Biome-specific effects of nitrogen and phosphorus on the photosynthetic characteristics of trees at a forest-savanna boundary in Cameroon

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Abstract  Photosynthesis/nutrient relationships of proximally growing forest and savanna trees were determined in an ecotonal region of Cameroon (Africa). Although area-based foliar N concentrations were typically lower for savanna trees, there was no difference in photosynthetic rates between the two vegetation formation types. Opposite to N, area-based P concentrations were—on average—slightly lower for forest trees; a dependency of photosynthetic characteristics on foliar P was only evident for savanna trees. Thus savanna trees use N more efficiently than their forest counterparts, but only in the presence of relatively high foliar P. Along with some other recent studies, these results suggest that both N and P are important modulators of woody tropical plant photosynthetic capacities, influencing photosynthetic metabolism in different ways that are also biome specific. Attempts to find simple unifying equations to describe woody tropical vegetation photosynthesis-nutrient relationships are likely to meet with failure, with ecophysiological distinctions between forest and savanna requiring acknowledgement.

Keywords  Tropical rain forest · Nutrient · Global change · Terrestrial productivity · Photosynthesis
Introduction

Forests and savannas are the dominant vegetation types of tropical regions (Walter and Mueller-Dombois 1971) and differ fundamentally in their structural characteristics and species composition (Torello-Raventos et al. 2013). Tree species associated with forest vs. savanna differ in numerous physiological characteristics, such as fire survivorship (Hoffmann et al. 2009; Ratnam et al. 2011), as well as in their wood and foliar characteristics (Gotsch et al. 2010; Hoffmann et al. 2005; Rossatto et al. 2013; Schrodt et al. 2014). We have, however, an incomplete knowledge on how the species differ in photosynthesis characteristics, especially in relation to nutrient availability. Although it does now seem clear that although tropical forests are more productive and comprise larger C stocks than tropical savannas, they tend to have lower maximum photosynthetic C assimilation rates per area of leaf area (Bloomfield et al. 2014; Domingues et al. 2010; Hoffmann et al. 2005; Rossatto et al. 2013).

Although it is well established that photosynthetic capacity can be modulated by leaf N concentrations (Evans 1989; Field and Mooney 1986), in the tropics, where soils are often old and weathered, P limitation may be more typical (Reich and Oleksyn 2004; Reich et al. 2009), with links to stand-level productivity (Mercado et al. 2011; Quesada et al. 2012). On the basis of several lines of evidence, it has, however, also been suggested that, in contrast to tropical forests, savannas may be more likely to be limited by N than P (Lloyd et al. 2009).

Materials and methods

Study location

Measurements were made during the end of the 2007 wet season (October/December) at the Mbam–Djerem National Park, central Cameroon (Electronic Supplementary Material Fig. S1). The area encompasses a transitional zone between the Guinea–Congo/Sudan formations (Maisels 2004; White 1983) where savannas co-exist with tall canopy forest and gallery forest in a mosaic characterised by relatively sharp boundaries (Mitchard et al. 2009). Mean annual precipitation is estimated at about 1.6 m year$^{-1}$ (Hijmans et al. 2005).

Study plots

Measurements were made in seven permanent 1-ha plots chosen to contain three vegetation groupings recognizable on the basis of structure and species composition, as classified by Torello-Raventos et al. (2013), viz.: (1) ‘long-grass savanna woodland’ (three plots; MDJ-02, MDJ-04 and MDJ-08); (2) three plots within the broad ‘forest’ groupings (MDJ-01, MDJ-03 and MDJ-07); and finally, (3) ‘transitional forest’ as represented by a single plot (MDJ-05). This plot was once savanna, but has recently been invaded by forest species as described for our study area (Mitchard et al. 2011). For the interested reader, photographs of this site as well as MDJ-04 (long-grass savanna) and the forested MDJ-01 and MDJ-03 are provided in Fig. 6 of Torello-Raventos et al. (2013).

Site characterisation

Biodiversity indices and measurements of plot structure were determined as detailed in Torello-Raventos et al. (2013). Soil sampling and associated measurements were made as described in Quesada et al. (2010) and Veenendaal et al. (2014).
Gas exchange characteristics

Sampling leaves on excised upper canopy branches with the assistance of a tree climber, data were obtained from 196 leaves fully exposed to the sun sampled from 69 individuals representing 42 species of adult perennial C3 trees and shrubs. Within each plot the quantitatively dominant species were selected, and measurements made for photosynthetic capacity using a LI-COR-6400 portable photosynthesis system (A–Ci curves at high photon irradiance), leaf nutrients and leaf mass per unit area (Mf). Methodological details follow Domingues et al. (2010), with a simple modification introduced for the estimation of the two key photosynthetic capacity parameters (Vcmax, the maximum rate of carboxylation and Jmax, the maximum rate of electron transport) optionally incorporating a mesophyll conductance term (g m) into the parameter estimation routine. The parameter g m is difficult to estimate from CO2 response curves and the approach adopted in the present work followed two steps. A curve fit based on CO2 concentrations at the intercellular air spaces (C i) as reported in Domingues et al. (2010) was performed first to generate initial values of the photosynthetic capacity parameters (Vcmax, Ci and Jmax–Ci). Next, a second curve fit was performed incorporating g m in order to calculate CO2 concentrations at the sites of carboxylation (C i) using the Vcmax–Ci and Jmax–Ci values as a starting point for the iteration process. To make our data comparable, the parameter fits for Vcmax and Jmax, as estimated from A–Ci curves at ambient temperatures (typically 28–33 °C), were scaled to a reference temperature (25 °C) as described in Bernacchi et al. (2001).

Usually three replicates (leaves) were sampled from each individual plant sampled in this study, and up to three, but sometimes one or two individuals of the same species, were sampled at a given plot (Electronic Supplementary Material Table S1). When possible, measurements were taken directly from tree branches, but often branches were detached from trees and smaller stems were then immediately re-cut under water.

Statistical and modelling analysis

For statistical comparisons of leaf traits among plots, species’ averages within each plot were computed after first taking averages from replicated samples of individual plants. Statistical inferences on the relationships of photosynthetic capacity parameters and associated leaf traits (nutrients and/or structure) were based on both simple and multiple linear regressions using derived values from determinations on individual leaves. Data were log10 transformed before standardized major axis (SMA) (Warton et al. 2006) analyses but not before the application of an area version of a dual-limitation model of N and P introduced by Domingues et al. (2010) and here employed on an area basis viz.

\[
V_{\text{max}} = \min \left\{ a_N + b_N [N]^a, \frac{a_P + b_P [P]^a}{[N]} \right\},
\]

where Vmax is either Vcmax or Jmax, aN and ap are intercepts and bN and bp are slopes empirically derived from fitting the model to the data. Model comparisons were based on evaluations of Akaike information criteria (AIC) and Bayesian information criteria (BIC). Bootstrapping analysis (Chernick and LaBudde 2011) was applied in order to derive confidence intervals for parameters which originated from the application of the dual-limitation model (Eq. 1). All statistical analysis was conducted using the statistical environment R (R Development Core Team 2011).

For these Ci-based analyses of the nutrient dependencies of Vcmax and Jmax, we also included data from the West African transect ZOT in Ghana sampled with an identical methodology (Domingues et al. 2010) so as to increase both the sample size and the variation of N and P observed.

Results

Assignment of species to the forest or savanna guilds

As described in detail by Torello-Raventos et al. (2013), species found within the forest-savanna ecotone can usually be classified as belonging to ‘forest’ or ‘savanna’ based on their observed distribution, although a small degree of overlap inevitably occurs. This is illustrated in Fig. 1 where the distributions of tree/shrub species (stem diameter at
breast height > 0.1 m) are represented using a Venn–Euler diagram. Here, the number of plant species found in more than one vegetation type is represented numerically and proportionally by the areas of intersection among the circles. Only eight out of the 164 species observed in the seven study plots occurred in both forest and savanna [see also Table E1 of the Supplementary Information of Torelloraventos et al. (2013)]. The transitional forest (MDJ-05) did, however, contain many savanna species, as well as several unique species not found in the nearby forest or savanna plots.

Stand properties

Consistent with Fig. 1, a larger variety of families, genera and species were found at the forest sites (Table 1). Not surprisingly, the forest plots also had larger stem density and larger basal area (Table 1). The transitional forest plot MDJ-05 had the highest stem density but that added to a low total basal area (Table 1). That plot also had a relatively large number of dead standing savanna trees (data not shown).

Upper layer soil physical and chemical properties (0.0–0.3 m) also varied substantially amongst plots but—with the exception of soil C/N ratio—not consistently between the two main vegetation formation types (Table 1). As an example, effective cation exchange capacity (the sum of exchangeable bases plus Al) was highest at plot MDJ-01 (forest) and MDJ-08 (savanna) with other forest and savanna plots having only about one-third of these values while total soil P varied between 307 and 977 μg g⁻¹ for the forest plots and 316 and 997 μg g⁻¹ for the savanna plots.

Table 1 Soil and vegetation properties of the study plots

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
|----------|--------|--------|--------|--------|--------|--------|--------|
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Number of Families | 25 | 30 | 28 | 21 | 15 | 12 | 12 |
| Number of Genera | 43 | 56 | 54 | 32 | 23 | 16 | 19 |
| Number of Species | 59 | 79 | 69 | 44 | 23 | 19 | 19 |
| Shannon index | 3.05 | 3.09 | 3.42 | 2.53 | 2.34 | 2.02 | 2.15 |

| Vegetation structure | Basal area, m² ha⁻¹ | Canopy area index, m² m⁻² | Tree density, ha⁻¹ | Sand fraction | Silt fraction | Clay fraction | pH (H₂O) | [N], mg g⁻¹ | [C], mg g⁻¹ | C/N ratio | Total P, μg g⁻¹ | ECEC, mmol eq kg⁻¹ |
|----------------------|---------------------|--------------------------|-------------------|---------------|--------------|--------------|----------|-------------|-------------|----------|----------------|------------------|
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Leaf traits (mean ± standard deviation) | Mₐ, g m⁻² | Vₐ max, μmol m⁻² s⁻¹ | Jₐ max, μmol m⁻² s⁻¹ | Nₛ, g m⁻² | Pₛ, g m⁻² | δ¹³C, ‰ |
|----------------------------------------|-------------|-----------------|-----------------|-------------|-------------|--------------|
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |
| Location | MDJ-01 | MDJ-03 | MDJ-07 | MDJ-05 | MDJ-02 | MDJ-04 | MDJ-08 |

ECEC Effective cation exchange capacity, Mₐ leaf mass per unit area, V₂₅ estimated maximum rate of Rubisco limited carboxylation at 25 °C, J₂₅ estimated maximum rate of electron transport at 25 °C, Nₛ leaf nitrogen per unit area, Pₛ leaf phosphorus per unit area

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Leaf traits

A partitioning of the measured trait variation between plots, species, individual trees, and a residual component (representing the average variation between leaves within any given tree plus any experimental error) is shown in Fig. 2. For $M_a$ and $N$ per unit area ($N_a$), this shows most of the variation not due to plot location was attributable to species identity, with the proportion of variation between trees of the same species and ‘residual variation’ (i.e. attributable to within-tree variability and experimental error) being relatively small. By contrast, for $P_a$ and the light/CO$_2$ saturated assimilation rate ($A_{\text{max}}(a)$) most of this variation was within species or within individual trees themselves (Fig. 2). In view of this inconsistent pattern of variation among traits, we undertook all analyses on a leaf-wise basis rather than deriving individual tree means or some sort of (often necessarily cross-plot) species’ average value.

Despite often considerable overlap between leaf attributes found in forest versus savanna, some differences are striking (Fig. 3). For example, forest leaves typically had a lower $M_a$, higher $N_a$, a lower $P_a$ and a higher N:P ratio. Also shown in Fig. 3 are the equivalent data for forest and savanna from the ZOT component of the West African study of Domingues et al. (2010). This shows some interesting differences, the statistically significant of which are evaluated—along with a comparison for the Cameroon forest species with South American forest—in Table 2. Taken together, Table 2 and Fig. 4 show several intra- and cross-continental differences.

Focussing first on the current study (comparison 1) forest ($F$) leaves had a higher N content than savanna ($S$) leaves on both an area and a mass basis. The effect of vegetation formation type ($V$) on foliar P contents was, however, rather small. Despite the differences between $F$ and $S$ in both $N_a$ and $P_a$ (which we also point out were of opposite sign), there was no effect of $V$ on $A_{\text{sat}}(a)$ (Table 2: comparison 1).

Also in Table 2 (comparison 2) we compare the significance of differences between forest leaves from this study in Cameroon with the earlier study from West Africa. With the same methodology we find West African ZOT forest leaves to have had significantly lower $M_a$, $N_a$ and $A_{\text{sat}}(a)$ than for Cameroon, but with about the same $P$, $N$ and $A_{\text{sat}}$ on a mass basis.

The corresponding comparison for savanna also showed West African leaves to have a lower $M_a$, but with their N concentration and photosynthetic rates on a mass basis no lower than for Cameroon. Nevertheless, because of the lower $M_a$ in West Africa, $A_{\text{sat}}(m)$ were higher; this was also associated with higher $P_m$ and $N_m$ (Table 2).

Finally, to help gain a broader perspective we compared our Cameroon forest data with those obtained from the forests of the Amazon Basin (Fyllas et al. 2009, 2012). The latter study classified Amazonian sites into two soil fertility groups on the basis of their soil chemical properties and demonstrated that ‘low nutrient soil’ forests have...
lower leaf N and P on both an area and mass basis, and also higher N:P ratios than those of our Cameroon study area (Table 2). On the other hand, leaves from sites classified as ‘high nutrient soil’ by Fyllas et al. (2009) were very similar in composition to our Cameroon sites on both a mass and area basis. We therefore conclude that the African forest species sampled here are quite similar in their N and P concentrations to trees occurring on the more fertile soils of the Amazon Basin. As Ma are, on average, similar, this is true on both an area and mass basis, with the African forests studied here differing from the Amazon Basin forests on lower nutrient status soils mostly in terms of a higher foliar P status.

Bivariate relationships

Concentrating again on the Cameroon data, Fig. 4 shows the associations between A_sat(a), M_a, N_a and P_a, noting that all savanna species were deciduous—we have further differentiated forest species according to their leaf habit (evergreen vs. deciduous) as in Schrodt et al. (2014).

Although the relationship between A_max(a) and M_a was not significant for either of the forest habit types, for the deciduous savanna species (S_d), there was a statistically significant positive relationship (p = 0.038). Compared to the two forest types there was a (common) SMA slope of 0.13 μmol CO₂ g⁻¹ dry weight s⁻¹ but with a clear difference in intercept (Fig. 4a). That is to say, for any given M_a, S_d tend to have a consistently lower A_sat(a) than either of the forest habit types. When examined as a function of N_a (Fig. 4b), all three habitat groupings showed statistically significant relationships (p < 0.10) with S_d having a photosynthetic rate about 2.5 μmol CO₂ m⁻² s⁻¹ greater than the forest species at any given N_a (common slope of 5.90 μmol CO₂ g⁻¹ N s⁻¹). Relationships between A_sat(a) and P_a were significant only for S_d (slope = 74 μmol CO₂ g⁻¹ P s⁻¹; p < 0.05), with data for the forest evergreen leaves (F_e) even suggesting a (non-significant) negative relationship (Fig. 4c). The N_a:P_a relationship was statistically significant for both deciduous types, with a clear difference in elevation: at any given N_a, P_a was higher in the leaves of savanna trees.

For all four bivariate relationships investigated there were no clear indications of trees sampled from transitional vegetation being distinct from those of either the (non-transitional) forest or savanna vegetation types. Overall, we conclude from Fig. 4 that the strongest relationship is between A_sat(a) and N_a with deciduous savanna species being markedly different from both forest types: in particular, they exhibited a substantially higher mean A_sat(a) for any given N_a. Moreover, unlike forest species, for savanna species there is also a dependence of A_sat(a) on P_a. At any given N_a, P_a was higher in the leaves of savanna trees.
Table 2  Comparisons of the main leaf traits (shown as medians) between (1) forest and savanna in Cameroon (this study); (2) and (3) forest and savanna in this study as compared to a previous study in West Africa (Domingues et al. 2010); (4) forest in this study as compared to a previous study in Amazon Basin for which soils has been classified into two fertility groups (Fyllas et al. 2009)

| Location | Vegetation formation type | \( M_a \) (g m\(^{-2}\)) | \( N_a \) (g m\(^{-2}\)) | \( P_a \) (g m\(^{-2}\)) | \( A_{\text{sat}(a)} \) (\( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \)) | \( N_m \) (mg g\(^{-1}\)) | \( P_m \) (mg g\(^{-1}\)) | \( N:P \) (g g\(^{-1}\)) | \( A_{\text{sat}(m)} \) (\( \mu \text{mol} \text{ s}^{-1} \)) |
|----------|--------------------------|-----------------|-----------------|-----------------|------------------|----------------|----------------|----------------|----------------|
| Comparison 1. This study: Forests vs. Savanna  
Cameroon  
Forest | 95 | 2.12 | 0.10 | 10.3 | 23.5 | 1.11 | 20.9 | 0.105 |  
Cameroon  
Savanna | 119*** | 1.63*** | 0.12** | 11.8 ns | 12.8*** | 1.08* | 13.0*** | 0.085* |
| Comparison 2. Forests: Cameroon vs. West Africa  
Cameroon  
Forest | 95 | 2.12 | 0.10 | 10.3 | 23.5 | 1.11 | 20.9 | 0.105 |  
West Africa  
Forest | 75*** | 1.76** | 0.11 ns | 8.6*** | 24.7 ns | 1.37*** | 18.6* | 0.105 ns |
| Comparison 3. Savanna: Cameroon vs. West Africa  
Cameroon  
Savanna | 119 | 1.63 | 0.12 | 11.8 | 12.8 | 1.08 | 13.0 | 0.085 |  
West Africa  
Savanna | 92*** | 1.73 ns | 0.14 ns | 9.8 ns | 18.5*** | 1.68*** | 12.7 ns | 0.107* |
| Comparison 4. Forest: Cameroon vs. Amazon Basin  
Cameroon  
Forest | 95 | 2.12 | 0.10 | 10.3 | 23.5 | 1.11 | 20.9 | 0.105 |  
Amazon “low nutrient soil”  
Forest | 97 | 1.90*** | 0.06*** | ND | 20.1*** | 0.70*** | 28.9*** | ND |
| Amazon “high nutrient soil”  
Forest | 95 ns | 2.09 ns | 0.11 ns | ND | 21.6** | 1.11 ns | 19.4* | ND |

\( M_a \): leaf mass per unit area, \( N_a \): nitrogen per unit leaf area, \( P_a \): phosphorus per unit leaf area, \( A_{\text{sat}(a)} \): Net CO\(_2\) assimilation rate per unit leaf area at saturating light and ambient [CO\(_2\)], \( A_{\text{sat}(m)} \): Net CO\(_2\) assimilation rate per unit leaf mass area at saturating light and ambient [CO\(_2\)], \( N_m \): nitrogen per unit leaf mass, \( P_m \): phosphorus per unit leaf mass, \( N:P \): leaf nitrogen/phosphorus ratio (g g\(^{-1}\))

*Asterisks* denote the result of a Kruskal-Wallace test of significance (* \( p < 0.05 \), ** \( p < 0.01 \), *** \( p < 0.001 \))
Variations in Rubisco and electron transport capacities in relation to N and P

Although as noted in the Materials and methods one would ideally like to model variations in both $V_{cmax}$ and $J_{max}$ in terms of the partial pressure of CO$_2$ in the chloroplast ($C_c$), this requires some reliable measure of the leaf ‘internal’ conductance ($g_m$). Nevertheless, for the study here, both $V_{cmax}$ and $J_{max}$ were eventually simply estimated from the $A$–$C_i$ curve with the associated kinetic constants for $g_m = \infty$ applied (Von Caemmerer 2000). This decision was made on the basis of: (1) there being no significant relationship between our curve-fitting-derived estimates of $g_m$ and traits previously considered to covary with it [viz. $M_a$ or $\delta^{13}C$ (Niinemets (1999)]; (2) there being no consistent differences in apparent $g_m$ between vegetation types; and (3) there being little systematic difference observed between $C_i$- and $C_{i\text{-}}$ (intercellular spaces) based estimates of these photosynthetic parameters (Electronic Supplementary Material Fig. S1).

Details of area-based photosynthesis-nutrient relationships so derived for simple ordinary least squares (OLS) linear models and the more complex dual-limitation model of Eq. 1 are shown in Table 3. For $F_e$ the best fit according to the AIC was the simple linear model wherein $V_{25}$ is a simple function of $N_a$ ($r^2 = 0.17$, $p = 0.002$), with the BIC—similar to the AIC but with more severe penalties for extra terms—giving the same result. Of the linear models, a simple dependence of $V_{25}$ on $N_a$ also gave the best fit for $S_{ad}$ according to the BIC ($r^2 = 0.21$, $p = 0.001$) but with the alternative dual-limitation model (Domingues et al. 2010) being marginally better according to the AIC ($r^2 = 0.23$, $p = 0.001$). Note, however, that in this model the $P_a$ term is negative, implying an inhibitory effect of P on $V_{25}$.

Overall, the results for the two forest types were similar, so when they were combined there was, not surprisingly, an increase in the correlation coefficient values for the $N_a$-based models with the AIC suggesting the dual-limitation model ($r^2 = 0.29$) to be marginally superior to the simple $N_a$-based linear model (which was in turn unambiguously favoured when considering the BIC). Note that in no case was there any indication for a role for $P_a$ as a modulator of $V_{25}$ when considered on its own ($r^2 \leq 0.01$) for forest trees, with $P_a$ having only a marginal influence when considered in conjunction with $N_a$.

By contrast, for $S_{ad}$ it was found that $P_a$ was nearly as good a predictor as $N_a$ when considered on its own ($r^2 = 0.18$ vs. 0.19) and with the linear model fits including both terms being significantly better than either $N_a$ or $P_a$ on their own. Overall, the dual-limitation model was, however, found to be superior to the OLS models according to both the AIC and BIC ($r^2 = 0.30$, $p < 0.001$). Although a simple combination of the forest and savanna data suggest that the dual-limitation model is not the best when looking
Table 3 Comparisons of predictive models of area based maximum carboxylation capacity ($V_{25} = V_{\text{mec}}$-area 25 °C; μmol m$^{-2}$ s$^{-1}$) based on leaf nitrogen and/or phosphorus content

| Equation | $r^2$ | AIC  | BIC  | $p$   |
|----------|-------|------|------|-------|
| Forest evergreen | | | | |
| $V_{25} = 16.43 + 11.72N_a$ | 0.17 | 371.35 | 377.14 | 0.002 |
| $V_{25} = 35.53 + 19.03P_a$ | 0.01 | 381.21 | 387.01 | 0.495 |
| $V_{25} = 16.49 + 12.50N_a - 14.64P_a$ | 0.15 | 373.05 | 380.77 | 0.007 |
| $V_{25} = 28.22 + 5.82N_a - 134.72P_a + 65.97N_aP_a$ | 0.15 | 374.04 | 383.70 | 0.013 |
| $V_{25} = \min(16.43 + 11.72N_a; 50.23 + 24.52P_a)$ | 0.15 | 374.35 | 385.01 | 0.037 |
| Forest deciduous | | | | |
| $V_{25} = 23.62 + 10.41N_a$ | 0.21 | 830.27 | 838.23 | <0.001 |
| $V_{25} = 42.80 + 39.09P_a$ | 0.00 | 854.61 | 862.58 | 0.323 |
| $V_{25} = 25.50 + 10.91N_a - 26.49P_a$ | 0.20 | 831.75 | 842.36 | <0.001 |
| $V_{25} = \frac{7.71 + 19.37N_a + 143.95P_a - 78.49N_aP_a}{\text{(52.73 – 32.13 P_a)}}$ | 0.21 | 831.76 | 845.03 | <0.001 |
| $V_{25} = \min(16.77 + 14.00N_a; 57.83 – 32.13P_a)$ | 0.23 | 829.26 | 843.53 | <0.001 |
| Forest (evergreen and deciduous) | | | | |
| $V_{25} = 18.61 + 12.03N_a$ | 0.27 | 1208.24 | 1217.39 | <0.001 |
| $V_{25} = 38.95 + 46.50P_a$ | 0.01 | 1255.86 | 1265.01 | 0.080 |
| $V_{25} = 19.60 + 12.45N_a - 17.26P_a$ | 0.27 | 1209.73 | 1221.93 | <0.001 |
| $V_{25} = 11.02 + 16.96N_a + 64.75P_a$ | 0.27 | 1210.75 | 1226.00 | <0.001 |
| $V_{25} = \frac{a - 41.37N_aP_a}{57.43 – 34.33P_a}$ | 0.29 | 1206.40 | 1222.65 | <0.001 |
| Savanna (deciduous) | | | | |
| $V_{25} = 26.22 + 8.25N_a$ | 0.19 | 779.04 | 786.89 | <0.001 |
| $V_{25} = 25.30 + 111.17P_a$ | 0.18 | 780.01 | 787.86 | <0.001 |
| $V_{25} = 22.20 + 5.27N_a + 66.68P_a$ | 0.23 | 775.52 | 785.98 | <0.001 |
| $V_{25} = 1.57 + 17.67N_a + 167.62P_a - 57.46N_aP_a$ | 0.27 | 770.21 | 783.29 | <0.001 |
| $V_{25} = \min(34.87 + 5.83N_a; 9.79 + 251.86P_a)$ | 0.30 | 765.86 | 779.94 | <0.001 |
| Forest and savanna (deciduous and evergreen) | | | | |
| $V_{25} = 22.13 + 10.46N_a$ | 0.26 | 2151.39 | 2162.29 | <0.001 |
| $V_{25} = 36.03 + 57.33P_a$ | 0.04 | 2223.43 | 2234.33 | 0.001 |
| $V_{25} = 21.53 + 10.24N_a + 8.83P_a$ | 0.25 | 2153.07 | 2167.60 | <0.001 |
| $V_{25} = 6.44 + 17.70N_a + 118.70P_a$ | 0.29 | 2141.92 | 2160.10 | <0.001 |
| $V_{25} = \frac{71.98N_aP_a}{57.85 + 19.52P_a}$ | 0.25 | 2154.39 | 2173.56 | <0.001 |

$N_a$ nitrogen per unit leaf area (g m$^{-2}$), $P_a$ phosphorus per unit leaf area (g m$^{-2}$)

Models addressed in detail in the “Results” and “Discussion” sections are highlighted in bold

for a common (cross–biome) relationship—in this case it being surpassed by a model containing linear functions of $N_a$ and $P_a$ and their interaction term $N_a$ and $P_a$—a simple analysis of AIC/BIC and/or the residual sum of squares (RSS) according to a procedure outlined in Lloyd et al. (1989) also shows that this combined (forest + savanna) model provides an inferior fit compared to when forest (i.e. $F_d$ and $F_e$ together) and savanna ($S_d$) are considered separately ($p < 0.001$). That is to say, although for the forest species $V_{25}$ showed a simple dependency upon $N_a$, for $S_d$ an additional role for $P_a$ is clearly implicated.

A similar picture emerges when models for $J_{25}$ are sought with little evidence of a role for $P_a$ as a modulating factor for either $F_d$ or $F_e$ and with $N_a$ effects apparently dominant for these two forest types (Table 4). As for $V_{25}$ there is, however, a clear indication of a role for $P$ for $S_d$, and with the dual-limitation model giving the best fit. Likewise, when all data are combined, then comparisons of either AIC, BIC or RSS with the individual models show that in any analyses of their $J_{25}$ nutrient dependencies, forest and savanna species need to be considered separately.

Fitting separate relationships for both forest and savanna, the resulting goodness of model fit is shown for both $V_{25}$ and $J_{25}$ in Electronic Supplementary Material, Fig. S3. This shows that in all cases, model predictions involved a much smaller degree of variation than suggested by the observations. An examination of model residuals in terms of the predictor variables $N_a$ and $P_a$ along with a range of other potentially confounding covariates such as $M_a$ and area-based cations (see Electronic Supplementary Material, Figs. S4, S5) did not, however, suggest reasons for concern in terms of any trait-specific systematic bias for either $V_{25}$ or $J_{25}$. Also note that in Figs. S3 and S4 we have separately identified members of the Fabaceae which, although making up less than 5 % of our data set, are also unusual in their foliar N and P characteristics (Fyllas et al. 2009), especially in relation to photosynthesis (Cernusak et al. 2011). There were, however, no indications from this study that members of this family behaved in any way different to the population sampled as a whole.

For both $V_{25}$ and $J_{25}$ the observed relationships with $N_a$ and $P_a$ are shown in Fig. 5. Here, for forest, we have shown the fitted lines for the modelled simple linear $N_a$ dependencies for both $V_{25}$ and $J_{25}$ with the dual-limitation model predictions presented only for $S_d$. This differentiation has been made on the basis of a bootstrapping analysis (Chernick and LaBudde 2011), which showed that for both $V_{25}$ and $J_{25}$ the (apparently negative) $V_{25}$ and $P_a$ terms were not significantly different from zero (see Table S2 in Electronic Supplementary Material) for both forest types, the implication of this being that $P_a$ actually exerts no modulating role on the photosynthetic properties of both $F_d$ and $F_e$. For $V_{25}$ our model clearly suggests that savanna leaves with $N_a < 2.5$ g m$^{-2}$ have a higher carboxylation capacity than forest leaves at the same $N_a$ (Fig. 5a).

Consistent with the simple linear $V_{25} = f(N_a)$ model being applied for the forest species, no fitted lines are
shown for the forest species for the \( P_a \) relationships of Fig. 5b, d. In both cases, the bootstrapping analysis did, however, show the savanna co-limitation model \( P_a \) slope to be significant with a 0.95 confidence interval for \( V_{25} \) of 190–375 \( \mu \text{mol CO}_2\,\text{g}^{-1}\,\text{P}\,\text{s}^{-1} \) with the equivalent range being 246–539 \( \mu \text{mol CO}_2\,\text{g}^{-1}\,\text{P}\,\text{s}^{-1} \) for \( J_{25} \) (Electronic Supplementary Material, Table S2).

Also shown for all four parts of Fig. 5 are fitted relationships from the original application of the dual-limitation model of (Domingues et al. 2010) to a wide range of West African tree species and location, including those with a much drier climate (grey lines). In all cases the ‘West African’ slopes are much steeper than found here for Cameroon, where the analysis has been confined to two forest-savanna transition zones. Differences at high \( N_a \) and \( P_a \) are particularly marked.

### Discussion

Using as our individual unit of variation the individual leaf (rather than the tree or species), we found unequivocal support for our first hypothesis viz. that the scaling between foliar N and P and the nature of the photosynthesis-nutrient relationship would be different for forest and savanna species. This can be seen from Fig. 4d where at any given leaf N (area basis) savanna trees had significantly higher P than their forest counterparts and Fig. 5 where the equations of Tables 2 and 3 clearly shown different relationships of both \( V_c(max) \) and \( J_{max} \) with both N and P for forest vs. savanna species.

On the other hand, although we had also hypothesized that savanna trees should show more indications of being limited by N, if anything the opposite was the case. This

### Table 4
Comparisons of predictive models of area based maximum electron transport rate (\( J_{25} = J_{\text{max}-\text{area}} \) 25 °C; \( \mu \text{mol m}^{-2}\,\text{s}^{-1} \)) based on leaf nitrogen and/or phosphorus content

|                | \( r^2 \) | AIC     | BIC     | \( p \)  |
|----------------|----------|---------|---------|--------|
| Forest evergreen |          |         |         |        |
| \( J_{25} = 32.69 + 21.14N_a \) | 0.18 | 426.88 | 432.68 | 0.001 |
| \( J_{25} = 64.15 + 64.28P_a \) | 0.02 | 436.24 | 442.03 | 0.181 |
| \( J_{25} = 32.66 + 20.68N_a + 8.58P_a \) | 0.16 | 428.85 | 436.58 | 0.005 |
| \( J_{25} = 28.78 + 22.89N_a + 48.23P_a - 21.78N_aP_a \) | 0.15 | 430.81 | 440.47 | 0.015 |
| \( J_{25} = \min(32.69 + 21.14N_a; 78.99 + 64.40P_a) \) | 0.16 | 429.88 | 440.54 | 0.028 |
| Forest deciduous |          |         |         |        |
| \( J_{25} = 40.42 + 19.60N_a \) | 0.24 | 946.15  | 954.12 | <0.001 |
| \( J_{25} = 83.76 - 9.89P_a \) | −0.01 | 975.38 | 983.34 | 0.888 |
| \( J_{25} = 49.03 + 21.89N_a - 121.73P_a \) | 0.25 | 944.48 | 955.10 | 0.001 |
| \( J_{25} = 29.94 + 32.89N_a + 99.60P_a - 101.93N_aP_a \) | 0.26 | 945.34 | 958.61 | <0.001 |
| \( J_{25} = \min(30.05 + 24.93N_a; 105.64 - 55.54P_a) \) | 0.26 | 945.12 | 959.39 | <0.001 |
| Forest (evergreen and deciduous) |          |         |         |        |
| \( J_{25} = 35.21 + 21.30N_a \) | 0.29 | 1376.58 | 1385.73 | <0.001 |
| \( J_{25} = 73.34 + 62.94P_a \) | 0.01 | 1428.19 | 1437.34 | 0.172 |
| \( J_{25} = 38.25 + 22.88N_a - 52.86P_a \) | 0.29 | 1376.94 | 1389.14 | <0.001 |
| \( J_{25} = 15.48 + 34.54N_a + 164.81P_a - 109.80N_aP_a \) | 0.29 | 1376.58 | 1391.83 | <0.001 |
| \( J_{25} = \min(26.97 + 25.76N_a; 105.46 - 59.78P_a) \) | 0.30 | 1374.66 | 1390.91 | <0.001 |
| Savanna (deciduous) |          |         |         |        |
| \( J_{25} = 45.60 + 14.01N_a \) | 0.23 | 861.59  | 869.44 | <0.001 |
| \( J_{25} = 46.59 + 170.38P_a \) | 0.18 | 868.26  | 876.11 | <0.001 |
| \( J_{25} = 40.56 + 10.27N_a + 83.73P_a \) | 0.25 | 859.78  | 870.24 | <0.001 |
| \( J_{25} = 21.18 + 21.91N_a + 178.51P_a - 53.96N_aP_a \) | 0.26 | 859.05 | 872.12 | <0.001 |
| \( J_{25} = \min(51.28 + 13.06N_a; 29.55 + 337.17P_a) \) | 0.29 | 855.17  | 869.25 | <0.001 |
| Forest and savanna (deciduous and evergreen) |          |         |         |        |
| \( J_{25} = 38.23 + 19.42N_a \) | 0.30 | 2431.46 | 2442.36 | <0.001 |
| \( J_{25} = 68.53 + 68.45P_a \) | 0.02 | 2528.29 | 2539.19 | 0.017 |
| \( J_{25} = 40.06 + 20.09N_a - 26.70P_a \) | 0.30 | 2432.37 | 2446.90 | <0.001 |
| \( J_{25} = 15.87 + 32.06N_a + 149.52P_a - 83.38N_aP_a \) | 0.33 | 2421.91 | 2440.09 | <0.001 |
| \( J_{25} = \min(29.42 + 24.36N_a; 97.57 + 6.46P_a) \) | 0.33 | 2422.10 | 2441.28 | <0.001 |

\( N_a \) nitrogen per unit leaf area (g m\(^{-2}\)), \( P_a \) phosphorus per unit leaf area (g m\(^{-2}\))

Models addressed in detail in the “Results” and “Discussion” sections are highlighted in bold.
is because the best-fitting relationship between the photosynthetic parameters $V_{c(\text{max})}$ and $J_{\text{max}}$ for both evergreen and deciduous forest trees was a simple linear relationship with $N_a$ with no relationship at all when a linear model with $P$ content was tested. By contrast, the savanna species (all of which were deciduous) showed significant relationships with $P_a$ as well as with $N_a$—albeit with a different $N$ dependence to that found for the forest species. Thus, if anything, the indications were for a greater limitation by $P$ on photosynthesis in savanna as opposed to forest trees.

Biome history may be important in explaining these results. For example any forest refugia in Africa at the Last Glacial Maximum (Anhuf et al. 2006) would have been most likely to have occurred where both precipitation regime and soil conditions remained most favourable for forest tree function. So, with deeper tropical soils of a high water holding capacity also typically being of a low $P$ status due to their long history of extreme weathering (Quesada et al. 2010), specific adaptions to a chronically low $P_a$ for forest trees seem likely, for example in the replacement of phospholipids by galactolipids and sulpholipids under condition of low $P$ supply (Lambers et al. 2012; Tjellström et al. 2008; Zhang et al. 2014).

With leaves intercepting light on a per unit area basis and spurious correlations possible when two unrelated area-based entities are transformed to a mass basis—the so called ‘lulu effect’ (Lloyd et al. 2013)—we saw for the current paper no practical reason to analyse our photosynthesis-nutrient dependencies on per unit mass basis (see also Osnas et al. 2013). Nevertheless, for the purposes of illustration our area-based analysis is repeated on a mass basis as part of the Electronic Supplementary Material (Tables S3, S4). This shows—in addition to the inevitable higher correlations associated with a ‘common-element’ correlation (Lloyd et al. 2013)—that for the forest species it is more often than not the more complex models involving not only both $N_m$ and $P_m$ but also their interaction, that have the lowest $\text{AIC}$ and/or $\text{BIC}$. This is as opposed to the simple forest species linear $N$ dependency for both $V_{25}$ and $J_{25}$ for the area-based fits. Overall these results are consistent with the assertion that in multivariate cases a simple area-to-mass conversion can easily give rise to variables not actually associated with the dependent variable appearing to be functionally linked (Lloyd et al. 2013). We also note that whilst the area-based models showed little bias in their residuals when examined as a function of $M_a$, $N:P$ and a range of area based leaf-nutrient measures (Figs S3, S4), this was not the case for the mass-based models for which there was a bias towards positive residuals at low $M_a$ (Figs S5, S6). The lack of any obvious dependency of the model-fit residuals on leaf cation concentrations, area-based leaf $S$ or leaf $N:P$ ratios suggests that—at least in our case—there is no need to invoke additional factors such as variations in leaf $K$ (Battie-Laclau et al. 2014) into our dual-dependency

![Fig. 5](image-url)
N-P based model. Though that is not to say, of course, that such elements might not have important roles in influencing tropical vegetation structure and function independent of the photosynthetic process (Schrödt et al. 2014; Veenendaal et al. 2014).

With our earlier analyses using the formulation of Eq. 1 having actually focussed on mass-based model fits (Domingues et al. 2010), there does, however, remain the question: to what extent are some previous conclusions of Domingues et al. (2010) regarding the relative roles on N and P still valid? The answer is that, with only minor modifications, they still hold. For example, in that paper we also showed that area-based fits of the dual-limitation model implied a role for both N and P as alternate limiting factors for photosynthesis (in addition to the mass-based models) and with area-based comparisons with simple linear models also showing the min–min model to have the lowest AIC. Indeed, the analysis here should be best considered a refinement of the work of Domingues et al. (2010), probing further into the nature of the apparent different nutrient/photosynthesis relationships identified for species associated with the different rainfall environments first identified there.

It is unlikely that the differences between forest and savanna in their photosynthesis–N relations (Figs. 4a, 5a, c) were simply a consequence of the sampled forest tree leaves being from a lower light environment. This is because considerable effort was put into ensuring that leaves from both vegetation formation types were sampled only from upper-canopy sun-exposed environments (See “Materials and methods”). Rather, and especially as broadly similar results have also been reported for a forest-savanna comparison in tropical northern Australia (Bloomfield et al. 2014), this difference between the two vegetation formation types in their photosynthesis–nutrient relationships seems something more fundamental. Both Domingues et al. (2010) and (Bloomfield et al. 2014) discuss at some length possible reasons for forest trees having an apparently less efficient use of N, focussing on the idea of an increased allocation of N to non-photosynthetic compounds when conditions favouring a longer leaf longevity are also combined with a more variable light environment.

The question remains, however, as to the extent of the validity of the original parameterisation of Domingues et al. (2010), or the new forest parameterisation developed here, when applied to tropical forest trees growing on low-P availability soils, such as those which cover much of the eastern Amazon Basin (Quesada et al. 2011), especially as already investigated as part of the modelling studies of Mercado et al. (2011) and Fyllas et al. (2014). Trees on such soils do, nevertheless, typically have a foliage of a much lower $P_{\text{c}}$ than encountered here (Table 2), so it will only be with further dedicated measurements under the full spectrum of $N:P$ variability and across a range of different growth forms that we will be able to ascertain the generality (or most likely otherwise) of any photosynthesis–nutrient relationships developed.

Most likely the dual-limitation model applies because for some specific locations and/or for some particular times of the year, P is rate limiting, whilst for other times/places it is N which constrains photosynthetic productivity. As for the Amazon Basin forest case discussed above, these regional variations, arising mostly from soil variations— but also clearly depending on vegetation formation type—will give rise to variations in the rates of photosynthesis, these linking to variations in stand-level productivity (Fyllas et al. 2014; Mercado et al. 2011) and thus presumably important when parameterizing global vegetation models (e.g. Sitch et al. 2008 and Piao et al. 2013). This emphasizes a need for the development of new realistic models of ecosystem N and P cycling that include soil biogeochemical processes in a realistic manner (Fisher et al. 2010; Goll et al. 2012; Ostle et al. 2009; Thomas et al. 2013; Xu et al. 2012; Yang et al. 2013). But whatever the case, the results presented here along with those of other recent studies (Bloomfield et al. 2014; Domingues et al. 2010; Rossatto et al. 2013) clearly indicate that no single unifying woody tropical vegetation photosynthesis–nutrient relationship is likely to be found.

**Author contribution statement**  TFD: collected and analyzed data, wrote manuscript, prepare figures, FYI; collected data, field support TF; collected data, field support, JG; institutional support, discussion of results, manuscript structure, GS; collected data, field support, OS; botanical identification, field support, FS; collected data, field support, BS; logistical support, botanical identification HT; botanical identification, field support, EV; discussion of results, manuscript structure SL; logistical support, site selection, field activities planning, JL; Project coordinator, manuscript writing, discussion of results.

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