

Although an examination of the various bivariate relationships, as discussed in Sect. 4.1 has hopefully proved informative, it is also of additional interest to quantify the extent to which all the various traits examined coordinate in their variability as a whole. In this respect, PCA was considered the most appropriate approach, as the first dimension of a PCA analysis can also be considered (with data normalisations prior to analysis as undertaken here) as the multivariate equivalent of an SMA model fit (Warton et al. 2006). Moreover, as long as it is rigorously established that subsequent axes remain orthogonal to each other (as we have done here for example through the sphericity and residuals matrix analyses of Tables S4 and S6 in the Supplement as well as can be seen from the species scores for the first three axes in Fig. 8) then these Д can be considered to represent distinct integrated plant functional dimensions, although sometimes having individual traits in common (Fig. 8d, Table 2). In our analysis here we have also taken the additional step of allowing for the covariance matrices to vary between low and high fertility sites through the CPC approach of Flury (1988), this effectively being a multivariate extension of the allowance in an SMA analysis for different groups to have differences in slope and/or elevation (Warton et al., 2006) with analysis of the "Flury hierarchy" in Table S3 (Supplement) strongly suggesting that the CPC model presents a significant improvement over models assuming equality or strict proportionality between the two species groups. We thus interpret Table 2 as indicating five discrete integrated trait dimensions of tropical tree function and with the relative importance of these effects varying between high and low fertility species. This interpretation is made even though some of the measured properties such as M_A and ρ_x are modelled as having significant contributions to several dimensions. This is argued as reasonable on two counts. First, variations in some of the traits measured may have different underlying causes. For example, changes in M_A may be a consequence of variations in leaf thickness, tissue density or both (Witkowski and Lamont, 1991; Niinemets, 1999; Poorter et al., 2009) and likewise, variations in ρ_x could reflect differences in the proportions of gas, air and dry matter content (for hydrated tissue) in a wide range of combinations (Poorter, 2008). Second, as selective pressures are multiple, it is quite likely that contrasting combinations of individual traits have evolved for different reasons.

4.2.1 Д_{PDJ}: Leaf structural costs and lifespan

Although it is often considered that the primary dimension of the leaf economic spectrum is that proposed by Wright et al. (2004) viz. systematic variations in rates of photosynthetic carbon acquisitions (dry weight basis) being linked with foliar dry-weight concentrations of nitrogen, phosphorus, M_{A} and leaf longetivity, our analysis found that U_1 (accounting for the greatest component of the total variation in the dataset) did not involve nitrogen at all, and was actually dominated by leaf cation concentrations and (of opposite sign) a low carbon content. We suggest that this dimension, Д_{PDJ}, reflects different plant strategies in terms of leaf construction costs, with the tendency for low M_{A} in these leaves of high mineral content presumably attributable to a low tissue density associated with thinner, less lignified cell walls and with the higher cations content presumably also balanced by higher levels of organic acids (Poorter and de Jong, 1999) and with lower overall construction costs and less investment of phenols and other carbon rich compounds in defense (Poorter and Villar, 1997). Presumably associated with Д_{PDJ} are also variations in leaf water relations. For example, it seems reasonable to expect that, associated with lower levels of lignification and reduced tissue densities, would be relatively more flexible cell walls and a low bulk modulus of elasticity (Niinemets, 2001), also with the high cation concentrations, especially potassium making a substantial contribution (in association with organic acids) to leaf tissue osmotic potentials (Olivares and Medina, 1992). These attributes, combined with the likely relatively low allocation of carbon resources to defense associated compounds such as lignin and phenols suggests that in many ways leaves of trees with high Д_{PDJ} may be able to expand quite rapidly but also be shorter lived and with more "deciduous like" characteristics than their lower Д_{PDJ} counterparts (see also Sobrado, 1986).

4.2.2 Д_{RW}: an extension of the classic "leaf economic spectrum"

Our second identified CPC, Д_{RW} is that usually considered to be the principal dimension of the leaf economic spectrum (Wright et al., 2004), some aspects of which have

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

also been presented for tropical forest tree species (Sandquist and Cordell, 2007; Santiago and Wright, 2007; Fyllas et al., 2009; Baltzer and Thomas, 2010; Baraloto et al., 2010; Domingues et al., 2010). Although we did not measure the photosynthetic or respiratory components, our analysis does suggest that for tropical forest species, L_A should also be included as part of $Д_{RW}$, effectively incorporating the relationships between L_A and foliar [N] and/or [P] status (Fig. 7) within this dimension. Such an involvement of L_A in the classic resource acquisition/utilisation spectrum has also been suggested from a data analysis involving 29 sub-tropical montane tree species across 12 ha of permanent sample plots in Tucumán, Argentina (Easdale and Healey, 2009). Although not considered significant on the basis of penalty corrected p-values, correlations between leaf size and [N] and [P] of a similar strength to that reported here (and hence included as part of $Д_{RW}$) were also reported for tropical forest leaves sampled across a range of soil substrates in French Guiana (Baraloto et al., 2010). They concluded, however, that L_A was not closely linked with either [N] or [P]. This could be for several reasons. First, their sampling strategy covered a range of (undefined) soil types and as discussed in Sect. 4.3, these are likely to have modulated foliar nutrient levels but not L_A. Second, our sampling has covered a much wider range of environments and soils, presumably bringing wider species-level variation into the dataset as whole. Thirdly, our analysis shows the L_A is also an important component of $Д_{FW}$ which, not having been taken into account in the Baraloto et al. (2010) study may have confounded their results.

Also identified as part of $Д_{RW}$ was Φ_{LS}, this being consistent with the general trend of Φ_{LS} to increases with increasing L_A (Fig. 6d). Especially as there was little contribution of $\oslash$ to this dimension (Table 2), this suggests that trees with a higher $Д_{RW}$ should also have increased rates of water transport per unit A_S. With there being no large contribution of variations in ρ_x to this dimension, this suggests a higher K_S modulated by other means. Such a higher K_S coordinating with higher [N] and [P] without commensurate changes in ρ_x could be achieved through increased vessel lumen areas at the expense of water holding tissues and, indeed, analysis of individual species sapling stem data for a Bolivian forest presented by Poorter wt al. (2010) does indeed suggest an increase in the proportion of non-wood stem components occupied by the gas, (as oppossed to water fractions) as $Д_{\mathrm{RW}}$ increases (using leaf data from Poorter and Bongers (2006) with CO_2 assimilation rates (leaf mass basis) taken as a proxy for $Д_{\mathrm{RW}}$). Alternatively, variations in sap ionic content affecting stem-specific hydraulic conductivities through interactions with the pectic matrix of the xylem pit membranes (e.g., Nardini et. al., 2010) might also somehow be involved.

Also of note (though of lesser significance than the above) was the increase in both M_{A} and [Mg] with decreasing $Д_{\mathrm{RW}}$. The former is, of course, well documented and, for woody plants at least, seems to be associated with an increased foliar tissue density rather than changes in leaf thickness (Niinemets, 1999; Poorter et al., 2009) and with a concurrent reduction in photosynthetic nutrient efficiency when expressed on a dry weight basis (Niinemets, 1999; Domingues et al., 2010). One possibility to account for this is low internal conductances to CO_2 transfer for higher M_{A} species (Lloyd et al., 1992; Syvertsen et al., 1995; Warren and Adams, 2006), as perhaps evidenced by a small but significant positive contribution in $\oslash$ to this dimension (0.014 ± 0.05: Table 2). Alternatively, relatively more nitrogen being allocated to cells walls of low $Д_{\mathrm{RW}}$ species (Onoda et al., 2004; Takashima et al., 2004), much of which would be expected to be in the form of defense related proteins (Feng et al., 2009). The decrease in [Mg] with higher values of $Д_{\mathrm{RW}}$ does not seem to have been reported before and may be related to its role as a coordination compound within the chlorophyll molecule. This is because, in the absence of variation in the within-canopy light regime, leaf chlorophyll contents should being relatively conserved on an area (as oppossed to mass) basis (Rijkers et al., 2000, Lloyd et al., 2010), this giving rise to attendant reductions in mass based magnesium concentrations as M_{A}decreases.

4.2.3 $Д_{\mathrm{FW}}$: tree height and light acquisition

Unlike the previous two Д considered, $Д_{\mathrm{FW}}$ does not involve foliar nutrient concentrations, but incorporates into the one dimension, variations in H_{max}, Φ_{LS}, $\oslash$, M_{A} and to a lesser extent ρ_{x}. This linkage is most likely through the hydraulics/plant height considerations already discussed as part of Sect. 4.1.1 and 4.1.2. That is to say, as H_{max} increases, a suite of trait adjustments occur; these including a reduction in Φ_{LS} with estimates of $\oslash$ also suggesting that leaves with a high H_{max} also tend to operate at a lower $c_{\mathrm{i}}/c_{\mathrm{a}}$. As it seems likely that the higher M_{A} with increasing H_{max} is mostly attributable to increased leaf/mesophyll thickness and hence increases in photosynthetic capacity per unit leaf area, A_{max} (Sect. 4.1.1), this reduction in $c_{\mathrm{i}}/c_{\mathrm{a}}$ may be attributable to stomatal capacity increasing less with H_{max} than should A_{max} . Such a tendency to operate at a lower $c_{\mathrm{i}}/c_{\mathrm{a}}$ would also help to conserve water for species more likely to be higher-up in the canopy and hence exposed to higher levels of insolation and an associated greater evaporative demand (Lloyd et al., 2010).

Although H_{max} was not determined in their study, many of the above measured and/or inferred traits, viz. Φ_{LS} and A_{max}, were found to co-vary in a similar manner as for Д$_{\mathrm{FW}}$ across a range of tropical forest trees in Panama by Meinzer et al. (2008). Though in that case, variations in ρ_{x} were considered of key importance in terms of trait coordination, especially through linkages to plant hydraulic parameters such as K_{S}. Our observed contribution of ρ_{x} is likewise significant (-0.22 ± 0.10), though as discussed in Sect. 4.1.1 taken across a wide range of species and sites the strong relationship between ρ_{x} and/or ρ_{w} and K_{S} as observed by Meinzer et al. (2008) and also in some other studies (e.g., Santiago et al., 2004a) may not necessarily always apply.

Interestingly, in contrast to Д$_{\mathrm{RW}}$, variations in Φ_{LS} were not accompanied by commensurate changes in L_{A}. Indeed, if anything, L_{A} tend to increase with decreasing Φ_{LS} as H_{max} increases within Д$_{\mathrm{FW}}$. Thus, we find integrated together within Д$_{\mathrm{FW}}$ the tendency of potentially taller trees to have fewer but larger leaves than their more vertically challenged counterparts. But with a lower Φ_{LS} overall. This lower Φ_{LS} presumably serves to help maintain favourable water relations by counteracting greater resistances in the hydraulic pathway for potentially taller trees. Nevertheless, along with a higher $\oslash$, this lower Φ_{LS} must also serve to reduce overall rates of whole tree carbon gain such as otherwise might be expected on the basis of higher A_{max} and a greater probability of high levels of incoming radiation. This trade-off associated with a greater H_{max} may be one reason for the observation that light demanding species with a low ρ_{w} do not necessarily show higher above-ground growth rates than their more shade tolerant counterparts as reported by Keeling et al. (2008).

4.2.4 Д_{TS}: large seeds at the expense of leaf area

As mentioned in Sect. 4.1.3, a major factor in accounting for this trait dimension is the presence of many large seeded Fabaceae, especially on nutrient poor soils, for whom it turns out do not have as large a Φ_{LS} as they would otherwise be expected to have on the basis of their other integrated trait values. Thus species with a high Д_{TS} should best be regarded as those having a larger than average seed size with that being associated with a lower than average Φ_{LS} as compared to trees of an equivalent Д_{FW} and/or Д_{RW}. This lower Φ_{LS} is also accompanied by reduction in L_{A} suggesting that it is not so much competition for lateral meristems (Kleiman and Aarssen, 2007) that gives rise to the negative association between Φ_{LS} and S within this dimension. But rather some sort of mechanical constraint such as the total mass capable of being borne per unit stem weight (Westoby and Wright, 2003) or a simple competition for carbon as discussed in Sect. 4.1.2.

The small but significant contributions of M_{A}, [N] and [P] to Д_{TS} may be mostly phylogenetic associations as members of the typically large seeded Fabaceae typically have a lower M_{A} and higher [N] and [P] than members of other plant families (Fyllas et al., 2009). On the other hand, as is discussed in Sect. 4.1.3, the lower foliar [Ca] levels associated with larger seed size is probably functionally linked though high calcium requirements of developing fruits and seeds.

4.2.5 Д_{PFL}: shade tolerance and long-term viability

The fifth dimension identified, viz. Д_{PFL}, includes a significant positive contribution of increased M_{A}, presumably associated with a high tissue density (as oppossed to leaf thickness) and associated increased leaf toughness (Kitajima and Poorter, 2010) and with high [C] linked through higher than average levels of more reduced structural compounds such as lignin as well as the typically high C-content defense related compounds such as tannins and phenols (Fine et al., 2006; Read and Stokes, 2006; Read et al., 2009). Also associated with this is a higher $\oslash$, which may be suggestive of a greater internal resistance to CO_2 diffusion within the leaves of high tissue density woody species (Lloyd et al., 1992; Syvertsen et al., 1995; Warren and Adams, 2006). Interestingly, as well as these correlated leaf traits in this dimension there is the coordinated involvement of a lower H_{max}. Species with strong weightings along this trait dimension are also characterised by larger seeds as would be expected for shade adapted trees (Sect. 4.1.3). Along with a small but significant contribution of ρ_{x}, $Д_{\mathrm{PFL}}$ is thus strongly suggestive of a coordinated trait dimension associated with shade tolerance and longevity. Not surprisingly then, it seems to play a much greater role in accounting for the trait variations of species associated with low fertility as opposed to high fertility soils as indicated by the different values for the characteristic roots ($\lambda_{\mathrm{low}} = 698$, $\lambda_{\mathrm{high}} = 318$, Table 2).

4.2.6 Significance of integrated trait dimensions and their components

Although it is axiomatic that to be included in any of the above integrated dimensions that a trait would have had to be actually measured, what is perhaps more subtle, is that the mix of suites of traits coming together on any one PCA (or CPC) axis is also dependent on what is *not* measured. For example, our differentiation of the first two components of the CPC analysis of Table 2, viz. $Д_{\mathrm{PDJ}}$ and $Д_{\mathrm{RW}}$ occurred mainly as consequence of [C] varying positively with M_{A} for $Д_{\mathrm{PDJ}}$ (this being interpreted as less allocation of photosynthate to more reduced structural compounds such as lignin in low M_{A}/high cation leaves), but increasing with decreasing M_{A} within $Д_{\mathrm{RW}}$ (this likely being an effect of higher lipid contents in higher photosynthetic capacity leaves). If leaf [C] is omitted for the analysis, then these two dimensions actually collapse into the one due to the strong correlations between all of the cations, nitrogen and phosphorus and (negatively) M_{A} (results not shown). This seems likely to have been the case for the results of Easdale and Healey (2009) and Baraloto et al. (2010) where, along with M_{A}, cations, nitrogen and phosphorus were all considered part of the one dimension. Likewise, although L_{A} was found to be a key component of Д_{RW} it was also found to be part of Д_{FW}. Thus, if the latter were not to have been derived from the CPC analysis (for example through the absence of any H_{max} measurements) then probably the involvement of L_{A} in Д_{RW} would also have appeared more equivocal (and potentially missed) as confounding species potential height effects on L_{A} would have muddied it's role in this classic leaf resource acquisition dimension (see for example Baraloto et al., 2010).

It is thus clear, that in the presence of additional parameter measurements (for example direct determination of K_{S}) our derived dimensions may well have been different. Nevertheless, as discussed above, all five Д identified to relate in some way to previously identified trait groupings; though is some cases (as for example with S and M_{A} in Д_{PFL}) not previously specifically linked through the species dependent variance-covariance matrix. It would be of great interest to see how the identified trait combinations vary with phylogeny and if they trace back through evolutionary time as discrete combinations. Nevertheless, these ambitions may be confounded by the fact that traits such as M_{A} appear significant in almost all dimensions. As discussed at the start of Sect. 4.4 this may be because variations in M_{A} can be surrogates for variations in tissue density, leaf thickness or both, and similarly from the discussion in Sect. 4.1.1. to 4.1.5 above, variations in [C], Φ_{LS}, L_{A} and $\oslash$ are all potentially attributable to a range of different underlying causes. It is also probably for this reason that considerable ambiguity exists between different studies in terms of the significance (or even the sign) of some bivariate relationships. For example, if the primary source of variation in L_{A} and M_{A} were to be in association with Д_{FW} (this being similar in many ways to the light acquisition axis identified by Zhang and Cao (2009) for dipterocarps growing in a Chinese common garden) then a positive association between M_{A} and L_{A} would be expected, with leaves of upper canopy trees being both larger and thicker than those for trees lower down in the canopy (as was found to be the case for temperate deciduous trees, for example, by Niinemets, 1998). On the other hand, where foliar N and/or P dry weight concentrations are the main source of variation via Д_{RW}, then a negative relationship between M_{A} and L_{A} would be expected to be observed as, for example, was found to be the case for a range of herbaceous angiosperms by Shipley (1995). Or, as found in some cases by Pickup et al. (2005) we predict there should be no relationship between L_{A} and M_{A}, for example where Д_{PDJ} is be the primary source of variation in the latter (as L_{A} is effectively absent from this dimension). Indeed, although much touted as a fundamental plant trait (e.g., Poorter et al., 2009; Asner et al., 2011; Kattge et al., 2011) M_{A} seems to us to be too confounded a measurement to be practically useful in differentiating different plant growth strategies as evidenced by its contribution to the five Д above and future work would be better directed towards separate measurements of foliar tissue density and thickness as well as leaf dry matter content (Witkowski and Lamont, 1991; Wilson et al., 1999). It is probably because of its ambiguous nature that M_{A} does not seem to be as good a predictor of demographic rates as first thought, especially when comparisons are done across different sites (Poorter et al., 2008).

Our results give no support for the supposed "second dimension" of the leaf economics spectrum proposed by Baltzer and Thomas (2010). That study, primarily based on data from Bornean forest trees did, however, fail to differentiate between genetic versus soil effects on foliar properties as has been done here. And with their "second dimension" (hardly likely to be orthogonal to the first dimension in any case) most likely simply reflecting soil fertility effects on foliar [P] as already well documented by Fyllas et al. (2009) and considered further below.

4.3 Coordinated trait responses to environmental variability

As evidenced by the 0.3–0.4 portion of the total variance associated with the Φ_{LS}, ρ_{x} and $\oslash$ "plot effect" terms (Fig. 4) values of all these traits are not independent of where a species is growing and with there being strong "environmental" effect correlations between ρ_{x} and all of log[N], log[P], log[Ca] and log[K]. This results in this

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

structural parameter aligning itself along with elemental concentrations (including [C] with a negative weighting) in the first environmental PCA axis, $ɥ_1$ (Table 4), which was itself closely correlated with a PCA of soil chemical and physical properties (Fyllas et al., 2009; Quesada et al., 2010). This suggests a coordinated plant physiological and structural response to changes in soil fertility, with the concurrent increases in foliar cations and phosphorus not that surprising as their availability within soils tends to decline more or less in concert as part of the soil weathering process (Quesada et al., 2010). Such a decline is not necessarily the case for N, however (Quesada et al. 2010), though in this respect it should also be borne in mind that plot/environment has relatively less effect on foliar [N] than [P], [Ca] or [K] (Fyllas et al., 2009). Thus in a relative sense (i.e. compared to its total variation), nitrogen actually makes a lesser contribution to $ɥ_1$ than the other elements, the only exception being foliar [Mg] which, unlike foliar [K] or [Ca], seems to be more influenced by plant regulatory factors than by soil availability (Fyllas et al. 2009). This dimension relating to what seems to be a soil fertility mediated effect bears some resemblance to $Д_{\mathrm{RW}}$ but with a more easily discernible effect on ρ_{x}. As mentioned in Sect. 4.1.1, such a fertility effect on ρ_{x} has been seen before as mediated by soil phosphorus availability for eucalypt and mangrove (Thomas et al., 2005; Lovelock et al., 2006). Although working with Brazilian savanna trees, Bucci et al. (2006) found it was nitrogen (as opposed to phosphorus) fertitlisation that induced changes in ρ_{x} and K_{S} with in their case with N-fertilisation causing attendant increases in Φ_{LS} not detected here (Table 4).

It seems likely that higher foliar [P], especially in combination with the lower M_{A} also associated with $ɥ_1$ would give rise to higher photosynthetic rates on an area basis (Domingues et al., 2010; Mercado et al., 2011). Thus, with tropical forest tree hydraulics and photosynthetic capacity being closely linked (Brodribb and Field, 2000; Brodribb et al., 2002; Santiago et al., 2004a) the likely increase in K_{S} accompanying a decrease in ρ_{x} with improved nutrient status may serve to help maintain some homeostasis in leaf water relations, this offsetting the higher rates of water-use per leaf area that would be expected to accompany any increase in $ɥ_1$. This suggestion supported by the only modest contribution of ⊘ to this dimension (Table 4). As to how such a coordination could occur is currently not clear, although the greater rates of cambial activity in the wood of higher P status trees giving rise to a lower ρ_x might be attributable through sugar signalling mechanisms (Rolland et al., 2006; Hölttä et al., 2010), this resulting in less secondary thickening of vessels walls and a higher conduit area (Thomas et al., 2005). Other elements may also be involved though, for example effects of calcium and/or potassium on sapwood cambial activity (Fromm, 2010).

The second integrated environmental response dimension identified, ψ_2, essentially represents an integration of previous observed foliar trait responses to precipitation, viz. increased M_A, [C] and ⊘ and decreased [Mg] as mean annual precipitation increases as detailed in Fyllas et al. (2009). Although this response to P_A seems at odds with the general observation from inter-species analyses that leaves of more arid environments should have a higher M_A and often with a higher ⊘ (Miller et al., 2001; Santiago et al., 2004b) as discussed by Fyllas et al. (2009) this tendency towards more structurally rigid leaves at higher P_A may be an intra-specific response to increased disease pressure, possibly even as a result of the development of phenoptypically distinct provenances under different precipitation regimes – as seems to be the case for Costa Rican populations of *Cordia alliodora* in terms of susceptibilities to soil water deficit induced cavitation (but not other hydraulic properties: Choat et al., 2007). An aligned interpretation is that as severe dry season water deficits become increasingly less of a driving force in determining leaf lifetimes, leaves of any given species become more "evergreen" in their structural characteristics. And indeed it is worth noting that the distinction between evergreen and deciduous phenologies for tropical forest trees is a somewhat arbitrary one (Brodribb and Holbrook, 2005; Williams et al., 2008). In such an interpretation, an increase in ⊘ with P_A could be interpreted as either a tendency towards more conservative stomatal behavior in evergreen species where the precipitation regime is not strongly seasonal (Lloyd and Farquhar, 1994) or, alternatively to an increased resistance to CO_2 diffusion within higher M_A leaves due to a higher cell wall resistance (Syvertsen et al., 1995).

Although not emerging as any sort of integrated response through the PCA analysis of the derived environmental effects, the temperature responses of [N], [K] and ρ_x are all also of note; these have already been considered separately by Fyllas et al. (2009) and Patiño et al. (2009).

5 Conclusions

Extending beyond a simple bivariate analysis approach, this study has separated environmental from genetic effects for a range of structural and physiological traits for Amazon forest trees then using Common Principal Component Analysis to reveal as many as five discrete integrated axes of genetic variation. The relative weightings of the axes varies between low and high fertility soil associated species. The first component (accounting for the highest proportion of the total variance in the dataset) was not the classic "leaf economic spectrum", but rather to relate mostly to variations in leaf construction costs. The leaf economic spectrum was the second most important dimension identified in terms of variance accounted with our results suggesting that it also involves differences in leaf size as well as in leaf area: sapwood area ratios. Our third dimension brings together several structural traits, including species specific maximum height, individual leaf areas, leaf mass per unit area and xylem density and leaf magnesium concentrations. The fourth and fifth dimensions were interpreted as relating to a seed size/leaf area trade-off and shade tolerance characteristics respectively.

Several traits, in particular leaf mass per unit area, foliar carbon content and xylem density had significant weighting on many axes of variation, this being attributed to their somewhat ambiguous "proxy" nature for a range of underlying and more fundamental plant physiological properties. In particular, variations in twig xylem density may arise as a consequence of differences in a range of different underlying phenomena and with its generally poor correlation with other plant traits suggesting that it may not be as good a proxy for plant hydraulic conductivity as once thought.

Significant effects of environment on many plant traits were also identified. Some of these integrated into discrete dimensions of variation and with discrete but different changes being associated with variations in soil fertility versus differences in mean annual precipitation. Whether these differences relate to strict "environmental effects" or reflect systematic patterns in intra-specific trait variation with soils and/or climate remains to be established.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/8/5083/2011/ bgd-8-5083-2011-supplement.pdf.

Acknowledgements. We thank our many South American collaborators for help with logistics and practical help in the field. Much of the data collection phase of this work was supported through the EU FP6 "LBA-Carbonsink" project with subsequent data analyses supported by funding through the UK National Environment Research Council "QUERCC" and "TROBIT" consortia. We also thank David Warton (University of New South Wales) for pointing out to us the possibilities of CPC analysis and Patrick Phillips (University of Oregon) for making his CPC model estimation and evaluation programs freely available. Shiela Lloyd assisted with manuscript preparation.

The service charges for this open access publication
have been covered by the Max Planck Society.

References

Ackerly, D. D.: Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance, Ecol. Monogr., 74, 25–44, 2004.

Addington, R. N., Donovan, L. A., Mitchell, R. J., Vose, J. M., Pecot, S. D., Jack, S. B., Hacke, U. G., Sperry, J. S., and Oren, R.: Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats, Plant Cell Environ., 29, 535–545, 2006.

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Anten, N. P. R. and Schieving, F: The role of wood mass density and mechanical constraints in the economy of tree architecture, Amer. Nat., 175, 250–260, 2010.

Asner, G. P., Martin, R. E., Tupayachi, R., Emerson, R. Martinez, P., Sinca, F., Powell, G. V. N. Wright, S. J. and Lugo, A. E.: Taxonomy and remote sensing of leaf mass per area (LMA) in humid tropical forests, Ecol. Appl., 21, 85–98, 2011.

Augspurger, C. K.: Seedling survival of tropical tree species: interaction of dispersal distance, light gaps and pathogens, Ecology, 65, 1705–1712, 1984.

Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Nascimento, H., Monteagudo, A., Neill, D. A., Silva, J. N. M., Malhi, Y., López Gonzalez, G., Peacock, J., Quesada, C. A., Lewis, S. L., and Lloyd, J.: Do species traits determine patterns of wood production in Amazonian forests?, Biogeosciences, 6, 297–307, doi:10.5194/bg-6-297-2009, 2009.

Baltzer, J. L. and Thomas, S. C.: A second dimension to the leaf economics spectrum predicts edaphic habitat association in a tropical forest, PLoS ONE, 5(1), e13163, doi:10.1371/journal.pone.0013163, 2010.

Bangerth, F.: Calcium related disorders of plants, Ann. Rev. Phytopathol., 17, 97–122, 1979.

Baraloto, C., Timothy Paine, C. E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C., and Chave, J.: Decoupled leaf and stem economics in rain forest trees, Ecol. Lett., doi:10.111/j.1461-0248.2010.01517.x, 2010.

Bates, D. and Sarkar, D.: `lme4`: Linear Mixed–Effects Models Using S4 Classes. R package version 0.999375–27, 2007.

Bongers, F. and Popma, J.: Is exposure-related variation, in: leaf characteristics of tropical rain forest species adaptive?, edited by: Werger, M. J. A., van der Aart, P. J. M., During, H. J., and Verhoeven, J. T. A., Plant Form and Vegetation Structure, 191–200 pp., SPB. Academic Publishing, The Hague, 1988.

Brodribb T. J. and Field T. S.: Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests, Plant Cell Environ. 23, 1381–1388, 2000.

Brodribb, T. J. and Holbrook, N. M.: Leaf physiology does not predict leaf habit; examples from tropical fry forest, Trees, 19, 290–295, 2005.

Brodribb, T. J., Holbrook, N. M., and Gutiérrez, M. V.: Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees, Plant Cell Environ., 25, 1435–1444, 2002.

Bucci, S. J., Goldstein, F. C., Meinzer, F. C. Scholz, A., Franco, A. C. and Bustamante, M.

C.: Functional convergence in hydraulic architecture and water relations in tropical savanna trees: From leaf to whole plant, Tree Physiol., 24, 891–899, 2004.

Bucci, S. J., Scholz, F. G., Goldestein, G., Meinzer, F. V., Franco, A. C., Campanello, P. I., Villa Lobos-Vega, R., Bustamante, M., and Miralles-Wilhelm, F.: Nutrient availability constrains the hydraulic architecture and water relations of savanna trees, Plant Cell Environ., 29, 253–267, 2006.

Casper, B. B., Heard, S. B., and Apanius, V.: Ecological correlates of single–seededness in a woody tropical flora, Oecologia, 90, 212–217, 1992.

Cavaleri, M. A., Oberbauer, S. F., Clark, D. B., Clark, D. A., and Ryan, M. G.: Height is more important than light in determining leaf morphology in a tropical forest, Ecology, 91, 1730–1739, 2010.

Carter, J. L. and White, D. A.: Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation in ground water depth, Tree Physiol., 29, 1407–1418, 2009.

Cavender-Bares, J. and Holbrook, N. M.: Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats, Plant Cell Environ., 24, 1243–1256, 2001.

Cavender-Bares, J., Kitajima, K., and Bazzaz, F. A.: Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species, Ecol. Monog., 74, 635–662, 2004.

Chao, K.-J., Phillips, O. L., Gloor, E., Monteagudo, A., Torres-Lezama, A., and Vásquez-Martínez, R.: Growth and wood density predict tree mortality in Amazon forests, J. Ecol., 96, 281–292, 2008.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, E. R.: Towards a worldwide wood economic spectrum, Ecol. Lett. 12, 351–366, 2009.

Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L. E. O. C., Bonal, D., Châtelet, P., Silva-Espejo, J. E., Goret, J.-Y., von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M. C., Phillips, O. L., Stevenson, P., and Malhi, Y.: Regional and seasonal patterns of litterfall in tropical South America, Biogeosciences, 7, 43–55, doi:10.5194/bg-7-43-2010, 2010.

Choat, B., Sack, L., and Holbrook, N. M.: Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation, New Phytol., 175, 686–698, 2007.

Coomes, D. A., Jenkins, K. L., and Cole, L. E. S.: Scaling of three vascular transport systems along gradients of nutrient supply and altitude, Biol. Lett., 3, 86–89, 2007.

Corner, E.: The Durian theory, or the origin of the modern tree, Ann. Bot., 13, 368–414,1949.

Domingues, T. F., Meir, P., Feldpausch, T. R., Saiz, G., Veenendaal, E. M., Schrodt, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H., Diallo, A., Grace, J., and Lloyd, J.: Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands, Plant Cell Environ., 33, 959–980, 2010.

Easdale, T. A. and Healey, J. R.: Resource-use-related traits correlate within population turnover rates, but not stem diameter growth rates in 29 subtropical montane tree species, Persp. Plant Ecol. Evol. System., 11, 203–218, 2009.

Falster, D. S. and Westoby, M.: Leaf size and angle vary widely across species: what consequences for light interception ? New Phytol., 158, 509–525, 2003.

Falster, D. S. and Westoby, M.: Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia, J. Ecol., 93, 521–535, 2005.

Falster, D. S., Moles, A. T., and Westoby, M.: A general model for the scaling of offspring size and adult size, Amer. Nat., 172, 299–317, 2008.

Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T.: Carbon isotope discrimination and photosynthesis, Ann. Rev. Plant Biol., 40, 503–537. 1989.

Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. A., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bird, M., Brondizio, E. S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T. F., Drescher, M., Fearnside, P. M., França, M. B., Fyllas, N. M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M. O., Iida, Y., Salim, K. A., Kassim, A. R., Keller, M., Kemp, J., King, D. A., Lovett, J. C., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Marshall, A. R., Metcalfe, D. J., Mitchard, E. T. A., Moran, E. F., Nelson, B. W., Nilus, R., Nogueira, E. M., Palace, M., Patiño, S., Peh, K. S.-H., Raventos, M. T., Reitsma, J. M., Saiz, G., Schrodt, F., Sonké, B., Taedoumg, H. E., Tan, S., White, L., Wöll, H., and Lloyd, J.: Height-diameter allometry of tropical forest trees, Biogeosciences, 8, 1081–1106, doi:10.5194/bg-8-1081-2011, 2011.

Feng, Y.-L., Lei, Y.-B., Wang, R.-F., Callaway, R. M., Valiente-Banuet, A., Inderjit, Li, Y.-P., and Zheng, Y.-L.: Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant, P. Natl. Acad. Sci. USA, 106, 1853–1856, 2009.

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., Sääksjärvi, Schultz, J. C., and Coley, P. D.: The growth-defense trade-off and habitat specialization by plants in Amazonian forests, Ecology, 87, S150–S162, 2006.

Flury B.: Common Principal Components and Related Multivariate Models, Wiley, New York, 1988.

Foster, S. A. and Janson, C. T.: The relationship between seed size and establishment conditions in tropical woody plants, Ecology, 66, 773–780, 1985.

Foster, S. A.: On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis, Bot. Rev., 52, 260–299, 1986.

Fromm, J.: Wood formation in trees in relation to potassium and calcium nutrition, Tree Physiol, 30, 1140–1147, 2010.

Fyllas, N. M., Patiño, S., Baker, T. R., Bielefeld Nardoto, G., Martinelli, L. A., Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L., Jiménez, E. M., Luizzão, F. J., Neill, D. A., Silva, N., Prieto, A., Rudas, A., Silviera, M., Vieira, I. C. G., Lopez-Gonzalez, G., Malhi, Y., Phillips, O. L., and Lloyd, J.: Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate, Biogeosciences, 6, 2677–2708, doi:10.5194/bg-6-2677-2009, 2009.

Fyllas, N. M., Lloyd, J., and Quesada, C. A.: Deriving plant functional types for Amazonian forests for use in vegetation dynamics models, Persp. Plant Ecol. Evol. System., submitted, 2011.

Galwey, N. W.: Introduction to Mixed Modelling: Beyond Regression and Analysis of Variance, Wiley, Chichester, 2006.

Gentry, A. H. and Emmons, L. H.: Geographical variation in fertility, phenology, and composition of the understory of neotropical forests, Biotropica, 19, 216–227, 1987.

Givnish, T. J.: On the adaptive significance of compound leaves, with particular reference to tropical trees, in: Tropical Trees as Living Systems, edited by: Tomlinson, P. B. and Zimmermann, M. H., Cambridge University Press, Cambridge, UK, 351–380, 1978.

Givnish, T. J.: Comparative studies of leaf form: Assessing the relative roles of selective pressures and phylogenetic constraints, New Phytol., 106(Suppl.), 131–160, 1987.

Gonzalez, E. and Fisher, R. F.: Variation in selected wood properties of *Vochysia guatemalensis* from four sites in Costa Rica, Forest Sci., 44, 185–191, 1998.

Gower, J. C.: Some distance properties of latent root and vector methods used in multivariate analyses, Biometrika, 53, 325–338, 1966.

Grubb, P. J.: A reassessment of the strategies of plant which cope with shortages of resources, Persp. Plant Ecol. Evol. System., 1, 3–31, doi:10.1078/1433-8319-00049, 1998.

Grubb, P. J. and Coomes, D. A.: Seed mass and nutrient content in nutrient starved tropical rainforest in Venezuela, Seed Sci. Res., 7, 269–280, 1997.

Grubb, P. J., Coomes, D. A. and Metcalfe, D. J.: Comment on A Brief History of Seed Size, Science, 310, 783–783, 2005.

Hammond, D. S.: Guianan forest dynamics: geomorphological control and tropical forest change across diverging landscapes, in: Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World, edited by: Hammond, D. S., CABI Publishing, Wallingford, UK, 343–379, 2005.

Hammond, D. S. and Brown, V. K.: Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropcial forests, Ecology, 76, 2544–2561, 1995.

Hernández, R. A. and Restrepo, G.: Natural variation in wood properties of *Alnus acuminata* grown in Colombia, Wood Fiber Sci., 27, 41–48, 1995.

Hölttä, T., Mäkinen, H., Nöjd, P., Mäkelä, A., and Nikinmaa, E.: A physiological model of softwood cambial growth, Tree Physiol., 30, 1235–1252, 2010.

Hollander, M. and Wolfe, D. A.: Nonparametric Statistical Methods, J. Wiley and Sons, New York, 1999.

Houle, D., Mezey, J., and Galpern, P.: Interpretation of the results of common principal components analyses, Evolution, 56, 433–440, 2002.

Hughes, L., Dunlop, M., French, K., Leishman, M., Rice, B., Rogerson, L., and Westoby, M.: Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes, J. Ecol., 82, 933–950, 1994.

Ishida, A., Nakano, T., Yazaki, K., Matsuki, S., Koike, N., Lauenstein, D. L., Shimizu, M., and Yamashita, N.: Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms, Oecologia, 156, 193–202, 2008.

Jones, F. A., Chen, J., Weng, G.-J., and Hubbell, S. P.: A genetic evaluation of seed dispersal in the neotropical tree *Jacaranda copaia* (Bignoniaceae), Amer. Nat., 166, 543–555, 2005.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M., Reichstein, M., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender–Bares, J., Chambers, J., Chapin, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Durka, W., Elser, J., Enquist, B. J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernández, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R., Green, W., Gutierrez, A. G., Hickler, T., Higgins, S., Hodgson, J. G., Jalili, A., Jansen, S., Kerkhoff, A. J., Kirkup, K., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusià, J., Louault, F., Siyan Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A., Müller, S., Nadrowski, K., Naeem, S., Niinemets, U., Nöllert, S., Nüske, A. , Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W., Patiño, S., Paula, S., Pausas, J. G., Peñuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado, B., Sardans, J., Shiodera, S., Shipley, B., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, W., White, M., Wright, S. J., Sönke, B., Zaehle, S., Zanne, A. E., and Wirth, Ch.: TRY – a global database of plant traits, Global. Change Biol., in press, , 2011.

Keeling, H. C., Baker, T. R., Monteagudo, A., Vasquez Martinez, R., and Phillips, O. L.: Contrasting patterns of diameter and biomass increment across tree functional groups in Amazonian forests, Oecologia, 158, 521–534, 2008.

Kelly, C. K.: Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms, Oecologia, 102, 377–388, 1995.

Kenzo, T., Ichie, T., Watanabe, Y., Yoneda, R., Nonomiya, I., and Koike, T.: Changes in photosynthesis and leaf characteristics with tree height in five diperocarp species in a tropical rain forest, Tree Physiol., 26, 865–873, 2006.

King, D. A.: Load bearing capacity of understory treelets of tropical wet forest, Bull. Torrey Bot. Club, 114, 419–428, 1986.

Kirby, E. A. and Pilbeam, D. J.: Calcium as a plant nutrient, Plant Cell Environ., 7, 397–405, 1984.

Kitajima, K.: Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees, Oecologia, 98, 419–428, 1994.

Kitajima, K. and Poorter, L.: Tissue–level leaf toughness, but not laminar thickness predicts sapling leaf lifespan and shade tolerance of tropical tree species, New Phytol., 186, 708–721, 2010.

Kleiman, D. and Aarssen, L. W.: The leaf size/number trade off in trees, J. Ecol., 95, 376-382, 2007.

Legendre, P. and Legendre, L.: Numerical Ecology, 2nd edition, Elsevier, Amsterdam, 1998.

Lichstein, J. W., Simons, T. R., Shriner, S. A., and Franzreb, K. E.: Spatial autocorrelation and autoregressive models in ecology, Ecol. Monogr., 72, 445–463, 2002.

Lloyd, J. and Farquhar, G. D.: ^{13}C discrimination during CO$_2$ assimilation by the terrestrial biosphere, Oecologia, 99, 201–215, 1994.

Lloyd, J. and Farquhar, G. D.: Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees, Phil. Trans. Roy. Soc. Lond., 363B, 1811–1817, 2008.

Lloyd, J., Syvertsen, J. P., Kriedemann,P., and Farquhar, G. D.: Low conductances for CO_2 diffusion from stomata to the sites of carboxylation in leaves of woody species, Plant Cell Environ., 15, 873–889, 1992.

Lloyd, J., Patiño, S., Paiva, R. Q., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., Baker, T. R., Brand, W. A., Hilke, I., Gielmann, H., Raessler, M., Luizão, F. J., Martinelli, L. A., and Mercado, L. M.: Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees, Biogeosciences, 7, 1833–1859, doi:10.5194/bg-7-1833-2010, 2010.

Lovelock, C. E., Ball, M. C., Choat, B., Engelbrecht, B. J. Holbrook, N. M., and Feller, M. C.: Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*, Plant Cell Environ., 29, 793–802, 2006.

McKean, J. W., Terpstra, J. T., and Kloke, J. D.: Computational rank-based statistics, WIREs Comput. Stat., 1, 132–140, 2009.

Maghsoodloo, S. and Laszlo Pallos, L.: Asymptotic behavior of Kendalls partial rank correlation coefficient and additional quantile estimates, J. Statist. Comput. Simul., 13, 41–48, 1981.

Malhado, A. C. M., Malhi, Y., Whittaker, R. J., Ladle, R. J., ter Steege, H., Phillips, O. L., Butt, N., Arag ao, L. E. O. C., Quesada, C. A., Araujo-Murakami, A., Arroyo, L., Peacock, J., Lopez-Gonzalez, G., Baker, T. R., Anderson, L. O., Almeida, S., Higuchi, N., Killeen, T. J., Monteagudo, A., Neill, D., Pitman, N., Prieto, A., Salomão, R. P., Vsquez-Martnez, R., and Laurance, W. F.: Spatial trends in leaf size of Amazonian rainforest trees, Biogeosciences, 6, 1563–1576, doi:10.5194/bg-6-1563-2009, 2009.

Malhado, A. C. M., Whittaker, R. J., Malhi, Y., Ladle, R. J., ter Steege, H., Phillips, O. L., Arag ao, L. E. O. C., Baker, T. R., Arroyo, L., Almeida, S., Higuchi, N., Killeen, T. J., Monteagudo, A., Pitman, N. C. A., Prieto, A., Salomão, R. P., Vàsquez-Martnez R., Laurance, W. F., and Ramìrez-Angulo, H.: Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest, Global Ecol. Biogeog., 19, 852–862, 2010.

Markesteijn, L., Poorter. L., and Bongers, F.: Light-dependent leaf trait variation in 43 tropical dry forest tree species, Amer. J. Bot., 94, 515–525, 2007.

MacDonald, P. G., Fonesca, C. R., Overton, J. McC., and Westoby, M.: leaf–size divergence along rainfall and soil–nutrient gradients; is the method of size reduction common among clades?, Funct. Ecol., 17, 50–57, 2003.

Magnani, F., Grace, J., and Borghetti, M.: Adjustment of tree structure in response to the environment under hydraulic constraints, Funct. Ecol., 26, 385–393, 2002.

Martinéz-Cabrera, M., Jones, H. I., Espino, C. S., Shenk, S., and Jochen, H.: Wood anatomy and wood density in shrubs: Responses to varying aridity along transcontinental transects, Am. J. Bot., 96, 1388–1398, 2009.

Meinzer, F. C.: Functional convergence in plant responses to the environment, Oecologia, 134, 1–11, 2003.

Meinzer, F. C., Campanello, P. I., Domec, J.-C., Gatti, M. G., Goldstein, G., Villalobos-Vega, R., and Woodruff, D. R.: Constraints on physiological function associated with branch architecture on wood density of tropical forest trees, Tree Physiol., 28, 1609–1617, 2008.

Mercado, L. M., Patiño, S., Domingues, T. F., Fyllas, N. M., Baker, T. R., Weedon, G. P., Sitch, S., Phillips, O. L., Aragão, L. E. O. C, Malhi, Y., Dolman, A. J., Restrepo-Coupe, N., Saleska, S. R., Quesada, C. A., and Lloyd, J.: Is the observed variability in stem wood production rates for Amazon forests due different rates of photosynthetic carbon supply? Phil. Trans. Roy. Soc. Lond., in press, 2011.

Metcalfe, D. J. and Grubb, P. J.: Seed mass and light requirements for regeneration in Southeast Asian rain forest, Can. J. Bot., 73, 817–826, 1995.

Miller, J. M., Williams, R. J., and Farquhar, G. D.: Carbon isotope discrimination by a sequence of *Eucalyptus* species along a subcontinental rainfall gradient in Australia, Funct. Ecol., 15, 222–232, 2001.

Moles, A. and Westoby, M.: Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage?, Oikos, 90, 517–526, 2000.

Moles, A. T, Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., and Westoby, M.: A brief history of seed size, Science, 307, 576–80, 2005.

Muller-Landau, H. C.: Interspecific and inter–site variation in wood specific gravity of tropical trees, Biotropica, 36, 20–32, 2004.

Nardini, A., Grego, F., Trifilo, P., and Salleo, S.: Changes of xylem sap ionic content and stem hydraulics in response to irradiance in *Laurus nobilis*, Tree Physiol., 30, 628–635, 2010.

New, M., Lister, D., Hulme, M., and Makin, I.: A high-resolution data set of surface climate over global land areas, Climate Res. 21, 1–25, 2002.

Niinemets, U.: Are compound–leaved species woody species inherently shade tolerant? An analysis of species ecological requirements and foliar support costs, Plant Ecol., 134, 1–11, 1998.

Niinemets, U.: Components of leaf mass per unit area – thickness and density, alter leaf photosynthetic capacity in reverse directions in woody plants, New Phytol., 144, 35–47, 1999.

Niinemets, U.: Global scale climatic controls of leaf dry mass per unit area, density and thickness in trees and shrubs, Ecology, 82, 453–489, 2001.

Nogueira, E. M., Fearnside, P. M., Nelson, B. W., and França, M. B.: Wood density in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land–use change in Amazonia, For. Ecol. Manag., 248, 119–135, 2007.

Olivares, E. and Medina, E.: Water and nutrient relations of woody perennials from tropical dry forests, J. Veg. Sci., 3, 383–392, 1992.

Omolodun, O. O., Cutter, B. E., Krause, G. F., and McGinnes, E. A.: Wood quality in *Hidegardia berteri* (Mast.)Kossern – An African tropical pioneer species, Wood Fiber Sci., 23, 419–435, 1991.

Onoda, Y., Hikosaka, K., and Hirose, T.: Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency, Funct. Ecol., 18, 419–425, 2004.

Osunkoya, O. O., Sheng, T. K., Mahmud, N.-A., and Damit, N. Y.: Variation in wood density. Wood water content, stem growth and mortality among seven tree species in a tropical rainforest on Borneo Island, Austral Ecol., 32, 191–201, 2007.

Parolin, P. and Ferreira, L. V.: Are there differences in specific wood gravities between trees in varzea and igapo (Central Amazonia)?, Ecotropica, 4, 25–32, 2004.

Patiño, S., Lloyd, J., Paiva, R., Baker, T. R., Quesada, C. A., Mercado, L. M., Schmerler, J., Schwarz, M., Santos, A. J. B., Aguilar, A., Czimczik, C. I., Gallo, J., Horna, V., Hoyos, E. J., Jimenez, E. M., Palomino, W., Peacock, J., Peña-Cru, A., Sarmiento, C., Sota, A., Turriago, J. D., Villanueva, B., Vitzthum, P., Alvarez, E., Arroyo, L., Baraloto, C., Bonal, D., Chave, J., Costa, A. C. L., Herrera, R., Higuchi, N., Killeen, T., Leal, E., Luizão, F., Meir, P., Monteagudo, A., Neil, D., Núñez-Vargas, P., Peñuela, M. C., Pitman, N., Priante Filho, N., Prieto, A., Panfil, S. N., Rudas, A., Salomo, R., Silva, N., Silveira, M., Soares deAlmeida, S., Torres-Lezama, A., Vásquez–Martínez, R., Vieira, I., Malhi, Y., and Phillips, O. L.: Branch xylem density variations across the Amazon Basin, Biogeosciences, 6, 545–568, doi:10.5194/bg-6-545-2009, 2009.

Phillips, O. L., Baker, T., Arroyo, L., Higuchi, H., Killeen, T., Laurance, W. F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D., Núñez-Vargas, P., Silva, N., Terborgh, J., Vásquez-

Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J., Czimczik C. I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S. G., Nascimento, H. E. M., Palacios, M., Patiño, S., Pitman, N., Olivier, J., Quesada, C. A., Saldias, M., Torres Lezama, A., and Vinceti, B.: Pattern and process in Amazon tree turnover, 1976-2001, Phil. Trans. Royal Soc. Lond., 359B, 381–407, 2004.

Phillips, P. C. and Arnold S. J.: Hierarchical comparison of genetic variance–covariance matrices I. Using the Flury hierarchy, Evolution, 53, 1506–1515, 1999.

Pickup M., Westoby M., and Basden A.: Dry mass costs of deploying leaf area in relation to leaf size, Funct. Ecol., 19, 88–97, 2005.

Poorter, L.: The relationships of wood-, gas- and water fractions of tree stems to performance an life history variation of tropical trees, Ann. Bot., Ann. Bot., 102, 367–375, 2008.

Poorter, H. and Villar, R.: The fate of acquired carbon in plants: chemical composition and construction costs. edited by: Bazzaz, F. A., Grace, J., in: Plant Resource Allocation, San Diego, Academic Press, 39–72, 1997.

Poorter, H. and de Jong R.: A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity, New Phytol., 143, 163–176, 1999.

Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., and Villar, R.: Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis, New Phytol., 182, 565–588, 2009.

Poorter L. and Bongers, F.: Leaf traits are good predictors of plant performance across 53 rain forest species, Ecology, 87, 1733–1743, 2006.

Poorter, L. and Rozendaal, D. M. A.: Leaf size and display of thirty-eight tropical tree species, Oecologia, 158, 35–46, 2008.

Poorter L., Bongers L., and Bongers F.: Architecture of 54 moist forest tree species: traits, trade-offs, and functional groups, Ecology, 87, 1289–1301, 2006.

Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller–Landau, H. C., Penã–Claros, M., Webb, C. O., and Wright, I. J.: Are functional traits good predictors of demographic rates? Evidence from five neotropical forests, Ecology, 89, 1908–1920, 2008.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Penã-Claros, M. M., Sterck, F., Villegas, Z., and Sass–Klaassen, U.: The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species, New Phytol., 185, 481–492, 2010.

Prance, G. T.: Chrysobalanaceae, Flora Neotropica, 9, 1–409. 1972.

Preston, K. A., Cornwell, W. K., and Denoyer, J.: Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms, New Phytol., 170, 807–818, 2006.

Powers, J. S. and Tiffin, P.: Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches, Funct. Ecol., 24, 927–936, 2010.

Putz, F. E., Coley, P. D., Lu, K., Montalvo, A., and Aiello, A.: Uprooting and snapping of trees: structural determinants and ecological consequences, Can. J. For. Res., 13, 1011–1020, 1983.

Quesada, C. A., Lloyd, J., Schwarz, M., Baker, T. R., Phillips, O. L., Patiño, S., Czimczik, C., Hodnett, M. G., Herrera, R., Arneth, A., Lloyd, G., Malhi, Y., Dezzeo, N., Luizão, F. J., Santos, A. J. B., Schmerler, J., Arroyo, L., Silveira, M., Priante Filho, N., Jimenez, E. M., Paiva, R., Vieira, I., Neill, D. A., Silva, N., Peñuela, M. C., Monteagudo, A., Vásquez, R., Prieto, A., Rudas, A., Almeida, S., Higuchi, N., Lezama, A. T., López–González, G., Peacock, J., Fyllas, N. M., Alvarez Dávila, E., Erwin, T., di Fiore, A., Chao, K. J., Honorio, E., Killeen, T., Peña Cruz, A., Pitman, N., Núñez Vargas, P., Salomão, R., Terborgh, J., and Ramárez, H.: Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties, Biogeosciences Discuss., 6, 3993–4057, doi:10.5194/bgd-6-3993-2009, 2009.

Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., Fyllas, N. M., Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. A., Geilmann, H., Moraes Filho, J. O., Carvalho, F. P., Araujo Filho, R. N., Chaves, J. E., Cruz Junior, O. F., Pimentel, T. P., and Paiva, R.: Variations in chemical and physical properties of Amazon forest soils in relation to their genesis, Biogeosciences, 7, 1515–1541, doi:10.5194/bg-7-1515-2010, 2010.

R Development Core Team: R: A Language and Environment for Statistical Computing, Foundation for Statistical Computing, Vienna, Austria, ISBN3-900051-07-0, 2010.

Raymond, C. A. and Muneri, A.: Effect of fertilizer on wood properties of *Eucalyptus globulus*, Can. J. For. Res., 30, 136–144, 2000.

Read, J. and Stokes, A.: Plant biomechanics in an ecological context, Amer. J. Bot., 93, 1546–1565, 2006.

Read, J., Sanson, G. D., Caldwell, E., Clissold, F. J., Chatain, A., Peeters, P., Lamont, B. B., de Garine-Wichatitsky, M., Jaffré, T., and Kerr, S.: Correlations between leaf toughness and phenolics among species in contrasting environments of Australia and New Caledonia, Ann. Bot., 103, 757–767, 2009.

Reich, P. B., Ellsworth, D. S., and Uhl, C.: Leaf carbon and nutrient assimilation and conservation in species of different successional status in an oligotrophic Amazonian forest, Funct. Ecol., 9, 65–76, 1995.

Reich, P. B., Walters, M. B., and Ellsworth, D. S.: From tropics to tundra: Global convergence in plant functioning, P. Natl. Acad. Sci. USA, 94, 13730–13734, 1997.

Rijskers, T., Pons, T. L., and Bongers, F.: The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance, Funct. Ecol., 14, 77–96, 2000.

Roderick, M. L. and Berry, S. L.: Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water, New Phytol., 149, 473–485, 2001.

Rolland, F., Baena-Gonzalez, E., and Sheen, J.: Sugar sensing and signalling in plants: conserved and novel mechanisms, Annu. Rev. Plant Biol., 57, 675–709, doi:10.1146/annurev.arplant.57.032905.105441, 2006.

Roque, R. M.: Effect of management treatment and growing regions on wood properties of *Gmelina arborea* in Costa Rica, New Forests, 28, 325–330, 2004.

Rozendaal, D. M. A., Hurtado, V. H., and Poorter, L.: Plasticity in leaf traits of 38 tropical tree species in response to light: relationships with light demand and adult stature, Funct. Ecol., 20, 207–216, 2006.

Russo, S. E., Jenkins, K. L., Wiser, S. K., Uriate, M., Duncan, R. P., and Coomes, D. A.: Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand, Funct. Ecol., 24, 253–262, 2010.

Sandquist, D. R. and Cordell, S.: Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawaii, Am. J. Bot., 94, 1459–1469, 2007.

Santiago, L. S. and Wright, I. J.: Leaf functional traits of tropical forest plants in relation to growth form, Funct. Ecol., 21, 19–27, 2007.

Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., and Jones, T.: Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees, Oecologia, 140, 543–550, 2004a.

Santiago, L. S., Kitajima, K., Wright, S. J., and Mulkey, S. S.: Co–ordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest, Oecologia, 139, 495–502, 2004b.

Sarmiento, C., Patiño, S., Paine, C. E. P., Beauchêne, J., Thibaut, A., and Baraloto, C.: Within-individual variation of trunk and branch xylem density in tropical trees, Amer. J. Bot., 98, 140-149, doi:10.3732/ajb.1000034, 2011.

Schuldt, B., Leuschner, C., Horna, V., Moser, G., Köhler, M., and Barus, H.: Change in hydraulic properties and leaf traits of a tall rainforest tree species subjected to long-term throughfall exclusion in the perhumid tropics, Biogeosciences Discuss., 7, 8553–8589, doi:10.5194/bgd-7-8553-2010, 2010.

Sheil, D. and Burslem, D. F. R. P.: Disturbing hypotheses in tropical forests, Trends Ecol. Evol., 18, 18–26, 2003.

Shipley, B.: Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms, Func. Ecol., 9, 312–319, 1995.

Sobrado, M. A.: Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species coexisting in tropical dry forests, Oecologia, 68, 413–416, 1986.

Stratton, L., Goldstein, G., and Meinzer, F. C.: Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest, Plant Cell Environ., 23, 99–106, 2000.

Sterck, F., van Gelder, H. A., and Poorter, L.: Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest, J. Ecol. 94, 1192–1200, 2006.

Sungpalee, W., Itoh, A., Kanzaki, M., Sringeryuang, K., Noguchi, H., Mizuno, T., Teejunuk, S., Hara, M., Chaiudon, K., Yamakura, T., and Sornngai, A.: Intra-and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest, J. Trop. Ecol., 25, 359–370, 2009.

Swenson, N. G. and Enquist, B. J.: Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community–wide variation across latitude and elevation, Amer. J. Bot., 94, 451–459, 2007.

Swenson, N. G. and Enquist, B. J.: The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area, Amer. J. Bot., 95, 516–519, 2008.

Syvertsen, J. P., Lloyd, J., McConchie, C., Kriedemann, P. E., and Farquhar, G. D.: On the site of biophysical constraints to CO2 diffusion through the mesophyll of thick hyperstomatous leaves, Plant Cell Environ., 18, 149–157, 1995.

Syversten, J. P., Goñi, C., and Otero, A.: Fruit load and canopy shading affect leaf characteristics and net gas exchange of Spring navel orange trees, Tree Physiol., 23, 899–906, 2003.

Takahashi, K. and Mikami, Y.: A weak relationship between crown architectural and leaf traits in saplings of eight tropical rain–forest species in Indonesia, J. Trop. Ecol., 24, 425–432, 2008.

Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J.: ADE–4: a multivariate analysis and graphical display software, Statistics and Computing, 7, 75–83, 1997.

ter Steege, H. and Hammond, D. S.: Character convergence, diversity, and disturbance in tropical rainforest in Guyana, Ecology, 82, 3197–3212, 2001.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M. F., Spichiger, R., Castellanos, H., Hildebrand, P., and Vásquez, R.: Continental–scale patterns of canopy tree composition and function across Amazonia, Nature, 443, 444–447, 2006.

Takashima, T., Hikosaka, K., Hirose, T.: Photosynthesis or persistence: Nitrogen allocation in leaves of evergreen and deciduous *Quercus* species, Plant Cell Environ. 27, 1047–1054, 2004.

Thomas, D. S., Montangu, K. D., and Conroy, J. P.: Why does phosphorus limitation increase wood density in *Eucalyptus grandis* seedlings?, Tree Physiol., 26, 35–42, 2005.

Thomas, S. C.: Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species, Oikos, 76, 145–154, 1996.

Thomas, S. C. and Bazzaz, F. A.: Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees, Ecology, 80, 607–1622, 1999.

van Gelder, H. A., Poorter, L., and Sterk, F. J.: Wood mechanics, allometry and life-history variation in a tropical rain forest tree community, New Phytol., 171, 367–378, 2006.

Vander Willigen, C., Sherwin, H. W., and Pammenter, N. W.: Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions, New Phytol., 145, 51–59, 2000.

Warren, C. A. and Adams, M. A.: Internal conductance does not scale with photosynthetic capacity: implications for carbon isotope discrimination and the economics of water and nitrogen use in photosynthesis, Plant Cell Environ., 29, 192–201, 2006.

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

Weber, J. C. and Montes, C. S.: Geographic variation in tree growth and wood density of *Guazuma crinita* Mart, in the Peruvian Amazon, New Forests, 36, 29–52, 2008.

Webb, L. J.: Environmental relationships of the structural types of Australia rain forest vegetation, Ecology, 49, 296–311, 1968.

Westoby, M. and Wright, I. R.: The leaf size–twig–size spectrum and its relationship to other important spectra of variation amongst species, Oecologia, 135, 621–628, 2003.

Westoby, M., Falster, D., Moles, A., Vesk, P., and Wright, I.: Plant ecological strategies: some leading dimensions of variation between species, Ann. Rev. Ecol. Syst., 33, 125–159, 2002.

Williams, L. J., Bunyavejchewin, S., and Baker, P. J.: Deciduousness in a seasonal tropical forest in western Thailand, Oecologia, 155, 571–582, 2008.

Williamson, G. B. and Wiemann, M. C.: Measuring wood specific gravity... Correctly, Amer. J. Bot., 97, 207–215, 2010.

Wilson, P. J., Thompson, K., and Hodgson, J. G.: Specific leaf area and leaf dry matter content as alternative predictors of plant strategies, New Phytol., 143, 155–162, 1999.

Witkowski, E. T. F. and Lamont, B. B.: Leaf specific mass confounds leaf density and thickness, Oecologia, 88, 486–493, 1991.

Wright, I. R., Falster, D. S., Pickup, M., and Westoby, M.: Cross–species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics, Physiol. Plant., 127, 445–456, 2006.

Wright, I. R., Ackerly. D. D., Bongers, F., Harms, K. E., Ibarra–Manríquez, G., Martínez–Ramos, M., Mazer, S. J., Muller–Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M., Vriesendorp, C. F., Webb, C. O., Westoby, M., and Wright, S. J.: Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests, Ann Bot., 99, 1003–1015, 2007.

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

Wright, S. J., Jaramillo, M. A., Pavon, J., Condit, R., Hubbell, S. P., and Foster, R. B.: Reproductive size thresholds in tropical trees; variations amongst individuals, species and forests, J. Trop. Ecol., 21, 307–315, 2005.

Yates, M. J., Verboom, G. A., Rebelo, A. G., and Cramer, M. D.: Ecophysiological significance of leaf size variation in Proteaceae from the Cape Floristic Region, Funct. Ecol., 24, 485–492, 2010.

Zach, A., Schuldt, B., Brix, S., Horna, V., Culmsee, H., Leuschner, C.: Vessel diameter and xylem hydraulic conductivity increase with tree height in tropical rainforest trees in Sulawesi Indonesia, Flora, 205, 506–512, 2010.

Zanne, A. R., Westoby, M., Falster, S., Ackerly, D. D., Loarise, S. R., Arnold, S. E. J., and Coomes, D. A.: Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity, Amer. J. Bot., 92, 207–215, 2010.

Zhang, J.-L. and Cao, J.-F.: Stem hydraulics mediates leaf water status, carbon gain, nutrient efficiencies and plant growth rates across dipterocarp species, Funct. Ecol., 23, 658–667, 2009.

Table 1. Relationships between the derived genetic components of the observed plant traits. with M_A = leaf mass per unit area (g m^{-2}); elemental concentrations are on a dry weight basis (mg g^{-1}), L_A = leaf area (m^2), ℓ_A = leaflet area (m^2), Φ_{LS} = leaf area:sapwood area ratio (cm^2 g^{-1}), ρ_x = branch xylem density (kg m^{-3}), $\oslash$ = stomatal limitation index (see Eq. 1), S = seed mass (g), H_{max} = species maximum height (m). Values above the diagonal represent the slope of the relationship (y axis as columns labels, x axis as row labels). Values below the diagonal represent the correlation coefficient, r. Values significant at $P < 0.05$ are given in bold. NS = no slope estimated as the relationship was not significant.

Variable	M_A	[C]	log[N]	log[P]	log[Ca]	log[K]	log[Mg]	$\log(L_A)$	$\log(\ell_A)$	$\log(\Phi_{LS})$	ρ_x	$\oslash$	$\log(S)$	H_{max}
$\log(M_A)$	–	**0.37**	**−1.01**	**−1.21**	NS	**−1.65**	**−2.18**	NS	**4.32**	**−1.27**	**0.88**	NS	**19.2**	**167**
[C]	**0.15**	–	NS	NS	**−6.28**	**−4.43**	**−5.85**	**17.30**	NS	NS	NS	NS	**51.4**	NS
log[N]	**−0.43**	0.07	–	**1.20**	NS	**1.63**	NS	**6.36**	**−4.18**	**1.22**	NS	0.22	**−18.6**	NS
log[P]	**−0.41**	-0.02	**0.66**	–	**1.93**	**1.36**	**1.79**	**5.37**	NS	**1.03**	**−0.72**	**0.19**	NS	NS
log[Ca]	−0.07	**−0.51**	0.02	**0.14**	–	**0.7**	**0.93**	NS	NS	NS	**−0.37**	**0.10**	**−8.3**	NS
log[K]	**−0.28**	**−0.45**	**0.18**	**0.46**	**0.46**	–	**1.32**	NS	**2.60**	NS	**−0.52**	NS	**−11.4**	NS
log[Mg]	**−0.14**	**−0.45**	0.05	**0.18**	**0.65**	**0.59**	–	**−2.98**	**1.97**	NS	**−0.40**	**0.10**	**−8.8**	NS
$\log(L_A)$	−0.09	**0.14**	**0.27**	**0.37**	−0.03	−0.01	−0.14	–	**0.65**	**0.19**	**−0.13**	**0.04**	NS	NS
$\log(\ell_A)$	**0.17**	−0.08	**−0.11**	0.04	0.07	**0.18**	0.15	0.41	–	NS	−0.2	NS	NS	NS
$\log(\Phi_{LS})$	**−0.24**	0.06	**0.20**	**0.14**	0.00	0.04	−0.09	**0.26**	0.01	–	NS	NS	NS	NS
ρ_x	**0.13**	0.07	−0.08	**−0.20**	**−0.21**	**−0.24**	**−0.12**	**−0.10**	**−0.22**	0.07	–	NS	**21.6**	NS
$\oslash$	0.09	0.03	**0.23**	**0.27**	**0.12**	0.06	**0.09**	**0.12**	−0.08	−0.08	−0.09	–	**−81.8**	731
$\log(S)$	**0.12**	**0.18**	**−0.16**	−0.08	**−0.34**	**−0.23**	**−0.25**	0.02	0.00	−0.10	**0.25**	**−0.20**	–	**8.8**
H_{max}	**0.17**	0.04	−0.03	0.00	−0.06	−0.02	−0.08	−0.02	0.00	−0.07	−0.03	**0.11**	**0.14**	–

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀◀ | ▶▶
◀ | ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 2. Common principal component analysis of derived genetic effects for species associated with low and high fertility soils. Values in brackets represent standard errors for each component. Coefficients given in bold are either those whose absolute values are 0.50 or more, or 0.30 or more with a standard error or less than 0.1. M_A = leaf mass per unit area; elemental concentrations are on a dry weight basis, L_A = leaf area; Φ_{LS} = leaf area:sapwood area ratio, ρ_x = branch xylem density, ⊘ = diffusion limitation index (see Eq. 1), S = seed mass, H_{max} = species maximum height.

Variable	Component				
	U_1	U_2	U_3	U_4	U_5
log(M_A)	−0.22(0.05)	−0.23 (0.06)	**0.44 (0.07)**	−0.22 (0.11)	**0.35 (0.09)**
[C]	**−0.35 (0.05)**	0.24 (0.07)	0.01 (0.07)	0.06 (0.12)	**0.34 (0.09)**
log[N]	0.15 (0.10)	**0.53 (0.04)**	−0.02 (0.09)	0.22 (0.09)	−0.03 (0.08)
log[P]	0.25 (0.08)	**0.45 (0.05)**	0.12 (0.09)	**0.31 (0.05)**	0.08 (0.06)
log[Ca]	**0.42 (0.03)**	−0.13 (0.08)	0.15 (0.09)	**−0.31 (0.06)**	0.00 (0.08)
log[K]	**0.48 (0.02)**	−0.01 (0.09)	0.00 (0.08)	0.16 (0.09)	0.05 (0.11)
log[Mg]	**0.49 (0.04)**	−0.21 (0.09)	0.07 (0.06)	0.06 (0.07)	0.19 (0.07)
log(L_A)	−0.01 (0.09)	**0.48 (0.05)**	0.25 (0.13)	−0.35 (0.16)	−0.16 (0.10)
log(Φ_{LS})	−0.01 (0.07)	0.29 (0.06)	−0.44 (0.11)	**−0.53 (0.16)**	0.18 (0.11)
ρ_x	−0.14 (0.03)	−0.03 (0.05)	−0.22 (0.10)	0.12 (0.21)	0.26 (0.11)
⊘	0.10 (0.04)	0.14 (0.05)	**0.39 (0.09)**	−0.10 (0.13)	**0.60 (0.08)**
log(S)	−0.23 (0.03)	0.01 (0.06)	0.19 (0.10)	**0.48 (0.10)**	**0.59 (0.08)**
H_{max}	−0.10 (0.04)	0.07 (0.06)	**0.53 (0.10)**	−0.13 (0.22)	**−0.47 (0.09)**
Characteristic roots					
$\lambda_{low,j}$	1876 (259)	1472 (203)	641(89)	717 (99)	698 (96)
$\lambda_{high,j}$	2341 (237)	1641 (166)	898 (91)	564 (57)	318 (32)

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◂◂ ▸▸
◂ ▸
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 3. Bivariate relationships for the derived environmental component of the observed plant traits. M_A = leaf mass per unit area; elemental concentrations are on a dry weight basis, L_A = leaf area; ℓ_a = leaflet area, Φ_{LS} = leaf area/sapwood area ratio, ρ_x = branch xylem density, $\oslash$ = diffusion limitation index (see Eq. 1). For units, see Table 1.

Variable	$\log(M_A)$	[C]	log[N]	log[P]	log[Ca]	log[K]	log[Mg]	$\log(L_A)$	$\log(\ell_A)$	$\log(\Phi_{LS})$	ρ_x	$\oslash$
$\log(M_A)$	–	**0.31**	**−1.06**	NS	**−4.97**	NS	**−1.32**	NS	NS	**−3.49**	NS	**0.57**
[C]	**0.63**	–	**−3.38**	NS	**−15.86**	NS	**−4.22**	NS	NS	NS	**4.10**	**1.82**
log[N]	**−0.52**	**−0.30**	–	**2.69**	**4.68**	NS	**1.25**	NS	NS	**3.06**	NS	NS
log[P]	−0.04	−0.09	**0.48**	–	**1.74**	**1.53**	NS	NS	NS	NS	**−0.45**	**0.20**
log[Ca]	**−0.28**	**−0.54**	**0.28**	**0.50**	–	**0.88**	**0.27**	NS	NS	NS	**−0.26**	NS
log[K]	−0.01	−0.13	**0.23**	**0.74**	**0.49**	–	NS	NS	NS	NS	**−0.30**	**0.13**
log[Mg]	**−0.54**	**−0.72**	**0.28**	0.04	**0.50**	**0.05**	–	NS	NS	NS	NS	NS
$\log(L_A)$	0.08	−0.06	**−0.09**	−0.03	0.11	0.21	0.07	–	**0.85**	NS	NS	NS
$\log(\ell_A)$	0.07	−0.20	**−0.16**	−0.11	0.09	0.20	0.15	**0.90**	–	NS	**−0.79**	**−0.35**
$\log(\Phi_{LS})$	**−0.29**	−0.25	**0.36**	−0.07	−0.02	−0.21	0.10	0.07	0.08	–	NS	NS
ρ_x	0.08	**0.27**	**−0.22**	**−0.64**	**−0.46**	**−0.82**	−0.06	−0.25	**−0.31**	0.17	–	NS
$\oslash$	**0.32**	**0.27**	**0.24**	**0.49**	0.25	**0.31**	−0.22	−0.14	**−0.28**	−0.09	−0.18	–

Table 4. Summary of the Principal Components Analysis of the correlation matrix for the derived environmental/soil effects on observed structural and physiological traits. Coefficients given in bold are those whose values are 0.3 or more. M_A = leaf mass per unit area; elemental concentrations are on a dry weight basis, L_A = leaf area; Φ_{LS} = leaf area: sapwood area ratio, ρ_x = branch xylem density, $\oslash$ = diffusion limitation index (see Eq. 1).

Variable	Component	
	Υ_1	Υ_2
$\log(M_A)$	−0.196	**−0.443**
[C]	**−0.300**	**−0.412**
log[N]	**0.320**	0.111
log[P]	**0.406**	−0.276
$\log[C_A]$	**0.453**	0.099
log[K]	**0.392**	−0.300
$\log[M_g]$	0.245	**0.416**
$\log(L_A)$	0.087	−0.009
$\log(\Phi_{LS})$	0.025	0.271
ρ_x	**−0.383**	0.287
$\oslash$	0.174	**−0.340**
Eigenvalue	6.23	2.54
Proportion of variance explained	0.33	0.25

Table 5. Kendalls partial correlation coefficient, τ_P, for the environmental contribution (plot effect estimate) of each foliar property with the set of environmental predictors with their significance is computed based on Maghsoodloo and Laszlo Pallos (1981). Bold values indicate a very strong correlation ($p < 0.001$) and italics indicate significant correlations at $p < 0.01$; see text for details. M_A = leaf mass per unit area; elemental concentrations are on a dry weight basis, L_A = leaf area; ℓ_A = leaflet area, Φ_{LS} = leaf area/sapwood area ratio, ρ_x = branch xylem density, $\oslash$ = diffusion limitation index (see Eq. 1) and ψ_1 and ψ_2 are the first two principal components of the PCA analysis on the environmental effects correlation matrix (See Table 4).

	M_A	[C]	[N]	[P]	[Ca]	[K]	[Mg]	L_A	ℓ_a	log(Φ_{LS})	ρ_x	$\oslash$	ψ_1	ψ_2
Soil fertility PCA axis, ϕ_F	−0.20	−0.23	0.20	**0.48**	**0.48**	**0.33**	0.22	−0.09	−0.07	−0.04	**−0.32**	0.20	**0.56**	0.00
Soil texture PCA axis, ϕ_T	0.05	0.10	0.12	0.04	**−0.27**	−0.17	−0.18	−0.03	0.02	0.05	0.19	0.02	−0.22	−0.07
Mean annual temperature, T_a	0.11	0.051	**−0.38**	−0.26	−0.08	**−0.41**	0.03	−0.08	−0.04	0.07	**0.35**	−0.13	−0.23	0.21
Mean annual precipitation, P_a	**0.33**	**0.30**	−0.18	0.17	−0.01	0.11	**−0.31**	−0.01	−0.01	0.17	−0.12	**0.24**	−0.07	**−0.44**
Mean annual radiation, Q_a	−0.06	0.15	0.02	0.12	−0.14	0.08	0.00	−0.11	−0.10	0.08	0.02	0.12	−0.04	−0.11

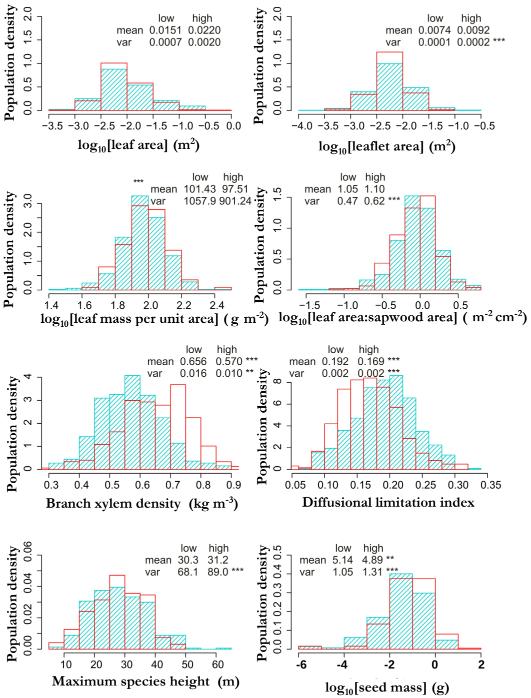

Fig. 1. Probability density histograms of raw data per fertility group for leaf area (L_A; m^2), leaflet area (ℓ_A; m^2), leaf mass per unit area (M_A; gm^{-2}), (m^2), leaf area:sapwood area ratio (Φ_{LS}; cm^{2}m^{-2}), branch xylem density (ρ_x; kg m^{-3}), $\oslash$ = stomatal limitation index (dimensionless; see Eq. 1), species maximum height (H_{max}; m) and seed mass (S; g). Open red bars represent low and blue dashed bars high soil fertility plots, as defined by the quantitative determinations of the level of total reserve bases from 0.0–0.3 m depth (Fyllas et al., 2009; Quesada et al., 2010). Also given for each histogram are the mean and the variance for each trait. Significant differences in mean values and/or variances between the two fertility groups were identified with Fligner-Killeen test respectively. Significance codes: *** <0.001, ** <0.01,* <0.05.

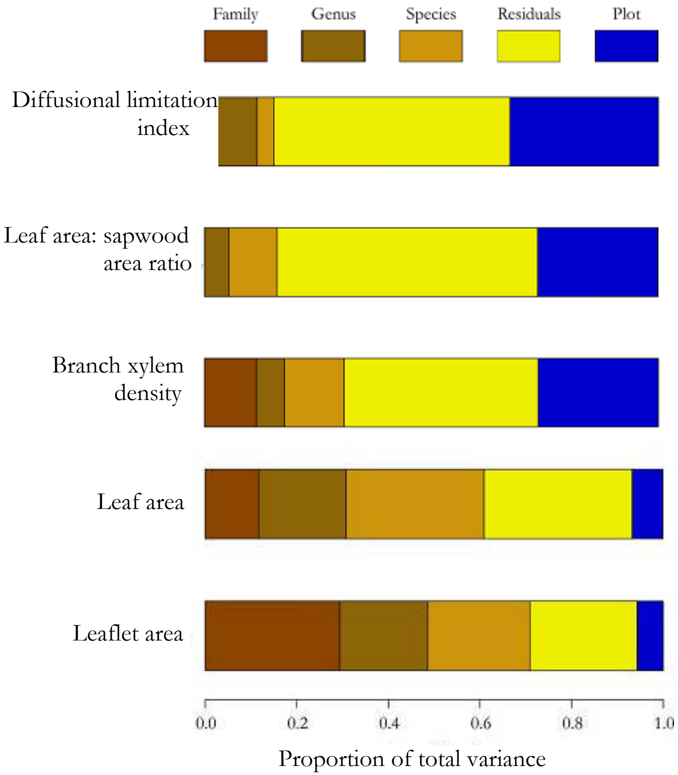

Fig. 2. Partitioning of the total variance for each structural property into genetic (family/genus/species), environmental (plot) and an error (residual) components. Foliar properties are sorted from less to more phylogenetically constrained. Significance of each variance component was tested with a likelihood ratio test (Galwey, 2006). Significance codes: *** < 0.001, ** < 0.01,* < 0.05.

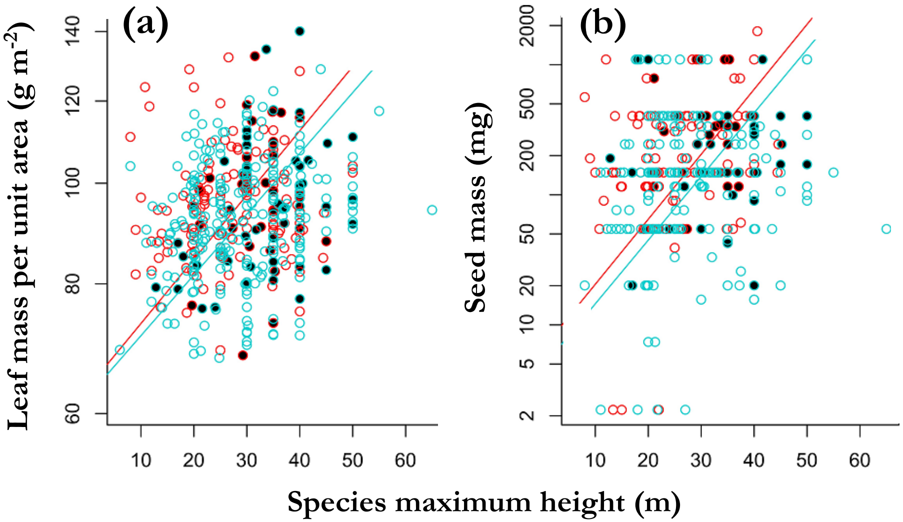

Fig. 3. Standard Major Axis (SMA) regressions lines between species maximum height (H_{max}) and the derived genetic components of leaf mass per unit area (M_{A}) for the same species and the associated average seed mass (S) for the associated genus. Red open circles indicate species found on low fertility sites and the blue open circles indicate species found on high fertility sites. Species found on both soil fertility groups are indicated with closed circles (see text for details). Red solid lines show the SMA model fit which is significantly different to the blue solid lines for high fertility soil species.

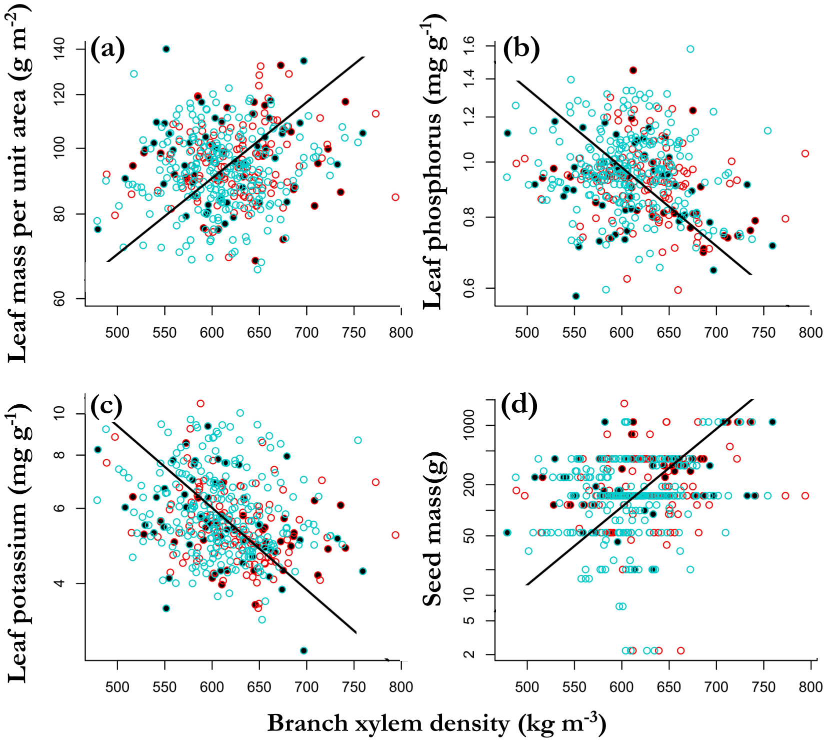

Fig. 4. Standard Major Axis (SMA) regressions lines between the derived species genetic components of branch xylem density (ρ_x) and those for mass per unit area (M_A), foliar [P] and foliar [K] for the same species and the average seed mass (S) for the associated genus. Red open circles indicate species found on low fertility sites and the blue open circles indicate species found on high fertility sites. Species found on both soil fertility groups are indicated with closed circles (see text for details). The black solid lines show the SMA model fit which did not depend on soil fertility.

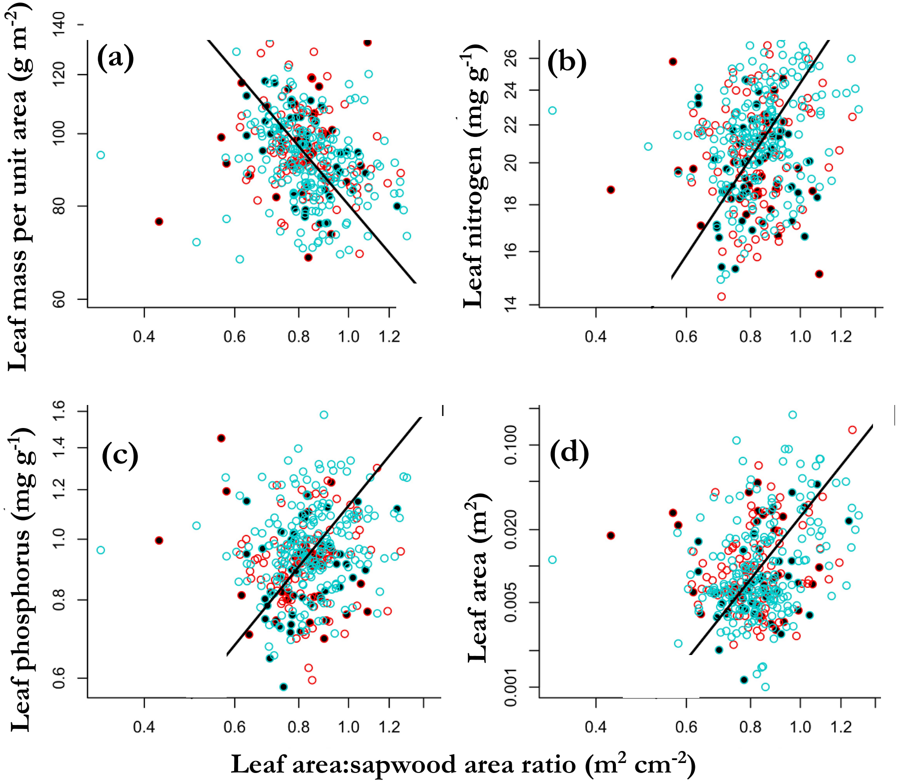

Fig. 5. Standard Major Axis (SMA) regressions lines between the derived species genetic components of leaf area/sapwood area ratio (Φ_{LS}) and those for mass per unit area M_A, foliar [N], foliar [P] and average leaf size for the same species.Red open circles indicate species found on low fertility sites and the blue open circles indicate species found on high fertility sites. Species found on both soil fertility groups are indicated with closed circles (see text for details). Solid lines show the SMA model fit which did not depend on soil fertility.

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀▮
▶▮
◀
▶
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

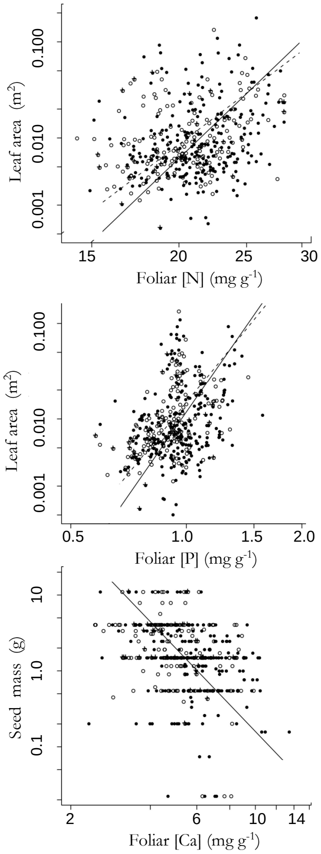

Fig. 6. Standard Major Axis (SMA) regressions lines between derived genetic components of foliar [N] and foliar [P] and leaf mass per unit area (L_A) for the top two panels and between species estimated foliar [Ca] associated average seed mass (S) for the associated genus. Open circles indicate species found on low fertility sites and the closed circles indicate species found on high fertility sites. Species found on both soil fertility groups are designated by a "+" (see text for details). For the top two panels, solid lines show the SMA fit for low fertility soil species which are significantly different to the dashed lines for high fertility soil species. For the bottom panel the solid lines shows the SMA model fit which did not depend on soil fertility.

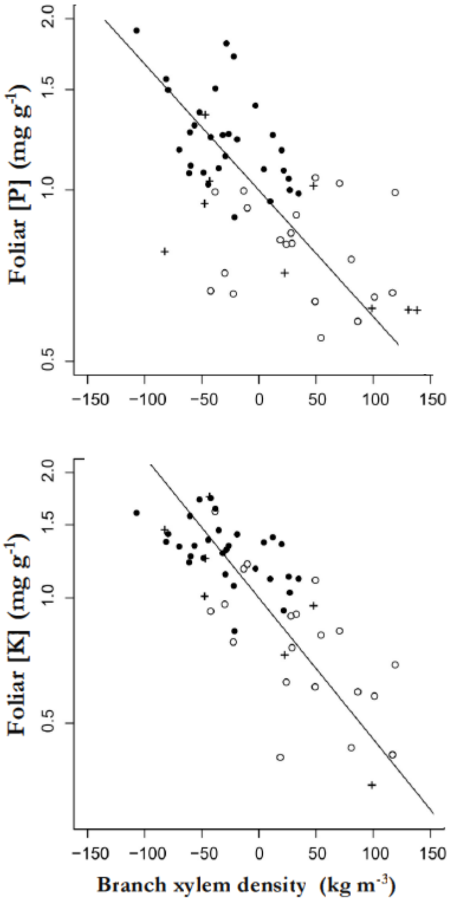

Fig. 7. Standard Major Axis (SMA) regressions lines between the derived environmental components of branch xylem density (ρ_x) and foliar [P] and foliar [K]. Open circles indicate species found on low fertility sites and the close circles indicate species found on high fertility sites. Species found on both soil fertility groups are designated by a "+" (see text for details). Solid lines show the SMA model fits.

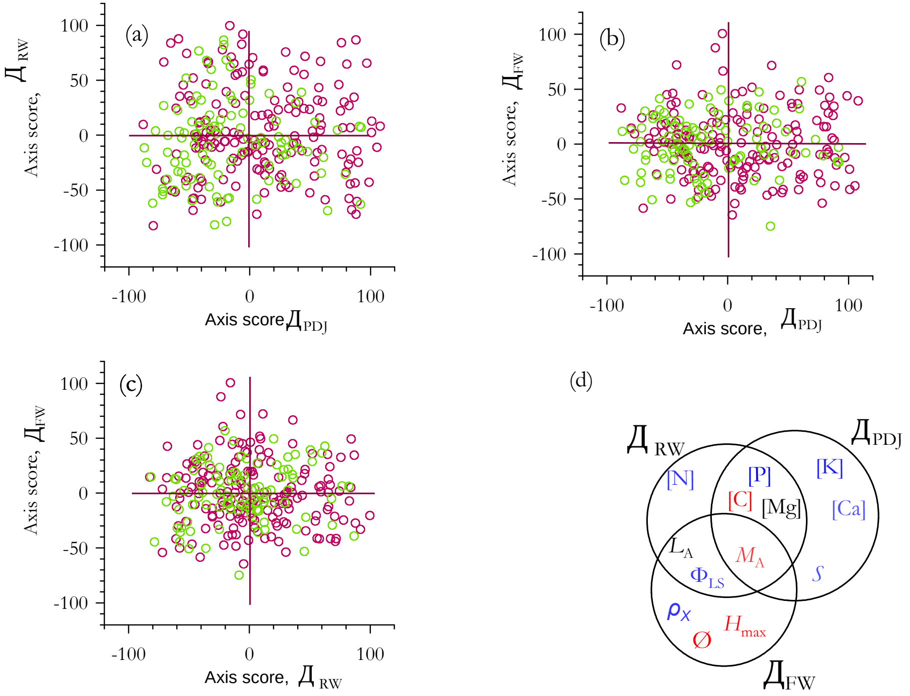

Fig. 8. Summary of CPC analysis results. **(a–c)** first three axis scores plotted against each other showing the lack of correlation required for a good model fit; green: species associated with low fertility soil, purple: species associated with high fertility soils **(d)** Euler diagram showing overlaps between the first three dimensions in terms for the individual measured traits (where significant): blue; positive relationship with dimension, red; negative relationship with dimension, black; of different sign depending on the dimension.

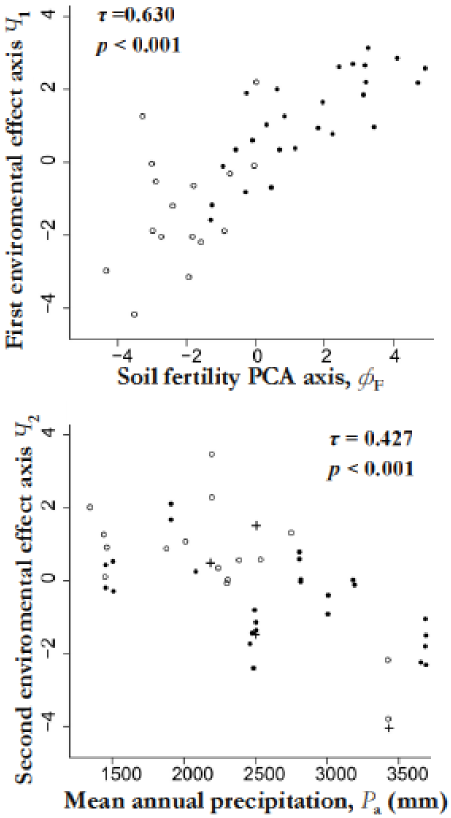

Fig. 9. Relationship between derived environmental effect principal components (Table 5) and soil/environmental parameters for various plots across the Amazon. Top panel, First principal component of the environmental effects versus the first principal component of the PCA of soil chemical and physical characteristics as derived by Fyllas et al. (2009) on the basis of data provided by Quesada et al. (2010). Second panel, second principal component of the environmental effects PCA versus mean annual precipitation. Open circles indicate low fertility sites and the closed circles indicate high fertility sites as defined by Fyllas et al. (2009).

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀▮
▶▮
◀
▶
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

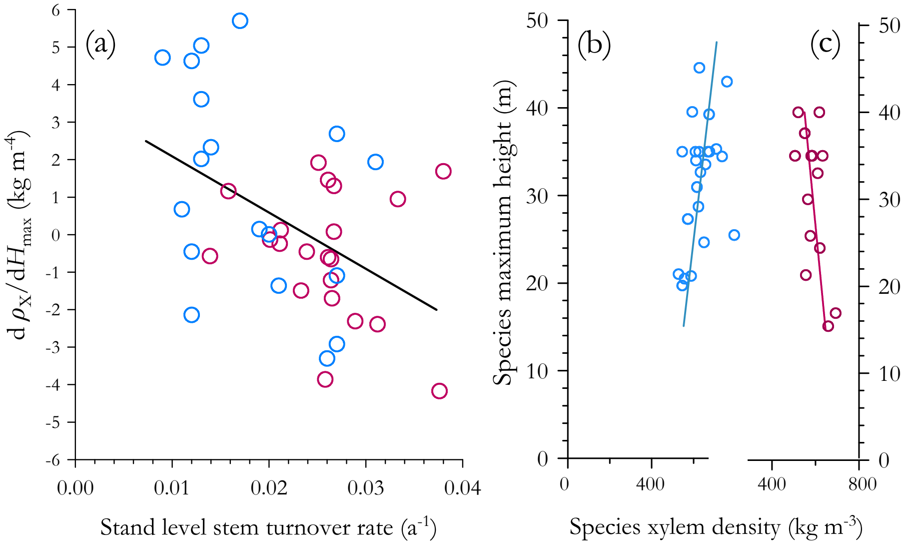

Fig. 10. Stand level variations in the relationship between species maximum height (H_{max}) and branch xylem density (ρ_x). **(a)** Slope of gradient describing variation in ρ_x with H_{max} as dependent on stand level turnover rate; **(b)** and **(c)** Specific examples for a low turnover and high turnover plots at Caixuana (Pará State, Brazil) and Jatun Sascha (Ecuador) respectively. Red open circles indicate species found on low fertility sites and the blue open circles indicate species found on high fertility sites. All lines have been fitted by SMA regression and are significant at $p \le 0.05$ or less.