Contrasting photosynthetic characteristics of forest versus savanna species (Far North Queensland, Australia)

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Abstract

Forest and savanna are the two dominant vegetation types of the tropical regions with very few tree species common to both. At a broad scale, it has long been recognised that the distributions of these two biomes are principally governed by precipitation and its seasonality, but with soil physical and chemical properties also potentially important. For tree species drawn from a range of forest and savanna sites in tropical far north Queensland, Australia, we compared leaf traits of photosynthetic capacity, structure and nutrient concentrations. Area-based photosynthetic capacity was higher for the savanna species with a steeper slope to the photosynthesis ↔ nitrogen (N) relationship compared with the forest group. Higher leaf mass per unit leaf area for the savanna trees derived from denser rather than thicker leaves and did not appear to restrict rates of light-saturated photosynthesis when expressed on either an area- or mass-basis. Median ratios of foliar N to phosphorus (P) were relatively high (>20) at all sites, but we found no evidence for a dominant P-limitation of photosynthesis for either forest or savanna trees. A parsimonious mixed-effects model of area-based photosynthetic capacity retained vegetation type and both N and P as explanatory terms. Resulting model-fitted predictions suggested a good fit to the observed data (R^2=0.82). The model's random component found variation in area-based photosynthetic response to be much greater among species (71% of response variance) than across sites (9%). These results suggest that, on a leaf area-basis, savanna trees of far north Queensland, Australia are capable of photosynthetically out-performing forest species at their common boundaries.

Key symbols and abbreviations

FNQ	Far north Queensland
N	Nitrogen
P	Phosphorus
$\mathbb{V}$	Vegetation type
$\mathbb{F}$	Forest
$\mathbb{S}$	Savanna
Φ	Plant functional type
A_{max}	Rate of CO_2 assimilation, light and CO_2 saturated
A_{N}	Photosynthetic nitrogen-use efficiency
A_{P}	Photosynthetic phosphorus-use efficiency
g_{s}	Stomatal conductance to CO_2 diffusion
d	Leaf (lamina) thickness
ρ	Leaf density
M_{a}	Leaf mass per unit area
ξ	Leaf dry matter content
Subscripted "a"	Per unit leaf area
Subscripted "m"	Per unit leaf dried mass

1. Introduction

Forests and savannas dominate the tropical vegetated regions of the Earth covering 15-20% of the Earth's surface (Torello-Raventos et al., 2013). At a broad scale, it has been long recognised that the distribution of these two biomes, each with its own structural characteristics and species composition, is principally governed by precipitation and its seasonality (Schmimper, 1903), but with soil chemical characteristics also important (Lloyd et al., 2008; Lloyd et al., 2009; Lehmann et al., 2011). Edaphic conditions are especially influential in regions where the two biomes intersect – often referred to as 'ecotones' or 'Zones of (Ecological) Tension' (ZOT) - both forest and savanna existing as discrete 'patches' under similar climatic conditions (Cochrane, 1989; Ratter, 1992; Thompson et al., 1992; Hoffmann et al., 2009; Lehmann et al., 2011; Saiz et al., 2012; Veenendaal et al., 2014). The patchiness of the ZOT mosaic at small spatial scales has led some to argue that disturbances, principally fire, must interact with climatic/edaphic boundaries in determining transition between the two alternative vegetation types (e.g. Lehmann et al., 2011; Hoffmann et al., 2012). Whatever the drivers, feedbacks associated with changes to distributions of these biomes in response to anthropogenic climate change have the potential to substantially modify the rate of future global warming (e.g. Malhi et al., 2009).

The underlying causes of variation in photosynthetic carbon acquisition across and within these two biomes remain, however, poorly understood. There is, nevertheless, accumulating evidence that for tropical forest species phosphorus (P) availability may limit photosynthetic rates and productivity (Vitousek, 1984; Domingues et al., 2010; Mercado et al., 2011; Quesada et al., 2012). Whereas in savanna ecosystems nitrogen (N) may be more important as a limiting nutrient (Lloyd et al., 2009). Soils in Australia are generally highly weathered with the consequence that plant performance, even in the sub-tropical and temperate regions, is often considered more limited by the supply of P than of N (Beadle, 1962, 1966; Webb, 1968). Nevertheless, in far north Queensland (FNQ), where almost all the Australian tropical forest occurs, recent volcanic activity (0.01 to 4.5 Ma BP) has produced some very young soils. These young basaltic soils cover about 60% of FNQ's land area (Whitehead et al., 2007) and display higher levels of organic matter and total P when compared with other parent material groupings such as granitic or metamorphic (Spain, 1990). Direct links from soil P status to measures of forest productivity are not straightforward, however, and inter-specific variations in P use efficiency are likely to have contributed to the varied composition of local plant communities (Gleason et al., 2009). Likely selection pressures, on infertile soils, for enhanced P use efficiency coupled with FNQ's recent volcanic history mean that primacy here for P as the major limiting nutrient to photosynthetic capacity is still hypothetical.

The forest and savanna vegetation types ($\mathbb{V}$) have very few plant species in common (Torello-Raventos et al., 2013) and the edaphic determinants of the ZOT are of particular interest in Australia (Beadle, 1962, 1966; Russell-Smith et al., 2004). The savannas of FNQ are distinctive globally being dominated by eucalypts (Myrtaceae). Here, species of the closely related genera *Eucalyptus* and *Corymbia* are characterised by sclerophyllous (hard) leaves with relatively low leaf [N], but a high oil content and correspondingly high heat of combustion (Beadle, 1966) – traits that contribute to a highly flammable leaf litter. In contrast to the tree species of the moist forests, such evergreen savanna species are expected to be able to withstand periods of water shortage and high water vapour pressure deficit. Sclerophylly imparts both structural and physiological leaf traits, but, to date, most research has focused on the structural aspects: leaf thickness and density combining in the ratio leaf mass per unit area (M_a, g m^{-2}). Sclerophyllous leaves are often amphistomatous (i.e. with stomata abundant on both the adaxial and abaxial surfaces) displaying an isobilateral mesophyll distribution (Burrows, 2001) - characteristics thought to be associated with both high photosynthetic potentials (Mott et al., 1982) and high insolation environments (Pyykko, 1966; Parkhurst, 1978). Such eco-physiological associations are expected on theoretical grounds, especially under conditions of low water availability (Buckley et al., 2002) and it may be that sclerophyllous eucalypt leaves display an 'investment strategy' that at once combines resilience with high photosynthetic return (Cernusak et al., 2011).

Broad overlap in leaf traits has been reported for savanna and forest tree species, but, due to different soils and the drier conditions typical of savannas, we might expect differences between the two vegetation types in leaf N and P content, rates of photosynthesis, morphology and longevity (Wright et al., 2001; Buckley et al., 2002; Meir et al., 2007; Domingues et al., 2010). It remains unclear, however, whether such differences persist within the relatively narrow boundaries of a ZOT. In addition, within individual tropical forest stands, leaves can vary markedly in their physiological and structural properties depending on canopy position and the availability of gaps (Popma et al., 1992; Lloyd et al., 2010). Indeed tropical forest tree species are often grouped according to their degree of shade tolerance and/or light requirement (e.g. Swaine and Whitmore, 1988; but see Poorter, 1999). Shade tolerant species in the understory may receive less than 2% of full light at the canopy crown (Chazdon, 1992) whilst pioneer species typically require high light for germination and survival and depend on the creation of canopy gaps (Turner, 2001). As a result, species characteristic of differing light niches have commonly been considered to display distinctive photosynthetic traits linked to nutrient investment, allocation and leaf architecture (Niinemets, 1997; Carswell et al., 2000; Wright et al., 2001). In the context of P availability, a study in the forest of Guyana, on relatively infertile Ferralsols, found that pioneer tree species exhibited higher photosynthetic nitrogen and phosphorus use efficiencies than neighbouring climax species (defined here as those species whose seeds can germinate and establish in the shade) (Raaimakers et al., 1995). Fyllas et al. (2012), in describing forest tree species of the Amazon Basin, derived four discrete PFTs aligned with the species' stature, canopy position and pioneering ability. It remains to be seen whether such an attractively simple system can be applied to tropical forest species of FNQ.

In this study we contrast leaf photosynthetic traits for tree species from forest and savanna communities of northern Australia addressing the following questions:

1. Are there differences in photosynthetic capacity and nutrient use efficiency between adjacent forest and savanna vegetation types?
2. And if so, are these distinctions associated with systematic differences in leaf structural traits?
3. Is there evidence of a greater role for P rather than N (or vice versa) in determining photosynthetic capacity across both sites and species?
4. Can a simple classification system based on light requirement and adult stature help to describe observed variation in photosynthetic traits of tropical forest trees?

2. Materials and method

2.1. Sites and species

A series of sites was selected in FNQ, Australia in an arc from the Atherton Tablelands, inland from Cairns, to Cape Tribulation, north of the Daintree River. The series, which forms part of the *Tropical Biomes in Transition* (TROBIT) network, was designed to provide a contrast of vegetation types, specifically forest ($\mathbb{F}$) and savanna ($\mathbb{S}$), and occurring on diverse soils (Table 1). Further descriptions of all sites and the rationale (both structural and floristic) for our distinction between $\mathbb{F}$ and $\mathbb{S}$ are available in Torello-Raventos et al. (2013). Seven sites were visited in six weeks of fieldwork during April and May 2009 and measurements were performed on 125 trees representing 30 species. A full list of species by site is presented in Table S1 (Supplementary information).

2.2. Gas exchange measurements

Leaf gas exchange measurements were performed using a portable photosynthesis system (Li-Cor 6400, Li-Cor, Lincoln, NE, USA) on young, fully developed leaves. During the measurements, chamber conditions were set with block temperature (mean 27 °C) held slightly above ambient air temperature to avoid problems of condensation; relative humidity remained close to ambient (mean = 67%). The rate of air flow to the sample cell was held constant at 500 μmol s^{-1}, but exceptionally, and when faced with very low stomatal conductance, this was reduced (minimum 250 μmol s^{-1}). Light ($A \leftrightarrow Q$) curves were generated for each tree species to determine the saturating light level for adoption in subsequent CO_2 response curves ($A_a \leftrightarrow C_i$ curves). Those saturating light levels ranged from 500 to 2,000 μmol m^{-2} s^{-1}. Measurements of light-saturated net CO_2 assimilation per unit leaf area (A_a) were then obtained for a range of intercellular CO_2 concentrations (C_i) by varying chamber CO_2 concentration (C_a). The $A_a \leftrightarrow C_i$ curves provided area based values of light-saturated photosynthesis under ambient and elevated atmospheric [CO_2] ($A_{sat,a}$ and $A_{max,a}$ respectively). For the purposes of modelling photosynthetic capacity we focus on variations in A_{max} - preferred over A_{sat} in this context as less susceptible to limitations of stomatal conductance (g_s).

In the absence of cranes or suspended walkways, branches had to be cut from trees. Sun exposed branches for low trees were reached using hand-held secateurs or forestry shears on telescopic poles; for taller trees branches were pulled down using a weighted line shot from a catapult. Trees of sub-canopy species were rarely found growing in full sunlight and so these leaves, although sampled from upper branches free of self-shading, had developed in a relatively low-light environment. Once detached, the stem was re-cut under water in order to re-establish the xylem water column (Domingues et al., 2010). Performing gas exchange measurements on excised branches can affect subsequent calculations where stomatal conductance is heavily depressed (Santiago and Mulkey, 2003). The $A_a \leftrightarrow C_i$ curves were reviewed for such instances and where necessary the data excluded from all further analysis (n=11). A further check on data integrity proposed by Kattge et al. (2009) rejects those measurements where $A_{sat}/[\mathrm{N}]_m$ is < 2 μmol CO_2 g^{-1}N s^{-1} : any such curves were likewise excluded (n=2).

2.3. Leaf morphology and nutrient analysis

At the completion of gas exchange measurements, the leaf (gas leaf) was cut from the branch and leaf thickness (d, μm) taken by averaging repeated measurements (Mitutoyo dial thickness gauge, n=6) alternating back and forward across the mid-vein and proceeding down the lamina from tip to base. A series of discs (6.6 mm, diameter) was then punched from the leaf avoiding veins and necrosis or other damage. The discs with the remainder of the leaf (petiole and mid-vein discarded) were oven dried at 70 °C for a minimum of 48 h before their dried mass was recorded. The combination for the discs of known area and dried mass allowed the calculation of leaf mass per unit area (M_a, g m^{-2}). Leaf density (ρ, g cm^{-3}) was estimated using the equation:

$$\rho = M_a / d \quad . \tag{1}$$

In addition to the gas leaf, the opposing leaf was also cut from the branch, petiole and mid-vein discarded, and placed in a zip-lock plastic bag with moist cotton-wool until fresh mass could be measured that evening (or exceptionally the next day). The leaf was then placed in an envelope, oven-dried as above and dried mass recorded. The ratio of the leaf's dried to fresh mass is termed leaf dry matter content (ξ). All subsequent references to ξ relate to opposing and not gas leaves. Logistical constraints imposed by repeated changes of base camp and lack of electricity supply meant that delays were experienced between harvesting the leaves and oven drying (maximum delay 30 days).

Oven-dried material was used for determination of total leaf [N] and [P]: dried ground leaf material was acid-peroxide digested before colorimetric analysis using a segmented flow analyser (Skalar San$^+$ System, Breda, The Netherlands). The photosynthetic efficiency of nutrient use was estimated as the maximal rate of carbon gain per unit of leaf N and P (A_N and A_P respectively).

2.4. Statistical analyses

All statistical analysis and modelling was conducted using the open-source statistical environment R (R Development Core Team, 2011). As initial data exploration revealed wide variation in many trait values across the different sites, non-parametric Kruskal-Wallis tests were used to test for differences among the categorical factors of Site and $\mathbb{V}$ using the `coin` package (Hothorn et al., 2008). Where significant, differences among factor levels were assigned using Tukey's HSD post-hoc tests ($p < 0.05$) applied to data rankings. After exclusion of poor $A_a \leftrightarrow C_i$ curves (n=13, described above) and replicates with other missing values (n=3), the revised dataset of 109 leaf measurements contained many more observations for $\mathbb{F}$ (n=85) than $\mathbb{S}$ (n=24) and so there is an element of imbalance in the test specification where $\mathbb{V}$ is adopted as the fixed factor. Bivariate relationships were described using Standardised Major Axis (SMA) line fits using smatr-3 (Warton et al., 2006). Relationships between replicated foliar traits (photosynthesis, nutrient content) and site-dependent variables (soil, climate) were quantified using Kendall's non-parametric rank-order correlation (tau, τ); especially appropriate in cases with many replicated response values for each value of the predictor variable (Legendre and Legendre, 2012).

2.4.1. Mixed effects linear model of photosynthetic capacity

The study involved replicated measurements of tree species within and across forest and savanna plots. Such a design introduced the strong likelihood that measurements within the same site would be influenced by spatial proximity. In specifying a model that attempted to explain differences in photosynthetic capacity between $\mathbb{V}$ it was necessary to recognise this hierarchical structure in order to avoid systematic variation in the residuals leading to potentially biased interpretation (Zuur et al., 2009). The sites and species selected, rather than considered of primary interest per se, were viewed as representative of a wider population and focus placed on their variance. The model's random component therefore included the categorical variables of species nested within sites. Unfortunately, because not all tree species at all sites were measured with replication (see instances of n=1 at Table S1), convergence problems meant that the random component of the model could not accommodate differing slopes as well as intercepts for species within a site.

The final model (fitted using the `nlme` package in R) may be expressed as:

$$A_{\max,\mathrm{a}[ijk]} = \alpha + \beta_1 b_{jk} + \beta_2 [\mathrm{N}]_{\mathrm{a}[ijk]} + \beta_3 [\mathrm{P}]_{\mathrm{a}[ijk]} + a_k + a_{j|k} + \varepsilon_{ijk} \; . \qquad (2)$$

Here response variable $A_{\max,\mathrm{a}[ijk]}$ denotes the maximum rate of area-based photosynthesis for observation i of species j at site k with b being a categorical variable taking a base value of 0 for species in plots classified as "forest" ($\mathbb{F}$) and a value of 1 for "savanna" ($\mathbb{S}$). The term a_k is a random intercept and allows for variation among sites. The term $a_{j|k}$ allows for interspecific variation at the same site. The term ε_{ijk} is the residual (unexplained) error and represents the variation within-site, variation among plants of the same species and measurement error. Each of the variation terms is assumed to be normally distributed with mean zero. With the independent covariates centred (i.e., zeroed on the population mean), the fitted intercept term α thus represents the predicted forest tree $A_{\max,\mathrm{a}}$ at the ($\mathbb{F} + \mathbb{S}$) population mean $[\mathrm{N}]_\mathrm{a}$ and $[\mathrm{P}]_\mathrm{a}$. The term $\beta_1 b$ represents the difference in predicted $A_{\max,a}$ between the two $\mathbb{V}$ (in this case $A_{\max,\mathrm{a}}[\mathbb{S}]$ - $A_{\max,\mathrm{a}}[\mathbb{F}]$). The predicted $\mathbb{S}$ tree $A_{\max,\mathrm{a}}$ at the population mean $[\mathrm{N}]_\mathrm{a}$ and $[\mathrm{P}]_\mathrm{a}$ values is therefore $\alpha + \beta_1$.

2.5. Plant functional types

$\mathbb{F}$ species were assigned to one of four plant functional types (Φ) depending on their adult stature and light requirements for recruitment (Veenendaal et al., 1996). Three of the authors (DMC, AF and DJM), each with an extensive knowledge of Australian tropical forest trees, made independent Φ assignments before combined results were consolidated and minor discrepancies resolved. The Φ descriptions are provided in Table S2 (Supplementary information) and the relevant species designations in Table S1 (Supplementary information). All of the tropical moist forest species in this study are obligate evergreen.

3. Results

3.1. Key leaf traits: Forest versus Savanna trees

There was a ten-fold range across the dataset in photosynthetic capacity per unit leaf area ($A_{\mathrm{max,a}}$) from 4.9 to 52.0 μmol m^{-2} s^{-1} (Figure 1a). Mean values (treating each sampled tree as an independent variable) differed among sites ($p<0.0001$) and were significantly higher in the $\mathbb{S}$ plots (Figure 1b; $p<0.0001$). When expressed per unit leaf dried mass, photosynthetic capacity ($A_{\mathrm{max,m}}$) was also highly variable with significant plot-to-plot differences (Figure 1c; $p<0.0001$). Overall there was, however, no difference in mean $A_{\mathrm{max,m}}$ between $\mathbb{F}$ and $\mathbb{S}$ (Figure 1d; $p=0.11$). There were striking inter-site differences in leaf mass per unit area (M_a; Figure 1e) which was highly variable, spanning a five-fold range from lowest to highest observations. Overall, M_a was higher for $\mathbb{S}$ than for $\mathbb{F}$ (Figure 1f; $p<0.0001$). That contrast in M_a derived chiefly from variable leaf dry matter content ratios (ξ) with a three-fold variation in ξ observed. Of note were pronounced differences among sites (Figure 1g; $p<0.0001$) and, like M_a, higher mean values for $\mathbb{S}$ than for $\mathbb{F}$ (Figure 1h; $p=0.0035$). By contrast, there was no difference between $\mathbb{S}$ and $\mathbb{F}$ for measures of leaf thickness (d) (Figure 1j; $p=0.70$) which was also much less variable.

Both area- and mass-based leaf nitrogen levels were highly variable and this was most pronounced within the $\mathbb{F}$ plots. On an area basis, differences among sites (Figure 1m; $p<0.0001$) produced higher mean $[\mathrm{N}]_a$ values for $\mathbb{S}$ than for $\mathbb{F}$ (Figure 1n; $p=0.0002$) with this inter-site N variability even more pronounced on a mass basis (Figure 1o; $p<0.0001$). Overall, mean $[\mathrm{N}]_m$ was higher for $\mathbb{F}$ than for $\mathbb{S}$ (Figure 1p; $p<0.0001$). Broadly similar trends were observed for total leaf phosphorus with higher mean $[\mathrm{P}]_a$ for $\mathbb{S}$ versus $\mathbb{F}$ (Figure 1r; $p=0.003$), and with that ranking also reversed when expressed on a mass basis (Figure 1t; $p=0.0004$). Foliar ratios [N]:[P] ranged from 10.1 (*Neisosperma poweri*, KBL-01) to 39.1 (*Symplocos hayesii*, KBL-03), but on average did not differ across plots (Figure 1k; $p=0.29$) and with no systematic differences between $\mathbb{F}$ and $\mathbb{S}$ (Figure 1l; $p=0.74$).

Considering the dataset as a whole (i.e. $\mathbb{F}$ and $\mathbb{S}$ trees combined), significant correlations of $A_{\mathrm{max,a}}$ with environmental variables such as elevation, temperature and soil cation status were found. But with these mirrored by significant correlations of the same sign for both leaf $[\mathrm{P}]_a$ and $[\mathrm{N}]_a$ (Supporting Information Table S3). In investigating the underlying sources of our dataset's tree-to-tree variation in photosynthetic properties, we therefore focussed (using the mixed effects model) on associated tree-to-tree variations in leaf-based nitrogen and phosphorus concentrations; checking for any edaphic or climatic effect beyond that through an examination of model residuals in relation to the site-associated climate and soil covariates.

3.2. Leaf nutrient relationships

There was a strong positive linear relationship between leaf $[\mathrm{P}]_a$ and $[\mathrm{N}]_a$ for both $\mathbb{F}$ and $\mathbb{S}$ (Figure 2a), but with a steeper slope observed for $\mathbb{S}$. The shallower slope for $\mathbb{F}$ differs ($p=0.031$) from the mean relationship for tropical forests as suggested by Reich et al. (2009) as depicted by the dotted line passing through the origin in Figure 2a (slope = $10^3/18.8$). When expressed on a mass basis, there was a single, common P ↔ N relationship for both $\mathbb{V}$ (Figure 2b). Leaf nutrient investment on an area basis showed positive relationships with M_a for $\mathbb{F}$ only (Figure 2c and d).

To test for differences in the photosynthesis-nutrient relationships between the two $\mathbb{V}$, a series of standardised major axis (SMA) analyses were undertaken with photosynthetic capacity (A_{max}) as the response variable and leaf chemistry ([N] and [P]) as the explanatory bivariate (Table 2). For the combined dataset, linear relationships were strong for both nutrients irrespective of whether variables were expressed on a mass- or area-basis (r values ranging from 0.63 to 0.70, Table S4, Supplementary information).

The $A_{max,a} \leftrightarrow [N]_a$ association as shown in Figure 3a suggests two important differences between the two $\mathbb{V}$. First: across the (pooled) dataset the lowest 0.3 fraction $[N]_a$ are confined to $\mathbb{F}$ associated trees (as can also be inferred from Figures 1 and 2). Second: for the lowest $[N]_a$ for $\mathbb{S}$ associated trees (*ca.* 1.6 g m^{-2}) similar $A_{max,a}$ are observed for both $\mathbb{S}$ and $\mathbb{F}$, but as $[N]_a$ increases beyond that point $A_{max,a}$ for $\mathbb{S}$ rises with a sensitivity nearly three times that observed for $\mathbb{F}$. There was no difference between the two $\mathbb{V}$ in either the slope or the intercept of the $A_{max,a} \leftrightarrow M_a$ association (Table S4) and a single line ($r^2 = 0.3$) describes the common positive relationship (Figure 3c).

3.3. Nutrient use efficiency and leaf structure

Elevated rates of photosynthesis per unit N yielded higher photosynthetic use efficiencies (A_N) for $\mathbb{S}$ species (Figure 4a). Of the $\mathbb{F}$ trees only the tall pioneers showed an equivalent A_N to the $\mathbb{S}$ species and there was a significant difference between tall pioneers and shade tolerant species. On the other hand, although there was a clear distinction between $\mathbb{F}$ and $\mathbb{S}$ species in A_P, no such distinction could be made among the four $\mathbb{F}$ types.

The higher M_a values for the $\mathbb{S}$ trees (Figure 1f) suggested underlying differences in leaf structure between the two $\mathbb{V}$ and the range of M_a values for separate Φ classes showed distributions centred at different points along the M_a axis (Figure S1, Supplementary information). Whilst we found positive relationships for M_a with d and ρ, the slopes of those relationships were $\mathbb{V}$-dependent (Figure 5a and b) and the association was much stronger for the $\mathbb{S}$ group. Over common ranges of M_a, the $\mathbb{F}$ trees displayed the thicker leaves (measured fresh) – a result heavily influenced by the upper canopy group. Indeed, M_a was seldom greater than 75 g m^{-2} for either the small pioneer or sub-canopy classes, but for any given M_a the ratio of leaf dry mass to water content (φ, as an index of sclerophylly) was much higher for the small pioneers (Figure 5c). The slope of the relationship $\varphi \leftrightarrow M_a$ also differed among the Φ classes ($p<0.0001$) – being shallowest for the $\mathbb{S}$ trees (an increased ratio of 0.005 per unit M_a) and steepest for the small pioneers (an increase of 0.019). Such structural differences among classes of $\mathbb{V}$ and Φ appeared unrelated, however, to our measure of photosynthetic N allocation: A_N was independent of d ($p=0.46$) and an overall correlation with M_a ($p=0.0009$) disappeared upon controlling for $\mathbb{V}$ and Φ (Figure 5d).

3.4. Modelling photosynthetic capacity

In attempting to model variation in $A_{max,a}$ the starting, or maximal, fixed component of our linear mixed effects model (Model 1, Table 3) included, along with a V dependent term, those continuous variables spanning leaf morphology and chemistry suggested by pair-wise correlation plots at Figure S2 (Supplementary Information). The optimal fixed term, on *AIC* and likelihood ratio criteria, was provided by Model 4: with vegetation type a fitted categorical variable (through the $\beta_1 b$ term) along with the continuous variables $[N]_a$ and $[P]_a$. Model performance was not improved by adding interaction terms (see model variants 8 through 12, Table 3). Also of note is Model 6 which in dropping the vegetation ~~*b*~~ term (*b*) produces a significantly inferior model (p=0.002). That is to say, we could not account for the intrinsically higher area-based photosynthetic capacities of $\mathbb{S}$ affiliated trees (Fig. 1b) through systematic $\mathbb{F}$-$\mathbb{S}$ differences in any of our measured foliar traits. Comparisons against a model variant (Model 7, Table 3), excluding the vegetation ~~*b*~~ term, but reinstating available traits relating to leaf chemistry and structure confirmed that vegetation type ~~*b*~~ could not be substituted in this way.

The full model, fixed and random terms combined, explained 82% of variation in the observed values of $A_{max,a}$ and with all four forest Φ reasonably well predicted (Figure 6a). A plot of model residuals against fitted values raised no concerns for the model assumptions (Figure S3, Supplementary information). These model results also suggest, other things being equal, that photosynthetic capacities are intrinsically higher for $\mathbb{S}$ than $\mathbb{F}$ species (Figure 1b) - with estimated values at the dataset trait means of 29 and 18 µmol CO_2 m^{-2} s^{-1} (Table 4). Despite the relatively low *t* value for the fitted $[P]_a$ term, the predictive power of the overall model was improved by retaining $[P]_a$ as a fixed term (compare models 4 and 5 in Table 3). The greater significance attached by the final model to the $[N]_a$ term is confirmed when the two slope coefficients are standardised to allow for the difference in underlying units: $\beta_2{}'$ $[N]_a = 0.294$ and $\beta_3{}'$ $[P]_a = 0.172$ (interpreted as the relative effect on $A_{max,a}$ of one standard deviation change in the independent variable).

Model output indicated that, after controlling for vegetation type (*b*) and leaf nutrient levels, less than 10% of variation in $A_{max,a}$ was attributable to site effects. The environmental influence on photosynthetic capacity noted above (Table S3) was, however, adequately captured by our mixed model's fixed term (which incorporates leaf N and P), as shown by the absence of any relationship between model residuals and those same site variables relating to climate and soil conditions (Table S5 and Figure S4).

Broadly similar results were obtained when the mixed modelling approach was repeated for mass-based leaf traits (Table S6, Supplementary information). The fixed component of the final parsimonious model again included vegetation type (*b*), $[N]_m$ and $[P]_m$, but this time with a significant N:P interaction. The preferred random term was unchanged from that presented above.

3.5. Plant functional types

The area-based model's nested random component, which recognises the grouping of species within sites, allows the variance of the response ($A_{max,a}$) to be partitioned among the available terms. The fraction attributable to variance among plots (9%) is dwarfed by that among species (71%). Variation in $A_{\mathrm{max,a}}$ around the population mean was therefore influenced much more by a tree's taxonomy than the plot in which it was growing. One factor that may help explain this inter-specific variation is plant functional type (Φ, related to a tree's growth strategy and light requirements as described in Table S2). We examined model output for any Φ-related pattern in random intercepts for the different species. We found that tall pioneers displayed higher intercepts than sub-canopy species (p=0.0326) as is shown in Figure 6b. Thus, at any given $[\mathrm{N}]_{\mathrm{a}}$ and $[\mathrm{P}]_{\mathrm{a}}$ tall pioneers typically achieved a higher $A_{\mathrm{max,a}}$ than shade tolerant forest trees - as confirmed by their higher A_{N} and A_{P} (Figure 4). Small pioneers and shade tolerant canopy species were intermediate between these two extremes and showed intercepts close to the population mean.

4. Discussion

The main aim of this study was to compare photosynthetic traits for the tree species typical of adjacent tropical moist forest and savanna plots – a dynamic boundary potentially sensitive to changes in global climate (Sitch et al., 2008; Booth et al., 2012; Gloor et al., 2012; Huntingford et al., 2013). Our findings include higher photosynthetic capacity and nutrient use efficiencies for the savanna species, but our prediction of a primary photosynthetic role for P rather than N across the forest sites was not supported. Our preferred area-based model retained only three fixed terms: vegetation type, leaf N and P yet accounted for 82% of variation in $A_{\mathrm{max,a}}$. Model output revealed a stronger relationship $A\leftrightarrow$N than $A\leftrightarrow$P and found variability among species much more pronounced than among sites. For $\mathbb{F}$ there was qualified support for the expectation that pioneer species would show higher photosynthetic traits of $A_{\mathrm{max,a}}$ and A_{N} compared to late successional shade tolerant species (Raaimakers et al., 1995).

4.1. Forest and savanna comparisons

Values reported here for key leaf traits such as $A_{\mathrm{max,a}}$, M_{a} and levels of foliar N and P fell within previously published ranges for $\mathbb{F}$ and $\mathbb{S}$ trees (e.g. Medina, 1984; Prior et al., 2005; Harrison et al., 2009; Cernusak et al., 2011). There were, however, significant differences among sites and between $\mathbb{F}$ and $\mathbb{S}$ in all these traits (Figure 1). In particular, a recently cyclone-affected $\mathbb{F}$ site south of Ravenshoe (KBL-01) stood out as high in leaf nutrients and photosynthetic capacity when expressed on a mass basis. Due to lower M_{a}, however, that prominence was all but removed when area-based traits were examined.

Our study included measurements of 30 tree species across seven sites; these sites and species being viewed as representative of wider populations and our modelling treatment of those terms therefore focusing on their influence on the variance of the photosynthetic response rather than mean values. The linear mixed effects model (Table 4), through its random component of species nested within sites, showed that most of the variance in the data occurred among species (71%). Once levels of leaf N and P had been included in the model, variation among sites represented less than 10% of total variation. This corresponds with the findings of other Australian studies where within-site variation has proved much larger than that across sites (e.g. Wright et al., 2004; Asner et al., 2009). For this study, it could be argued, however, that the climatic and topographical ranges spanned by the seven sites (Table 1) were rather modest – mean annual precipitation, for example, is nowhere lower than 1.3 m and the range in mean annual temperatures is only 6 °C.

Lower mass-based leaf nutrient values for $\mathbb{S}$ species have traditionally been linked to their higher M_a associated with contrasts in leaf longevity and economic strategy. In the Australian literature, these species are widely described as sclerophyllous, characterised by tough leaves and adaptations to limit water loss. We argue, however, that on theoretical grounds it is area- rather than mass-based concentrations of N (and presumably also P, where relevant for photosynthetic carbon gain) that should be modulated by differences in water availability (Buckley et al., 2002). With declining precipitation therefore, an increase in area-based photosynthetically important nutrients (in our case $\mathbb{S} > \mathbb{F}$) seems to be the general case (Buckley et al., 2002; Cernusak et al., 2011; Domingues et al., 2014; Schrodt et al., 2014). It is non-systematic variations in M_a with precipitation, in turn probably attributable to differences in rainfall seasonality, that produce contradictions in mass-based N ↔ precipitation relationships (Schrodt et al., 2014).

4.2. Linking leaf structure to metabolism

At the leaf level, A_N is dependent upon a number of factors including N allocation, conductance and Rubisco kinetics and no single cause has been found to explain observed interspecific differences (Hikosaka, 2004; Hikosaka and Shigeno, 2009). The idea that species with high M_a exhibit low A_N due to greater structural investment (e.g. Takashima et al., 2004) has been countered by later studies that found no relationship between A_N and the proportion of leaf N allocated to cell walls (Harrison et al., 2009; Hikosaka and Shigeno, 2009). Indeed, our general positive association between area-based photosynthetic capacity and M_a - also observed by Domingues et al. (2014) - challenges the general notion that thick sclerophyllous leaves should be characterised by low photosynthetic rates and/or low photosynthetic nutrient use efficiencies (Wright et al., 2004; Westoby and Wright, 2006). Certainly, it has long been known that typically sclerophyllous eucalypt species can have exceptionally high photosynthetic rates (Larcher, 1969) with Denton et al. (2007) also finding very high nutrient use efficiencies for numerous xeromorphic Proteaceae species that exhibit some of the very highest M_a worldwide. Maximov (1929) noted: “the drier the habitat, the smaller and more leathery the leaves, and the higher their rate of transpiration”.

Interestingly, our best-fit photosynthesis model was not improved by the inclusion of morphological traits such as M_a, leaf thickness or the ratio of leaf dry to fresh mass. Although M_a was much higher for the $\mathbb{S}$ plots, there was no difference in leaf thickness between $\mathbb{S}$ and $\mathbb{F}$ sites (p=0.95) suggesting that most of the difference in M_a between the two vegetation types was attributable to a higher leaf density for $\mathbb{S}$. But, as noted above, with no adverse effects on photosynthetic nutrient use efficiencies.

4.3. The role of phosphorus

It has long been considered that vegetation differentiation in Australia is strongly influenced by edaphic constraints and specifically soil P status (Webb, 1968; Russell-Smith et al., 2004). The widely observed positive correlation leaf [N] ↔ [P] (e.g. Wright et al., 2001) is evident here as well (Figure 2a), but the slope of the relationship differed between $\mathbb{F}$ and $\mathbb{S}$. Despite their situation in the Atherton basalt province (Whitehead et al., 2007), the mean foliar N:P ratios for all of the sites visited in this study were far above thresholds believed to constitute P-deficiency (Townsend et al., 2007; Cernusak et al., 2010). This is particularly striking since the forests studied here, even after excluding the sub-canopy trees, had median $[\mathrm{N}]_{\mathrm{a}}$ of only 1.63 g m^{-2}. Such N levels are low compared to other tropical forests for which extensive data have recently become available - see Table 2 of Domingues et al. (2014). Values here are lower, for example, than Cameroon (2.12 g m^{-2}) and lower even than for trees growing on soils of low nutrient availability in the Amazon Basin (1.90 g m^{-2}). Foliar P levels, however, were lower still despite concentrations of total soil extractable P (P_{ex}) for our forest plots being relatively high (165-958 μg g^{-1}, Table 1). For what have been classed 'high nutrient' soils in the Amazon Basin, for example, Fyllas et al. (2009) reported median foliar P of 1.11 mg g^{-1} and 0.11 g m^{-2} with equivalent soil P_{ex} ranging from 52-422 μg g^{-1} (Quesada et al., 2010). In our study, however, upper canopy forest trees displayed median P values of only 0.76 mg g^{-1} and 0.08 g m^{-2}, much closer to Amazon forest trees growing on 'low nutrient status' soils for which soil P_{ex} ranges from 14-87 μg g^{-1} (Quesada et al., 2010) with foliar P median values of 0.7 mg g^{-1} and 0.06 g m^{-2}(Fyllas et al., 2009).

This apparent 'inability' of Australian forest trees to utilise high soil P availabilities could perhaps be related to their unique evolutionary history. Essentially of Gondwanan origin (Crisp et al., 1999), today's forests represent remnants of more temperate moist forests that covered much of the continent until the mid-Miocene (Adam, 1992). Presumably arising from a flora already adapted to the characteristically P-limited soils of much of Australia (McKenzie et al., 2004) it may be that many of the species occurring within the Australian tropical forest region suffer from an 'evolutionary hangover' lacking the ability to utilise high levels of soil P even where available. There is in addition, especially for the lowlands, a considerable Asia-derived element in the Australian tropical forest flora (Sniderman and Jordan, 2011; Crayn et al., 2014) and many soils of the Asian lowland tropical forest region are also of relatively low nutrient status (Acres et al., 1975; Tessins and Jusop, 1983; Ohta and Effendi, 1992; Banin et al., 2014). By comparison, despite the generally lower P status of the savanna soils (Table 1), the savanna trees in our study had a slightly higher median $[\mathrm{P}]_{\mathrm{a}}$ than those of the forest ($\mathbb{S}$ = 0.08 g m^{-2} and $\mathbb{F}$=0.06 g m^{-2}) and this was true also for $[\mathrm{N}]_{\mathrm{a}}$ ($\mathbb{S}$ = 2.09 g m^{-2} and $\mathbb{F}$=1.62 g m^{-2}). This finding for the Australian species contrasts with previous work in West Africa and Cameroon where area-based N and P concentrations were lower for savanna than for forest species (Domingues et al., 2014; Schrodt et al., 2014).

Despite these differences in area-based nutrient concentrations, there are notable consistencies between our results and the African studies mentioned above. First, albeit with different model constructs, there is clear evidence of a role for both N and P in the modulation of photosynthetic rates in the field. Second, other things being equal, it seems that savanna trees have higher N use efficiency than their forest counterparts. This higher A_{N} (Figure 4) may reflect differences in leaf construction linked to the higher light environment. Earlier studies have suggested that lower A_{N} values for sclerophytes may be caused by limitations to internal conductance caused by leaf structural factors linked to greater leaf longevity (e.g. Warren, 2008). Mesophyll conductance(g_{m}) is, however, the complex and variable product of at least three phases acting in series (Flexas et al., 2008): conductance through intercellular air spaces (g_{ias}), through cell walls (g_w) and through the liquid and membrane phases inside cells (g_{liq}). The most important constraint on g_m is thought to be g_{liq} which is the phase least affected by leaf structure.

Overall, our results suggest a complex effect of P on photosynthetic capacity for these Australian tree species. Foliar $[P]_a$ was only marginally significant in the preferred linear mixed effects model (Table 4), but its inclusion improved the overall predictive power. When examined on a mass basis, P did, however, appear more critical and with an N:P interaction term also included in the optimal model (Table S6). This mass- versus~~-~~ area-based inconsistency in the apparent importance of P as a modulator of photosynthetic rates was also noted by Domingues et al. (2014) who likewise found their mass-based models to include an N:P interaction term not present in the area-based version. The sudden appearance of apparently significant terms when transforming area-based entities to a mass basis is , however, to be expected (Lloyd et al., 2013).

4.4. Describing trait variation using plant functional types

Where possible in the $\mathbb{F}$ sites, tree species were selected in order to provide a contrast of light environment as described in the assigned categories of plant functional type (Φ). Such categorisation is often problematic and especially in the setting of boundaries from one group to another (e.g. Poorter, 1999). For Australian tropical moist forests, Webb developed a classification system of 20 structural vegetation types along climatic and edaphic gradients (1968). Faced with such complexity and subjectivity, many authors have instead argued for a spectrum of vegetation types or habits (e.g. Coste et al., 2005). The current study used Φ to attempt to explain residual patterns in the data after controlling for $\mathbb{V}$ (Figure 6b). As hypothesised, there was evidence that pioneer trees of the $\mathbb{F}$ showed higher photosynthetic capacity and nutrient use efficiency than those shade tolerant species which persist in the understory (Figure 4).

~~4.5.~~5. Conclusions

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Comparing tree species of neighbouring forest and savanna sites in far north Queensland, Australia we found higher photosynthetic capacity for savanna species linked to greater nitrogen use efficiency. Higher leaf mass per unit area for the savanna trees derived from greater leaf density rather than thickness, but did not inhibit photosynthetic capacity or A_N. Our mixed effects model accounted for 82% of variation in observed photosynthetic response and confirmed the importance of the $A \leftrightarrow N$ relationship. The model, whilst retaining leaf P as a key explanatory term, did not support the prediction of a dominant role for P rather than N in determining rates of photosynthesis for Australian tropical forest species.

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Table 1. Plot coordinates after Torello-Raventos et al. (2013), vegetation classification $\mathbb{V}$, elevation above sea level E_{V}, mean annual temperature T_{A}, mean annual precipitation P_{A}, 0.95 quantile upper stratum canopy height H^*, upper stratum canopy area index C_{U}, soil pH, soil exchangeable cations, soil extractable phosphorus and Wold Reference Base (WRB) soil classification for the study sites. Soil values represent the top 0.3 m of soil.

Plot	Lat.	Long.	$\mathbb{V}$	E_{V} (m)	T_{A} (°C)	P_{A} (m)	H^* (m)	C_{U} ($m^2\ m^{-2}$)	pH	$[\mathrm{Al}]_{\mathrm{e}}$	$[\mathrm{Ca}]_{\mathrm{ex}}$	$[\mathrm{K}]_{\mathrm{ex}}$	$[\mathrm{Mg}]_{\mathrm{ex}}$	$[\mathrm{Na}]_{\mathrm{ex}}$	$[\mathrm{P}]_{\mathrm{ex}}$	WRB Soil Classification
										$\mathrm{mmol_{eq}\ kg^{-1}}$					($\mu g\ g^{-1}$)	
CTC-01	16.103S	145.447E	Tall forest	90	25.2	3.20	38.9	2.36	5.56	0.48	17.94	0.71	7.65	0.65	208	Haplic Cambisol (Hyperdystric, Alumic, Skeletic)
KBL-01	17.764S	145.544E	Tall forest	761	20.5	1.75	38.0	1.45	4.79	0.27	4.71	0.35	2.58	0.36	952	Haplic Regosol (Siltic, Hyperdystric)
KBL-03	17.685S	145.535E	Tall forest	1055	19.1	1.34	35.8	2.30	4.38	4.84	0.90	0.47	1.82	0.62	227	Haplic Nitisol (Hyperdystric, Rhodic)
KCR-01	17.107S	145.604E	Tall forest	813	20.5	1.96	44.0	2.21	5.40	0.60	16.11	0.78	5.71	0.39	165	Haplic Cambisol (Dystric, Alumic)
DCR-01	17.026S	145.597E	Tall savanna woodland	683	21.2	1.45	26.2	1.63	5.65	0.90	8.78	0.71	6.93	0.71	79	Haplic Cambisol (Orthodystric, Alumic)
DCR-02	17.021S	145.584E	Tall savanna woodland	653	21.3	1.46	22.1	0.70	5.52	1.27	8.82	0.55	5.74	0.33	56	Arenic Cambisol (Epieutric)
KBL-02	17.849S	145.532E	Tall savanna woodland	860	20.1	1.43	28.1	0.77	5.28	0.26	4.78	0.17	7.66	0.77	216	Geric Acrisol (Hyperdystric, Rhodic)

Table 2: Coefficients for standardised major axis (SMA) bivariate relationships. Vegetation contrasts: forest and savanna; n, number of observations; r^2, correlation coefficient and associated *p*-value; Intercept; Slope and 95% confidence interval.

Response	Bivariate	Vegetation class	n	r^2	*p*	Intercept	Slope	Slope: Low 95% CI	Slope: High 95% CI
$[P]_a$ ↔	$[N]_a$	Forest	81	0.82	**<0.0001**	-11.01	47.92	43.58	52.68
		Savanna	24	0.51	**<0.0001**	-70.96	75.86	55.87	102.99
$[P]_m$ ↔	$[N]_m$	All	105	0.81	**<0.0001**	-0.097	0.046	0.042	0.050
$[N]_a$ ↔	M_a	Forest	81	0.43	**<0.0001**	0.299	0.018	0.015	0.021
		Savanna	24	0.08	0.1848				
$[P]_a$ ↔	M_a	Forest	81	0.38	**<0.0001**	3.31	0.84	0.71	1.00
		Savanna	24	0.00	0.8207				
$A_{max,a}$ ↔	$[N]_a$	Forest	81	0.47	**<0.0001**	-11.43	17.01	14.46	20.00
		Savanna	24	0.17	**0.0442**	-54.48	42.15	28.47	62.40
$A_{max,a}$ ↔	$[P]_a$	Forest	81	0.47	**<0.0001**	-7.52	0.35	0.30	0.42
		Savanna	24	0.09	0.1522				
$A_{max,a}$ ↔	M_a	All	105	0.30	**<0.0001**	-6.03	0.29	0.25	0.34
$A_{max,m}$ ↔	$[N]_m$	Forest	81	0.63	**<0.0001**	-192.81	18.47	16.12	21.16
		Savanna	24	0.31	**0.0049**	-100.47	21.87	15.26	31.35
$A_{max,m}$ ↔	$[P]_m$	Forest	81	0.61	**<0.0001**	-148.85	404.67	352.06	465.15
		Savanna	24	0.30	**0.0061**	-14.60	394.68	274.50	567.47
$A_{max,m}$ ↔	M_a	Forest	81	0.08	**0.0132**	607.15	-4.95	-6.13	-4.00
		Savanna	24	0.30	**0.0056**	628.00	-2.73	-3.93	-1.90
$DM:H_2O$ ↔	M_a	Forest	85	0.40	**<0.0001**	-0.063	0.009	0.007	0.010
		Savanna	24	0.30	**0.0056**	0.086	0.005	0.003	0.007
d ↔	M_a	Forest	82	0.26	**<0.0001**	107.77	3.91	3.23	4.72
		Savanna	24	0.74	**<0.0001**	152.77	1.86	1.48	2.32
ρ ↔	M_a	Forest	82	0.45	**<0.0001**	0.040	0.0020	0.0017	0.0024
		Savanna	24	0.66	**<0.0001**	0.141	0.0014	0.0011	0.0018
A_N ⍰ ↔	M_a	Forest	81	0.00	0.6122				
		Savanna	24	0.00	0.9268				

Table 3. Stepwise selection process for the fixed component of the linear mixed effect model: photosynthetic capacity ($A_{max,a}$) as response variable. Categorical variable Б has two levels: forest and savanna for the contrasting vegetation types. Continuous explanatory variables are $[N]_a$, $[P]_a$, leaf mass per unit area (M_a), leaf dry matter content (ξ) and leaf thickness (d). The effect of dropping sequential terms was tested by comparing the nested model variants. Model variants were all run using the Maximum Likelihood method; the models' random component was identical in all variants. Test parameters and statistics are df, degrees of freedom; AIC, Akaike information criteria; BIC, Bayesian information criteria; logLik, Maximum Likelihood; the Likelihood Ratio statistic and associated p-value. Models with the same degrees of freedom are not nested one in the other.

Model	Fixed component	df	AIC	BIC	logLik	Test	L.Ratio	p-value
1	Б + $[N]_a$ + $[P]_a$ + M_a + d + ξ	11	735.51	765.12	- 356.76			
2	Б + $[N]_a$ + $[P]_a$ + M_a + d	10	733.52	760.44	- 356.76	*1 vs 2*	0.011	0.915
3	Б + $[N]_a$ + $[P]_a$ + M_a	9	731.94	756.16	- 356.97	*2 vs 3*	0.417	0.519
4	Б + $[N]_a$ + $[P]_a$	8	730.58	752.11	- 357.29	*3 vs 4*	0.640	0.424
5	Б + $[N]_a$	7	732.96	751.80	- 359.48	*4 vs 5*	4.383	**0.036**
6	$[N]_a$ + $[P]_a$	7	738.39	757.23	- 362.20	*4 vs 6*	9.814	**0.002**
7	$[N]_a$ + $[P]_a$ + M_a + d + ξ	10	742.94	769.86	- 361.47	*1 vs 7*	9.432	**0.002**
8	Б + $[N]_a$ + $[P]_a$ + Б:$[N]_a$ + Б:$[P]_a$ + $[N]_a$:$[P]_a$ + Б:$[N]_a$:$[P]_a$	12	734.73	767.02	- 355.36	*4 vs 8*	3.852	0.426
9	Б + $[N]_a$ + $[P]_a$ + Б:$[N]_a$ + Б:$[P]_a$	10	733.15	760.07	- 356.58	*7 vs 9*	2.426	0.297
10	Б + $[N]_a$ + $[P]_a$ + Б:$[N]_a$	9	731.37	755.59	- 356.68	*8 vs 10*	0.213	0.645
11	Б + $[N]_a$ + $[P]_a$ + Б:$[P]_a$	9	731.49	755.71	- 356.75	*8 vs 11*	0.339	0.561
12	Б + $[N]_a$ + $[P]_a$ + $[N]_a$:$[P]_a$	9	732.53	756.75	- 357.26	*4 vs 12*	0.050	0.823

Table 4. Output of the linear mixed effects model (Eq. 2): fixed effects (top) and random effects (bottom). The top section shows fixed effect parameter estimates and associated standard error, degrees of freedom, test statistic and associated *p*-value. The final 'optimal' model is compared against a simpler 'null' model that includes only vegetation type (Б) in the fixed component, but has an identical random term of Species nested within Site. Continuous explanatory variables were centred on their respective means (i.e. zero re-set to the trait average).

		Final model					**Null model**				
Fixed effect		Estimate	S.E.	DF	t value	*p value*	Estimate	S.E.	DF	t value	*p value*
Forest (if other variables were zero)		18.06	1.57	73	11.537	**<0.0001**	17.08	2.47	75	6.925	**<0.0001**
Savanna (Vegetation contrast)	β_1	11.18	3.08	5	2.076	**0.0151**	14.15	4.54	5	3.119	**0.0263**
Leaf[N]$_a$	β_2	6.66	2.07	73	3.472	**0.0020**					
Leaf[P]$_a$	β_3	0.07	0.03	73	1.618	0.0502					
Random effect		Variance	% of total				Variance	% of total			
Intercept variance: Among sites	a_k	3.56	9.4%				12.06	13.9%			
Intercept variance: Among species	$a_{j\|k}$	26.77	70.8%				66.39	76.2%			
Residual (within species, within sites)	ε_{ijk}	7.49	19.8%				8.64	9.9%			
		37.82	100.0%				87.10	100.0%			
AIC				726.7					746.5		
Likelihood ratio test				-355.4					-367.2		

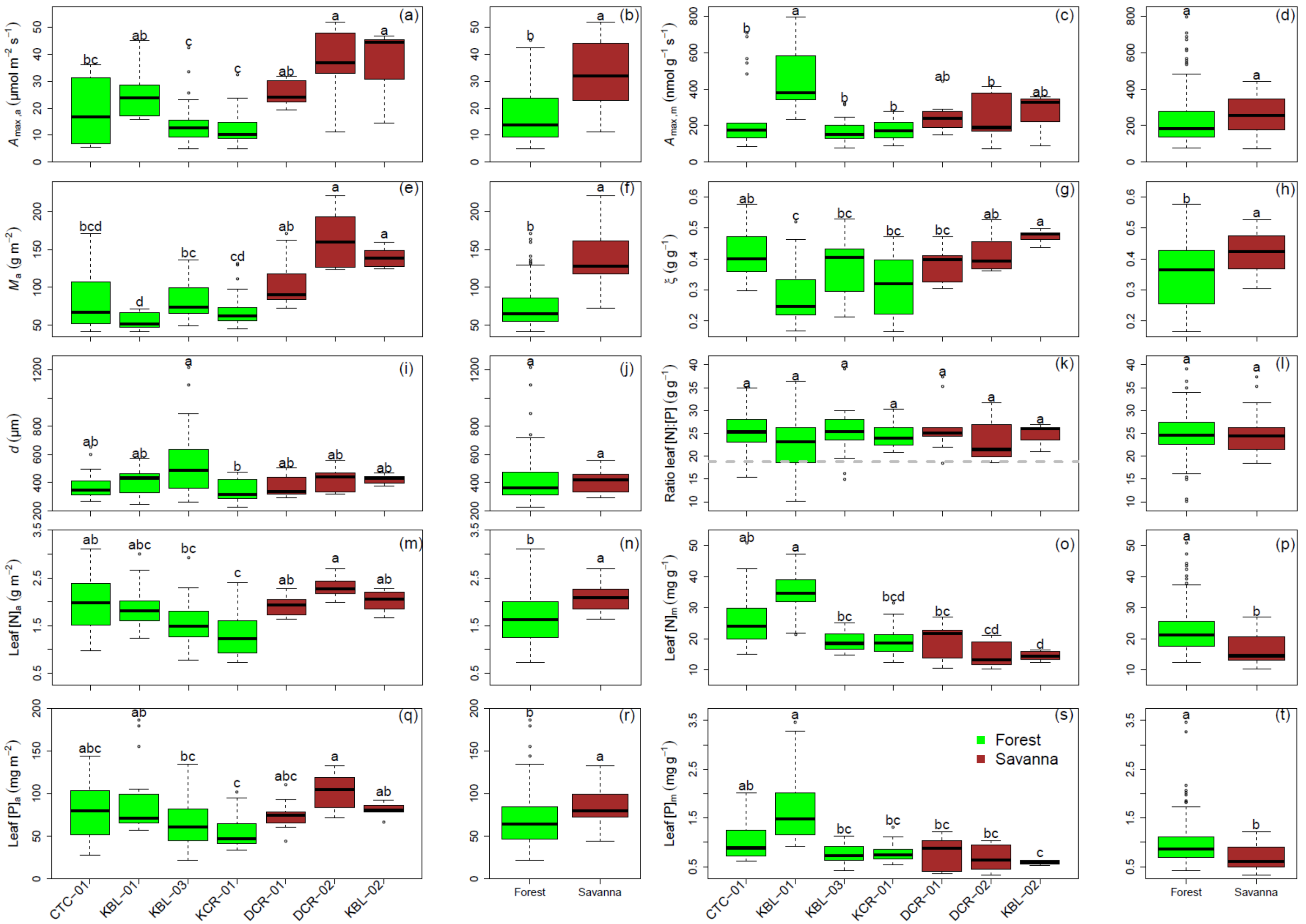

Figure 1 Paired boxplots of key leaf traits (untransformed data) by site and vegetation type (𝕍). The two 𝕍 classes are distinguished by colour: green for forest and brown for savanna. Site abbreviations are laid out in Table 1. Leaf traits are photosynthetic capacity (a,b) per unit leaf area and (c,d) per unit leaf dried mass; (e,f) leaf mass per unit area; (g,h) leaf dried matter content; (i,j) leaf thickness; (k,l) ratio of total leaf nitrogen to phosphorus; total leaf nitrogen (m,n) per unit leaf area and (o,p) per unit leaf dried mass; total leaf phosphorus (q,r) per unit leaf area and (s,t) per unit leaf dried mass. The box and whiskers show the median result as a thick horizontal band, the ends of the box denote the inter-quartile range; the whiskers extend 1.5 times the inter-quartile range or to the most extreme value, whichever is smaller; any points outside these values are shown as outliers. The grey dashed line in plot k represents a mean N:P ratio of 18.8 reported for tropical forests by Reich et al. (2009).

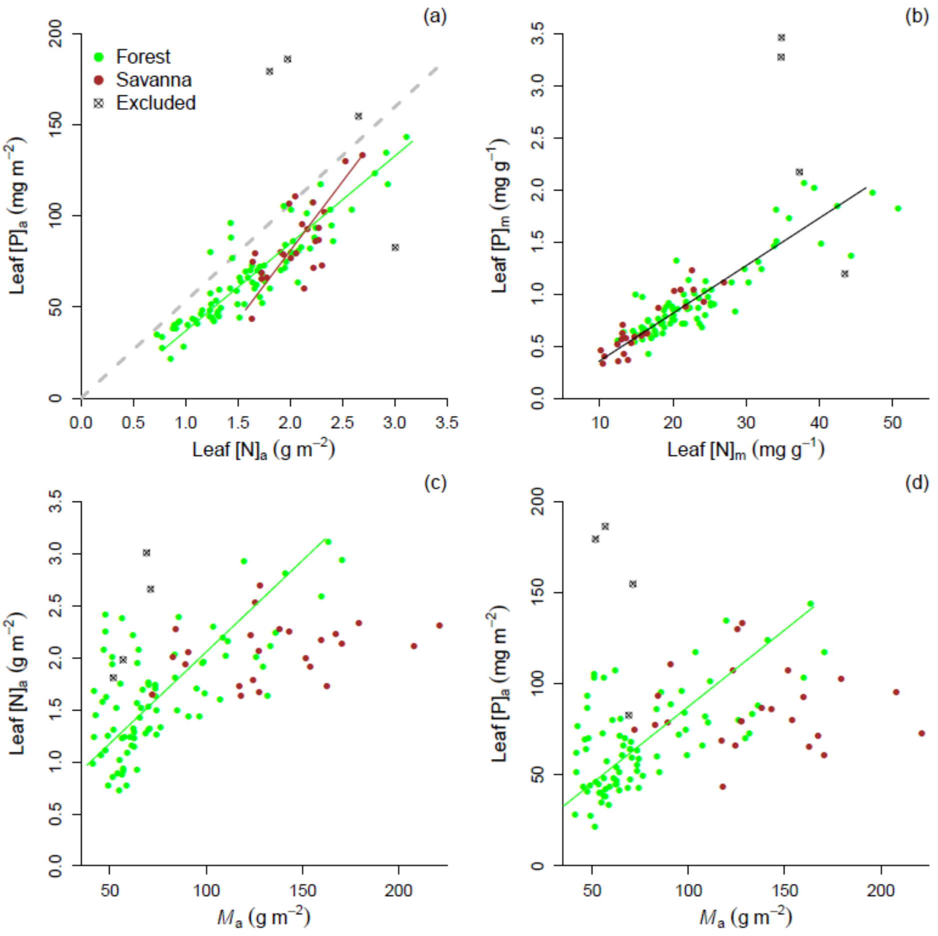

Figure 2. Scatterplots of the relationships between leaf phosphorus and leaf nitrogen (a) on an area basis and (b) on a mass basis. Plot (c) shows the relationship between leaf nitrogen on an area basis and leaf mass per unit area; plot (d) shows the equivalent relationship for leaf phosphorus. Each point corresponds to a single tree and vegetation types are distinguished by colour: green for *F* and brown for *S*. Standardised major axis (SMA) fitted lines are shown for the two vegetation types only where the bivariate relationship proved significant $p < 0.05$. Pearson's correlations testing the assumption of linearity are given at Table S4 (Supplementary Information) together with Likelihood ratio and Wald statistics testing the H_0 of common slope, elevation and axis shift for the two *V* classes. Intercept, slope and r^2 values for the SMA fitted lines are given in Table 2. In plot (a) a third fitted line (grey, dashed) displays a slope based on a mean N:P ratio of 18.8 typical for tropical forests as reported by Reich et al. (2009) and passing through the origin. In plot (b) there was a common slope to the $[P]_m \leftrightarrow [N]_m$ relationship for both vegetation types (black line). In reviewing residual plots of initial SMA fits (not shown), four data points were identified as outliers (crossed circles). The four outliers have been excluded from the re-run SMA fits shown here.

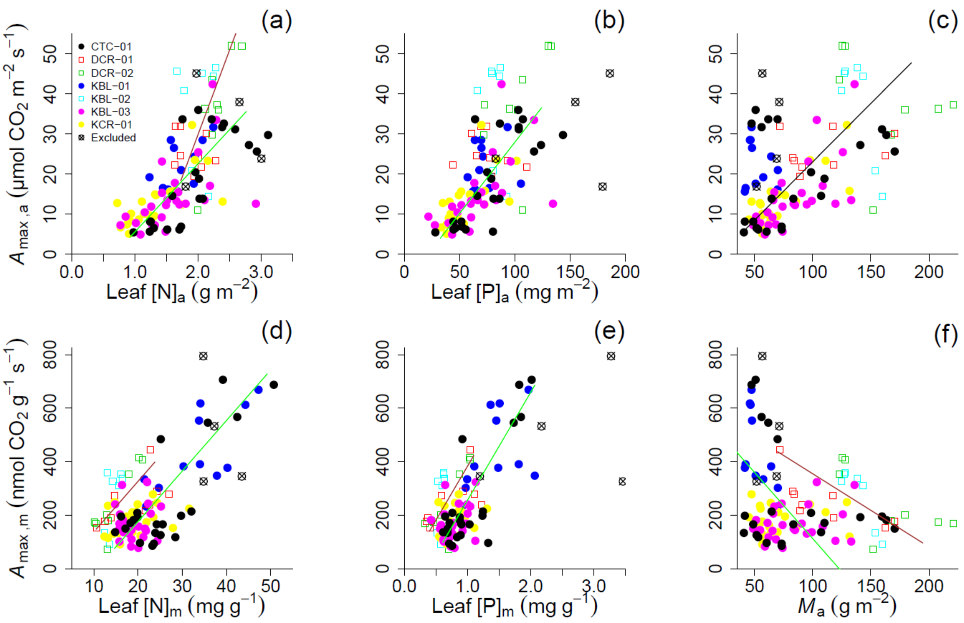

Figure 3. Top panel (plots a, b and c), scatterplots of the area-based relationships between photosynthetic capacity ($A_{\mathrm{max,a}}$) and (a) leaf nitrogen; (b) leaf phosphorus; (c) leaf mass per unit area (M_a). Bottom panel (plots d, e and f) the equivalent plots are expressed per unit leaf dried mass. Each point represents a single leaf; dots denote $\mathbb{F}$ sites and square symbols denote $\mathbb{S}$ sites; individual sites are distinguished by colour: CTC-01 black, DCR-01 red, DCR-02 green, KBL-01 royal blue, KBL-02 turquoise, KBL-03 pink, KCR-01 yellow. Standardised major axis (SMA) fitted lines are shown where significant: $\mathbb{F}$ (green), $\mathbb{S}$ (brown). Pearson's correlations testing the assumption of linearity are given at Table S4 (Supplementary Information) together with Likelihood ratio and Wald statistics testing the H_0 of common slope, elevation and axis shift for the two $\mathbb{V}$ classes. In plot (c) there was no difference in slope between the two $\mathbb{V}$ and so a common line is fitted (black). SMA intercept, slope and r^2 values are given in Table 2.

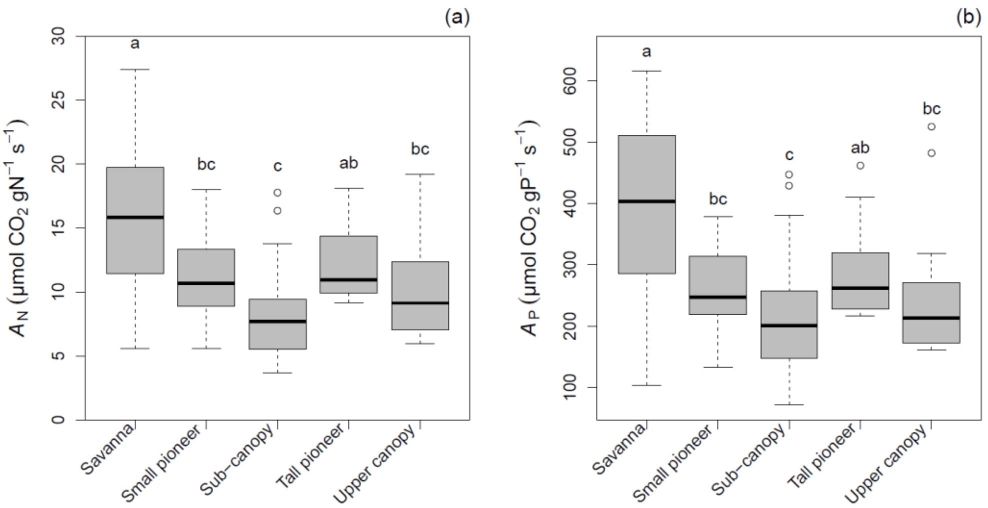

Figure 4. Boxplots of photosynthetic N use efficiency (A_N) and P use efficiency (A_P) by *Φ*. Boxes which share the same letter correspond to means that were not significantly different (Tukey's HSD on ranked values). Boxplot construction is explained in Figure 1.

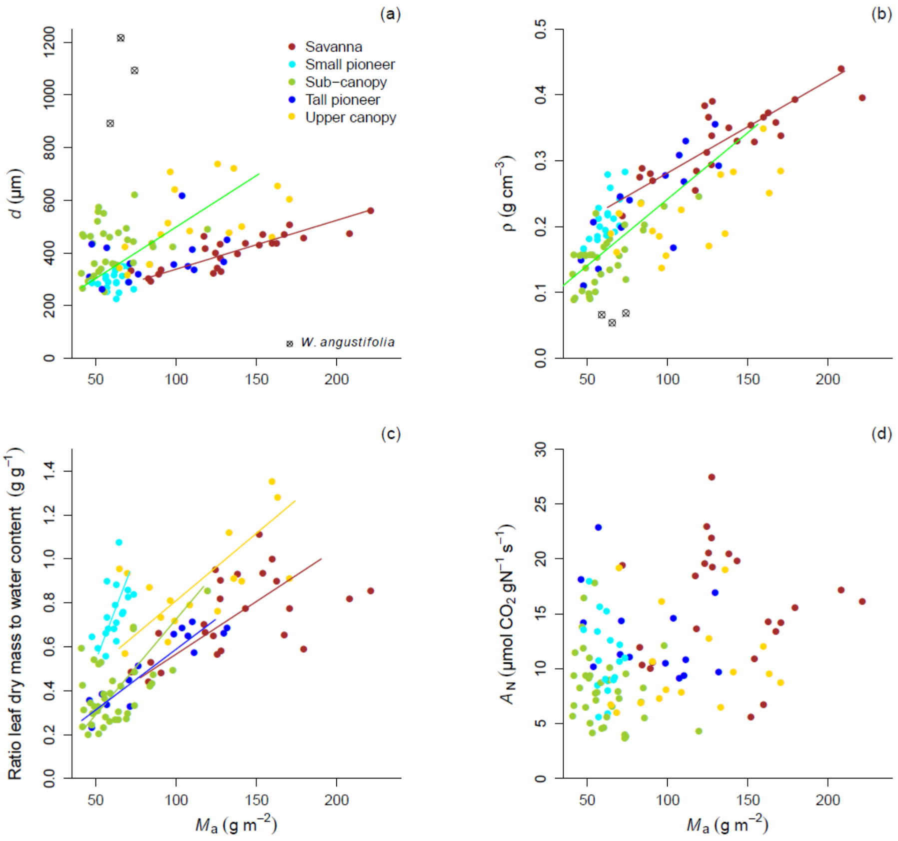

Figure 5: Scatterplots of the relationship with leaf mass per unit area for each of (a) leaf thickness (measured fresh), (b) leaf density (derived as M_a/d), (c) the ratio of leaf dry mass to water content and (d) photosynthetic N use efficiency. Each point represents one tree and separate Φ are distinguished by colour. Standardised major axis (SMA) fitted lines are shown in the top panel for the two vegetation types: $\mathbb{F}$ in green and $\mathbb{S}$ in brown. Outlying values for *Wilkiea angustifolia* (crossed circles) were excluded from the SMA analyses of plots (a) and (b). In plot (c) a separate fitted line is shown for each Φ. Pearson's correlations testing the assumption of linearity are given at Table S4 (Supplementary Information) together with Likelihood ratio and Wald statistics testing the H_0 of common slope, elevation and axis shift for the two $\mathbb{V}$ classes. SMA intercept, slope and r^2 values are given in Table 2. There was no relationship $A_N \leftrightarrow M_a$ for individual levels of $\mathbb{V}$ or Φ.

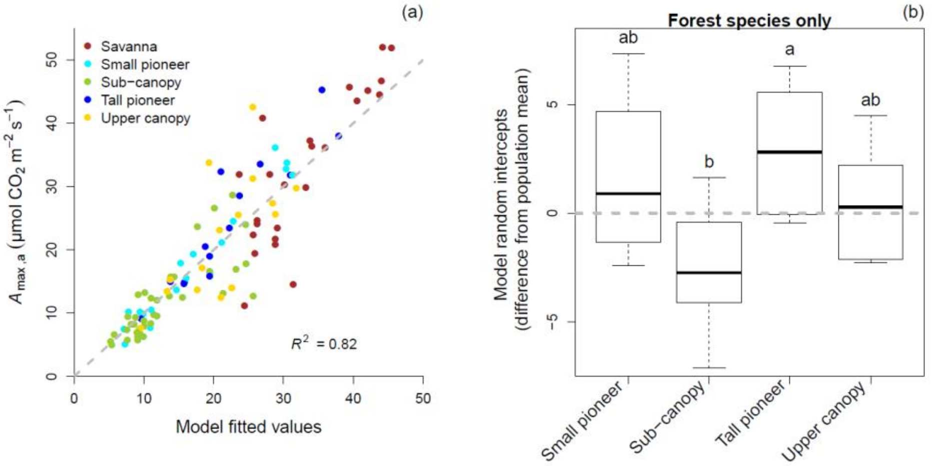

Figure 6. Output from linear mixed effects model (Eq. 2): (a) scatterplot of observed photosynthetic capacity ($A_{\text{max,a}}$) against the model fitted values as an indication of goodness of fit and (b) boxplot of model random intercepts ($A_{\text{max,a}} \leftrightarrow [\text{N}]_{\text{a}}$) by Φ for the $\mathbb{F}$ subset; boxes which share the same letter correspond to means that were not significantly different (Tukey's HSD on ranked values). Boxplot construction is explained in Figure 1.

Supplementary

Table S1. List of species measured with Site code (Table 1) and Φ (Table S2) for the tropical moist forest species.

Site	Type	*Species*	Φ (forest species)	*n*
KBL-01	Forest	*Alangium villosum*	Sub-canopy	4
KBL-01	Forest	*Aleurites rockinghamensis*	Tall pioneer	4
KBL-03	Forest	*Apodytes brachystylis*	Sub-canopy	4
KCR-01	Forest	*Ardisia brevipedata*	Sub-canopy	4
CTC-01	Forest	*Argyrodendron peralatum*	Upper canopy	4
KBL-03	Forest	*Beilschmiedia tooram*	Upper canopy	1
CTC-01	Forest	*Cardwellia sublimis*	Tall pioneer	4
KCR-01	Forest	*Cardwellia sublimis*	Tall pioneer	5
KBL-01	Forest	*Castanospora alphandii*	Upper canopy	1
CTC-01	Forest	*Cleistanthus myrianthus*	Upper canopy	3
DCR-02	Savanna	*Corymbia citriodora*		3
DCR-02	Savanna	*Corymbia clarksoniana*		3
DCR-01	Savanna	*Corymbia intermedia*		1
KBL-02	Savanna	*Corymbia intermedia*		4
KBL-01	Forest	*Elaeocarpus grandis*	Tall pioneer	1
KBL-03	Forest	*Elaeocarpus largiflorens*	Upper canopy	4
DCR-02	Savanna	*Eucalyptus portuensis*		4
KCR-01	Forest	*Eupomatia laurina*	Sub-canopy	5
CTC-01	Forest	*Haplostichanthus ramiflorus*	Sub-canopy	4
KBL-03	Forest	*Litsea leefeana*	Tall pioneer	1
DCR-01	Savanna	*Lophostemon suaveolens*		3
KBL-02	Savanna	*Lophostemon suaveolens*		4
CTC-01	Forest	*Mallotus mollissimus*	Small pioneer	4
KBL-01	Forest	*Neisosperma poweri*	Sub-canopy	4
KBL-01	Forest	*Neolitsea dealbata*	Small pioneer	4
KBL-03	Forest	*Neolitsea dealbata*	Small pioneer	4
KCR-01	Forest	*Neolitsea dealbata*	Small pioneer	6
DCR-01	Savanna	*Planchonia careya*		6
KCR-01	Forest	*Polyscias elegans*	Tall pioneer	4
CTC-01	Forest	*Pseuduvaria froggattii*	Sub-canopy	4
KBL-03	Forest	*Sloanea australis*	Upper canopy	4
KBL-03	Forest	*Symplocos hayesii*	Sub-canopy	4
KBL-03	Forest	*Synima cordierorum*	Sub-canopy	1
KCR-01	Forest	*Toechima erythrocarpum*	Sub-canopy	4
KBL-03	Forest	*Wilkiea angustifolia*	Sub-canopy	5
		Total number of $A \leftrightarrow C_i$ curves		**125**
		Number of Site + Species combinations with replicates ≥ 3		**28**

Table S2. Plant functional type (*Φ*) assigned to the forest species. The classification assigned to each species is based on light requirement and adult stature.

Plant functional type (*Φ*)	**Description**
Small pioneer	Small stature pioneer, light demanding
Sub-canopy	Sub canopy, shade tolerant
Tall pioneer	Tall pioneer, light demanding
Upper-canopy	Upper canopy, shade tolerant, but well adapted to sunlit conditions

Table S3: Kendall’s rank-order (tau, τ) correlations between site variables (elevation above sea level E_V, mean annual temperature T_A, mean annual precipitation P_A, soil pH, soil exchangeable cations, soil extractable phosphorus) and selected leaf traits (photosynthetic capacity, levels of nitrogen and phosphorus – all on an area basis). Soil values represent the top 0.3 m of soil horizon.

	$A_{max,a}$		Leaf $[N]_a$		Leaf $[P]_a$	
Site variable	Kendall's τ	*p* value	Kendall's τ	*p* value	Kendall's τ	*p* value
E_v (m)	**-0.197**	**0.0027**	**-0.241**	**0.0002**	**-0.199**	**0.0025**
T_A (°C)	**0.144**	**0.0318**	**0.212**	**0.0016**	**0.163**	**0.0155**
P_A (m)	0.064	0.3295	0.022	0.7404	-0.004	0.9490
pH	0.111	0.0914	0.166	0.0114	0.098	0.1362
$[Al]_e$ (mmol$_{eq}$ kg^{-1})	**-0.214**	**0.0011**	**-0.132**	**0.0442**	**-0.137**	**0.0378**
$[Ca]_e$ (mmol$_{eq}$ kg^{-1})	-0.010	0.8761	0.073	0.2690	0.014	0.8324
$[K]_e$ (mmol$_{eq}$ kg^{-1})	**-0.245**	**0.0002**	**-0.159**	**0.0169**	**-0.200**	**0.0027**
$[Mg]_e$ (mmol$_{eq}$ kg^{-1})	**0.206**	**0.0017**	**0.211**	**0.0013**	**0.148**	**0.0246**
$[Na]_e$ (mmol$_{eq}$ kg^{-1})	0.005	0.9432	0.048	0.4640	-0.029	0.6550
CEC (mmol$_{eq}$ kg^{-1})	-0.022	0.7418	-0.029	0.6656	-0.004	0.9590
$[P]_{ex}$ (μg g^{-1})	0.087	0.1845	0.013	0.8431	0.044	0.5024

Table S4. Results of standardised major axis (SMA) bivariate relationships testing the null hypothesis that there was no difference between Forest and Savanna trees in slope (LR, Likelihood ratio statistic), intercept or axis shift (Wald statistic). For each bivariate relationship the assumption of linearity, for the dataset as a whole, was tested using Pearson's correlation (r). The dataset here excludes the four outlying points identified on Figure 2a.

		Test for linear relationship			Significance of difference between Vegetation classes in					
					Slope		Elevation		Shift	
Response	Bivariate	df	r	*p*	LR	*p*	Wald	*p*	Wald	*p*
$[P]_a \leftrightarrow$	$[N]_a$	103	0.89	**<0.0001**	7.58	**0.0059**	NA	NA	NA	NA
$[P]_m \leftrightarrow$	$[N]_m$	103	0.90	**<0.0001**	3.41	0.0646	3.74	0.053	19.10	**<0.0001**
$[N]_a \leftrightarrow$	M_a	103	0.63	**<0.0001**	13.83	**0.0002**	NA	NA	NA	NA
$[P]_a \leftrightarrow$	M_a	103	0.53	**<0.0001**	3.08	0.0794	10.00	**0.002**	45.74	**<0.0001**
$A_{max,a} \leftrightarrow$	$[N]_a$	103	0.67	**<0.0001**	16.09	**<0.0001**	NA	NA	NA	NA
$A_{max,a} \leftrightarrow$	$[P]_a$	103	0.63	**<0.0001**	3.98	**0.0459**	NA	NA	NA	NA
$A_{max,a} \leftrightarrow$	M_a	103	0.55	**<0.0001**	0.02	0.8805	0.19	0.659	63.41	**<0.0001**
$A_{max,m} \leftrightarrow$	$[N]_m$	103	0.69	**<0.0001**	0.77	0.3809	40.36	**<0.0001**	4.33	**0.037**
$A_{max,m} \leftrightarrow$	$[P]_m$	103	0.70	**<0.0001**	0.02	0.8976	26.28	**<0.0001**	2.40	0.121
$A_{max,m} \leftrightarrow$	M_a	107	-0.23	0.017	7.53	**0.0061**	NA	**NA**	NA	NA
$DM:H_2O \leftrightarrow$	M_a	107	0.62	**<0.0001**	7.84	**0.0051**	NA	NA	NA	NA
$d \leftrightarrow$	M_a	107	0.24	**0.0113**	21.52	**<0.0001**	NA	NA	NA	NA
$\rho \leftrightarrow$	M_a	104	0.82	**<0.0001**	5.58	**0.0181**	NA	NA	NA	NA
$A_N \leftrightarrow$	M_a	103	0.34	**0.0004**	0.24	0.6249	0.86	0.353	58.44	**<0.0001**

Table S5 Kendall's rank-order (tau, τ) correlations between site variables (elevation above sea level E_V, mean annual temperature T_A, mean annual precipitation P_A, soil pH, soil exchangeable cations, soil extractable phosphorus) and standardised residual terms from the preferred mixed effects model (Eq. 2, Table 4). Soil values represent the top 0.3 m of soil horizon.

Site variable	Kendall's τ	*p* value
E_v (m)	0.002	0.974
T_A (°C)	-0.011	0.877
P_A (m)	-0.009	0.894
pH	-0.042	0.550
$[Al]_e$ ($mmol_{eq}$ kg^{-1})	-0.053	0.446
$[Ca]_e$ ($mmol_{eq}$ kg^{-1})	-0.018	0.794
$[K]_e$ ($mmol_{eq}$ kg^{-1})	-0.087	0.221
$[Mg]_e$ ($mmol_{eq}$ kg^{-1})	0.003	0.966
$[Na]_e$ ($mmol_{eq}$ kg^{-1})	-0.065	0.354
CEC ($mmol_{eq}$ kg^{-1})	-0.051	0.462
$[P]_{ex}$ (µg g^{-1})	0.051	0.465

Table S6: Output of a comparative linear mixed effects model (after Eq. 2) with leaf traits expressed on a mass basis: fixed effects (top) and random effects (bottom). The top section shows fixed effect parameter estimates and associated standard error, degrees of freedom, test statistic and associated *p*-value. The final 'optimal' model is compared against a simpler 'null' model that includes only vegetation class (*V*) in the fixed component, but has an identical random term of Species nested within Site. Continuous explanatory variables were centred on their respective means.

	Final model					**Null model**				
Fixed effect	Estimate	S.E.	DF	t value	*p value*	Estimate	S.E.	DF	t value	*p value*
Forest (with other variables at mean value)	210.04	14.81	71	14.181	**<0.0001**	262.78	55.87	74	4.703	**<0.0001**
Savanna (Vegetation contrast)	86.35	28.33	5	3.048	**0.0285**	-30.96	90.58	5	-0.342	0.7464
Leaf[N]$_m$	6.95	2.14	71	3.252	**0.0018**					
Leaf[P]$_m$	104.52	43.46	71	2.405	**0.0188**					
Leaf[N]$_m$: Leaf[P]$_m$	5.95	2.71	71	2.198	**0.0312**					
Random effect	Variance	% of total				Variance	% of total			
Intercept variance: Among sites	0	0.0%				10,328	38.8%			
Intercept variance: Among species	2,513	32.4%				11,645	43.8%			
Residual (within species, within sites)	5,251	67.6%				4,627	17.4%			
	7,763	100.0%				26,600	100.0%			
AIC			1,228					1,275		
Likelihood ratio test			-606					-632		

Figure S1. Kernel density plot showing smoothed probability distributions of leaf mass per unit area (g m^{-2}) for each plant functional type.

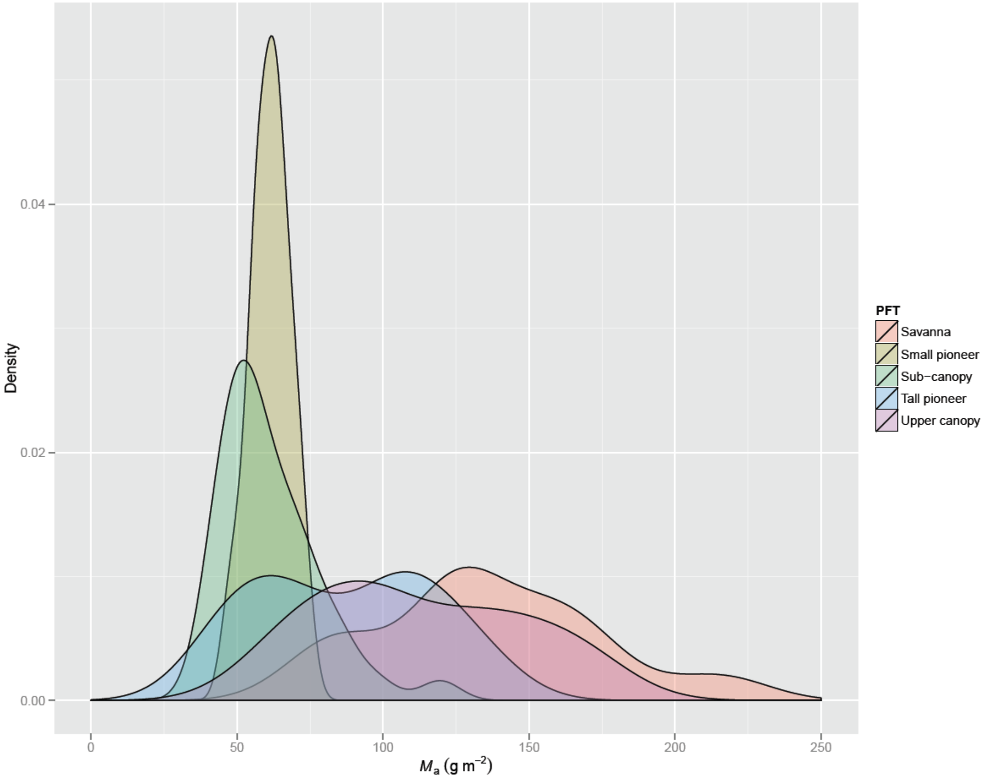

Figure S2. Pair-wise plot of response and explanatory variables. The upper panel contains estimated pair-wise correlations and the font size is proportional to the absolute value of the estimated correlation coefficient. Significance codes: *** <0.001, ** <0.01, * <0.05, . <0.01. The diagonal panel contains histograms and the lower panel scatterplots with a local regression smoother added to aid visual interpretation. The selected variables are photosynthetic capacity on an area basis as response with six continuous explanatory variables (spanning leaf morphology and nutrient levels). Trait units are $A_{\mathrm{max,a}}$ (µmol CO_2 m^{-2} s^{-1}), Maximum conductance (mol m^{-2} s^{-1}), Leaf mass per unit area (g m^{-2}), Leaf dry matter content (g g^{-1}), Leaf thickness (µm), Total leaf nitrogen per unit area (g m^{-2}), Total leaf phosphorus per unit area (mg m^{-2}).

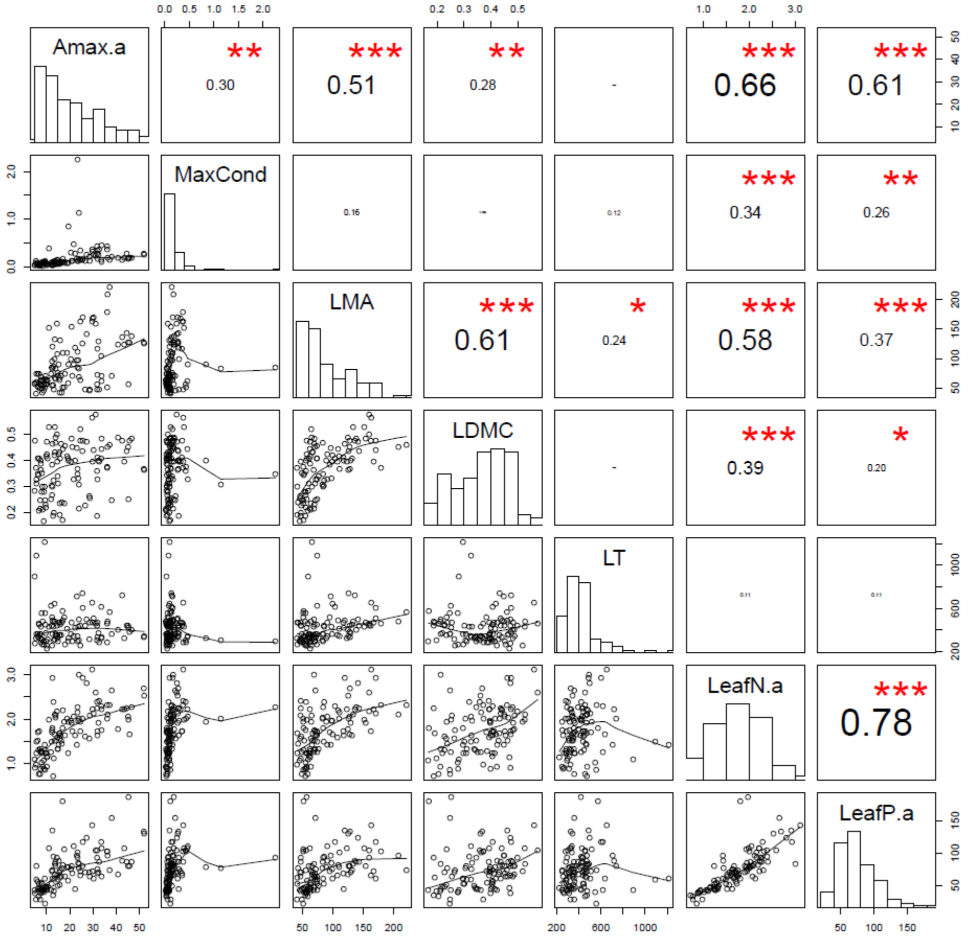

Figure S3: Model validation graphs for the random intercept mixed effects model (Eq. 2). Standardised residuals are plotted against fitted values and each of the explanatory factors and variables used in the model's fixed component.

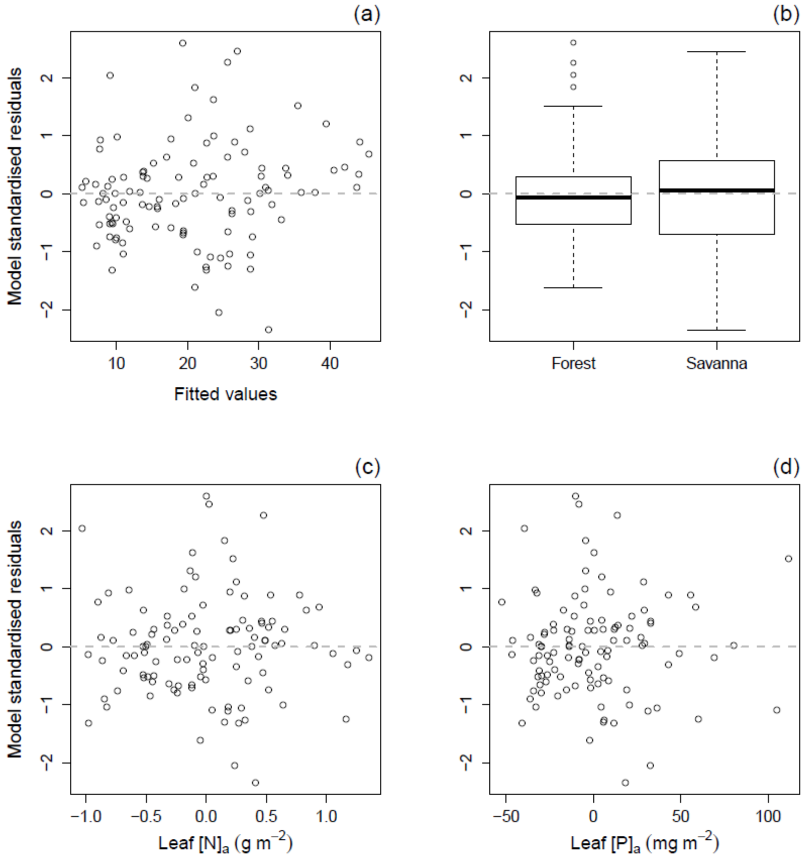

Figure S4 Scatterplots of model standardised residuals (Eq. 2, Table 4) and selected site variables of elevation, temperature and soil conditions. Corresponding Kendall's rank-order (tau, τ) correlations are shown in Table S5.