

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

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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; Schrodtt 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).

Our earlier work from West Africa demonstrated that, depending on their relative concentrations in the leaf tissue, both Rubisco activity and electron transport activity of African savanna and forest trees can potentially be limited by either N or P (Domingues et al. 2010). But in that study interpretations of forest/savanna differences were complicated by savanna measurements from a wide range of precipitation regimes across soil types that were extremely diverse.

Here we report on work from a naturally occurring forest/savanna mosaic in Central Cameroon where we investigate photosynthetic and associated foliar trait

characteristics of trees and shrubs for forest and savanna species growing in close proximity and thus the same climatic regime. We aimed to test the hypotheses that under similar climatic conditions in a zone of transition:

1. Scaling between foliar N and P, and its relationship with photosynthesis, is different for forest and savanna species.
2. Species growing in savannas show more indications of N limitation than forest species (which would, in turn, be more likely to be limited by P).

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).

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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 ($A-C_i$ curves at high photon irradiance), leaf nutrients and leaf mass per unit area (M_a). Methodological details follow Domingues et al. (2010), with a simple modification introduced for estimation of the two key photosynthetic capacity parameters (V_{cmax} , the maximum rate of carboxylation and J_{max} , 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 CO_2 response curves and the approach adopted in the present work followed two steps. A curve fit based on CO_2 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 (V_{cmax-C_i} and J_{max-C_i}). Next, a second curve fit was performed incorporating g_m in order to calculate CO_2 concentrations at the sites of carboxylation (C_c) using the V_{cmax-C_i} and J_{max-C_i} values as a starting point for the iteration process. To make our data comparable, the parameter fits for V_{cmax} and J_{max} , as estimated from $A-C_i$ 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 values derived from determinations on individual leaves. Data were \log_{10} 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

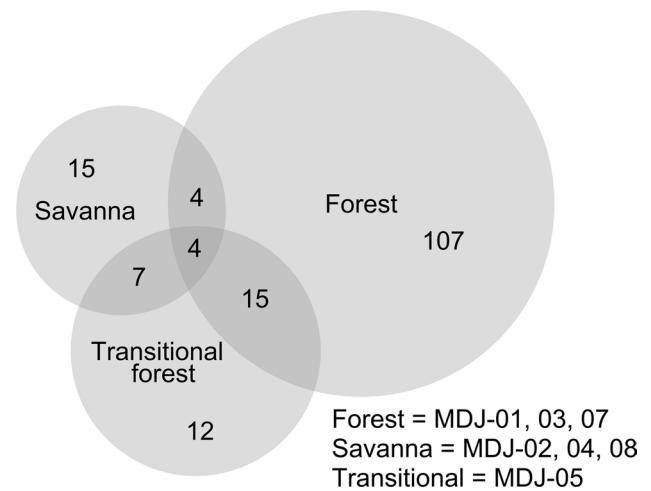


Fig. 1 Venn–Euler diagram showing the abundance of tree species across sample plots considered as ‘forest’, ‘savanna’ and ‘transitional forest’ according to the classification of Torello-Raventos et al. (2013). Numbers refer to number of individual species

introduced by Domingues et al. (2010) and here employed on an area basis viz.

$$V_{max} = \min \left\{ \begin{array}{l} a_N + b_N[N]_a \\ a_P + b_P[P]_a \end{array} \right\}, \quad (1)$$

where V_{max} is either V_{cmax} or J_{max} , a_N and a_P are intercepts and b_N and b_P 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 C_i -based analyses of the nutrient dependencies of V_{cmax} and J_{max} 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

Table 1 Soil and vegetation properties of the study plots

	Forest			Transition	Savanna		
Location	MDJ-01	MDJ-03	MDJ-07	MDJ-05	MDJ-02	MDJ-04	MDJ-08
Latitude	6.1683N	5.984N	6.007N	5.980N	6.164N	5.999N	6.213N
Longitude	12.825E	12.869E	12.887E	12.869E	12.824E	12.868E	12.749E
Biodiversity measures							
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, m ² ha ⁻¹	35.6	25.6	25.6	14.0	4.3	5.9	8.1
Canopy area index, m ² m ⁻²	3.24	2.98	1.75	2.85	0.45	0.36	0.48
Tree density, ha ⁻¹	611	467	465	684	136	213	241
Soil physical and chemical properties (0.0–0.3 m)							
Sand fraction	0.41	0.65	0.67	0.58	0.28	0.56	0.59
Silt fraction	0.38	0.23	0.16	0.18	0.33	0.16	0.28
Clay fraction	0.22	0.12	0.18	0.25	0.39	0.28	0.13
pH (H ₂ O)	6.53	4.88	4.70	4.50	5.32	4.92	5.81
[N], mg g ⁻¹	1.49	0.71	0.68	0.80	1.56	0.62	0.72
[C], mg g ⁻¹	19.4	8.6	9.0	12.0	26.5	9.8	11.5
C/N ratio	11.6	12.2	12.6	15.0	17.2	15.7	15.2
Total P, μg g ⁻¹	977	307	738	576	997	316	364
ECEC, mmol eq kg ⁻¹	21.1	10.5	7.3	1.6	9.3	5.2	16.4
Leaf traits (mean ± standard deviation)							
<i>M</i> _a , g m ⁻²	80 ± 31	97 ± 26	109 ± 21	113 ± 41	136 ± 23	127 ± 26	135 ± 32
<i>V</i> _{cmax} , μmol m ⁻² s ⁻¹	39.2 ± 13.6	42.3 ± 12.2	45.7 ± 12.1	44.8 ± 8.3	54.6 ± 11.8	39.2 ± 9.2	27.8 ± 0.1
<i>J</i> _{max} , μmol m ⁻² s ⁻¹	76.8 ± 20.5	79.3 ± 19.5	88.2 ± 17.8	81.0 ± 18.6	87.6 ± 17.5	67.9 ± 12.3	47.5 ± 10.2
<i>N</i> _a , g m ⁻²	1.97 ± 0.55	2.26 ± 0.67	2.13 ± 0.46	2.12 ± 0.56	2.67 ± 1.39	1.48 ± 0.27	1.44 ± 0.06
<i>P</i> _a , g m ⁻²	0.12 ± 0.05	0.10 ± 0.03	0.09 ± 0.02	0.10 ± 0.03	0.16 ± 0.08	0.13 ± 0.04	0.12 ± 0.07
δ ¹³ C, ‰	-29.8 ± 1.2	-30.0 ± 1.0	-30.6 ± 1.2	-30.0 ± 0.9	-30.5 ± 0.3	-30.3 ± 0.3	-29.3 ± 0.1

ECEC Effective cation exchange capacity, *M*_a leaf mass per unit area, *V*₂₅ estimated maximum rate of Rubisco limited carboxylation at 25 °C, *J*₂₅ estimated maximum rate of electron transport at 25 °C, *N*_a leaf nitrogen per unit area, *P*_a leaf phosphorus per unit area

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 Torello-Raventos 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.

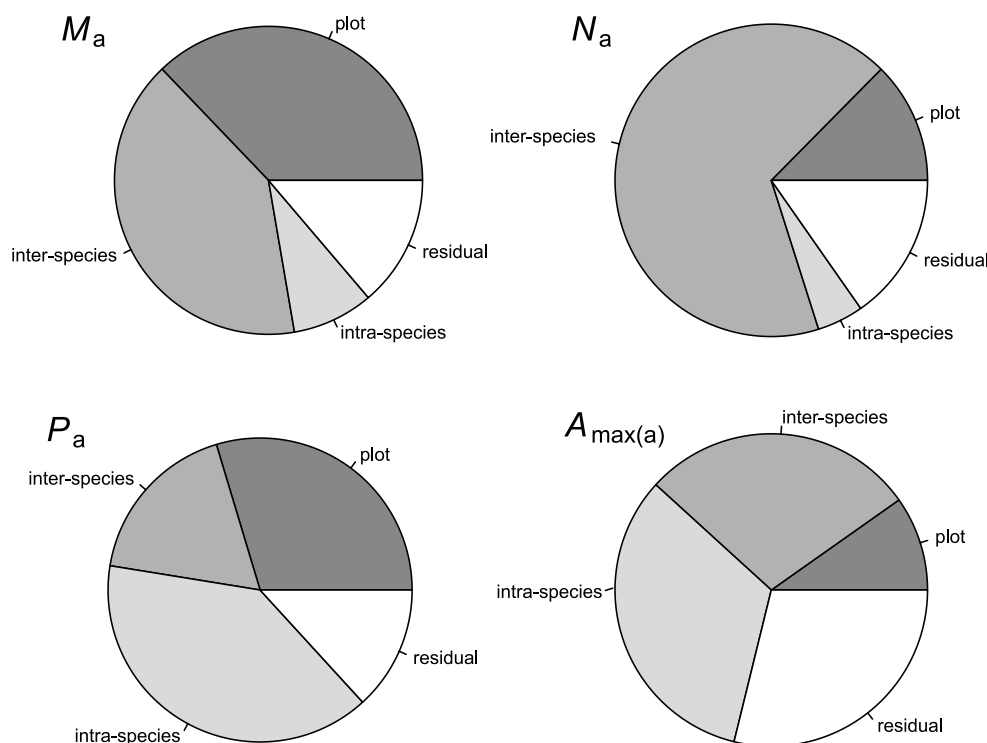
Stand properties

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.

Fig. 2 Partitioning of the total variance between plots, species, individual trees. The residual term includes between-leaf variation and experimental error. M_a Leaf mass per unit area, N_a N per unit leaf area, P_a P per unit leaf area, $A_{\max(a)}$ net CO_2 assimilation rate per unit leaf area at saturating light and $[\text{CO}_2]$



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 ($A_{\max(a)}$) 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_m , 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_{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

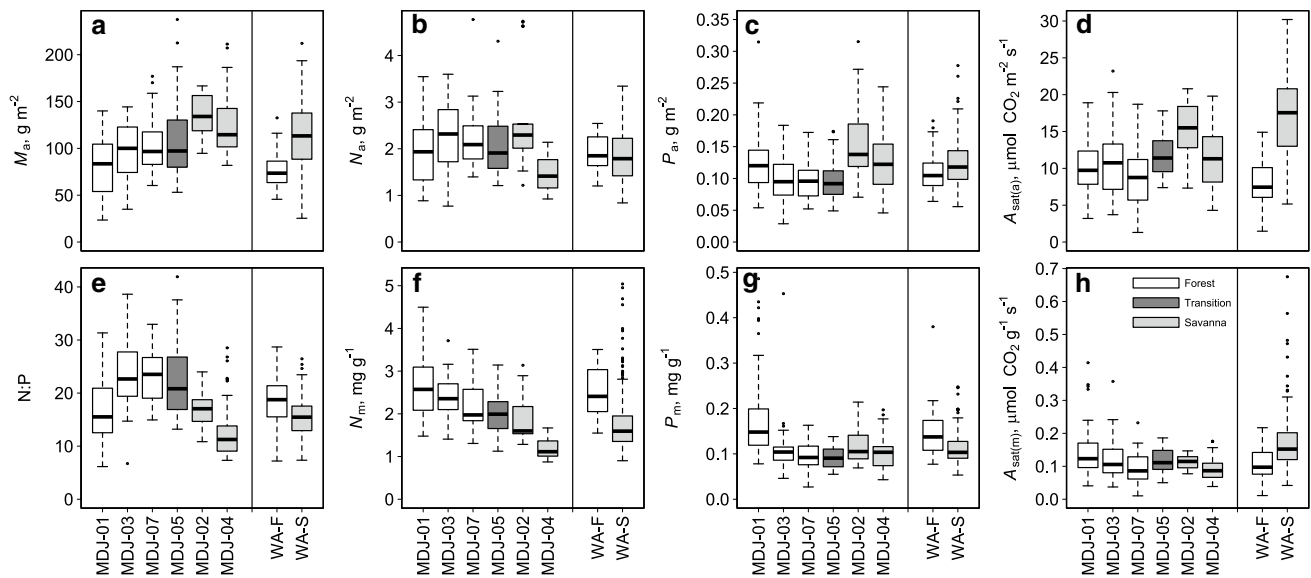


Fig. 3 Statistical comparison of leaf attributes of forest (white bars), savanna (light grey) and transitional forest (dark grey) sampled in central Cameroon. Also shown (right of vertical line) are forest (WA-F) and savanna data (WA-S) from a previous study in West Africa (Domingues et al. 2010). **a** M_a ; **b** N_a ; **c** P_a ; **d** net CO_2 assimilation

rate per unit leaf area at saturating light and ambient $[\text{CO}_2]$ [$A_{\text{sat}(a)}$]; **e** leaf N/P ratio (N:P; g g^{-1}); **f** N per unit leaf mass (N_m); **g** P per unit leaf mass (P_m); **h** net CO_2 assimilation rate per unit leaf mass area at saturating light and ambient $[\text{CO}_2]$ [$A_{\text{sat}(m)}$]; for other abbreviations, see Fig. 2

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 M_a 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 $A_{\text{sat}(a)}$, M_a , N_a and P_a where noting that all savanna species were deciduous—we have further differentiated forest species according to their leaf habit (evergreen vs. deciduous) as in Schrodtt et al. (2014).

Although the relationship between $A_{\text{max}(a)}$ 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 $0.13 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ dry weight s}^{-1}$ 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 $A_{\text{sat}(a)}$ 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 $2.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ greater than the forest species at any given N_a (common slope of $5.90 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$). Relationships between $A_{\text{sat}(a)}$ and P_a were significant only for S_d (slope = $74 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ P s}^{-1}$; $p < 0.05$), 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 , S_d typically had a P_a about 0.04 g m^{-2} greater than their deciduous forest counterparts (F_d) (Fig. 4d).

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 $A_{\text{sat}(a)}$ and N_a with deciduous savanna species were markedly different from both forest types: in particular, they exhibited a substantially higher mean $A_{\text{sat}(a)}$ for any given N_a . Moreover, unlike forest species, for savanna species there is also a dependence of $A_{\text{sat}(a)}$ on P_a . At any given N_a , P_a was higher in the leaves of savanna trees.

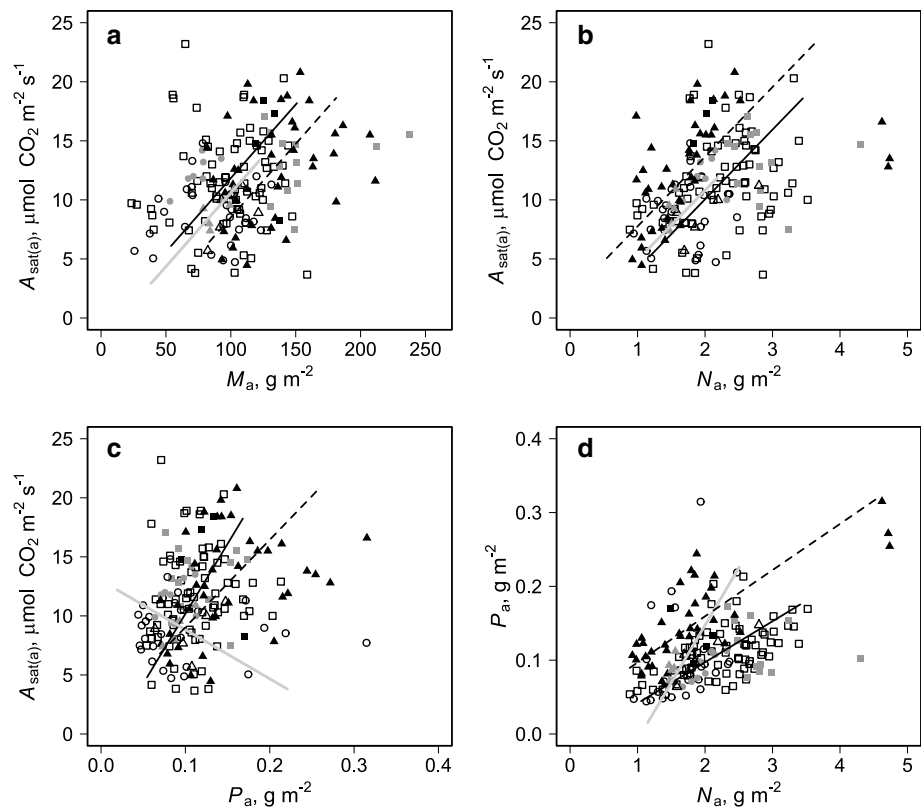
Table 2 Comparisons of the main leaf traits (shown as medians) between (1) forest and savanna in Cameroon (this study); (2) and (3) forest and savanna in this study as compared to a previous study in West Africa (Domingues et al. 2010); (4) forest in this study as compared to a previous study in Amazon 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 ($g\ m^{-2}$)	$A_{sat(a)}$ ($\mu mol\ m^{-2}\ s^{-1}$)	N_m ($mg\ g^{-1}$)	P_m ($mg\ g^{-1}$)	$N:P$ ($g\ g^{-1}$)	$A_{sat(m)}$ ($\mu mol\ s^{-1}$)
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, $A_{sat(a)}$ Net CO_2 assimilation rate per unit leaf area at saturating light and ambient $[CO_2]$, $A_{sat(m)}$ 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-Wallis test of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Fig. 4a–d Bivariate plots of observed relationships between area-based measures of light-saturated photosynthetic rate [$A_{\text{sat}(a)}$], N and P. Deciduous forest (squares), evergreen forest (circles) and savanna (triangles) with open, grey and black symbols indicating individuals in forest, transition and savanna environments, respectively. Lines are standard major axis (SMA) regression fits for forest deciduous (black line), forest evergreen (grey line), and savanna deciduous leaves (dotted line)



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 $\delta^{13}\text{C}$ (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_c - and C_i - (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_d 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 F_d 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_d 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 ($V_{25} = V_{\text{cmax-area } 25 \text{ } ^\circ\text{C}; \mu\text{mol m}^{-2} \text{ s}^{-1}$) 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
$V_{25} = 35.53 + 19.03 P_a$	0.01	381.21	387.01	0.495
$V_{25} = 16.49 + 12.50N_a - 14.64 P_a$	0.15	373.05	380.77	0.007
$V_{25} = 28.22 + 5.82N_a - 134.72 P_a + 65.97N_a P_a$	0.15	374.04	383.70	0.013
$V_{25} = \min(16.43 + 11.72N_a; 50.23 + 24.52 P_a)$	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
$V_{25} = 42.80 + 39.09 P_a$	0.00	854.61	862.58	0.323
$V_{25} = 25.50 + 10.91N_a - 26.49 P_a$	0.20	831.75	842.36	<0.001
$V_{25} = 7.71 + 19.37N_a + 143.95 P_a - 78.49N_a P_a$	0.21	831.76	845.03	<0.001
$V_{25} = \min(16.77 + 14.00N_a; 57.83 - 32.13 P_a)$	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
$V_{25} = 38.95 + 46.60 P_a$	0.01	1255.86	1265.01	0.080
$V_{25} = 19.60 + 12.45N_a - 17.26 P_a$	0.27	1209.73	1221.93	<0.001
$V_{25} = 11.02 + 16.96N_a + 64.75 P_a - 41.37N_a P_a$	0.27	1210.75	1226.00	<0.001
$V_{25} = \min(12.83 + 15.22N_a; 57.43 - 34.33 P_a)$	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
$V_{25} = 25.30 + 111.17 P_a$	0.18	780.01	787.86	<0.001
$V_{25} = 22.20 + 5.27N_a + 66.68 P_a$	0.23	775.52	785.98	<0.001
$V_{25} = 1.57 + 17.67N_a + 167.62 P_a - 57.46N_a P_a$	0.27	770.21	783.29	<0.001
$V_{25} = \min(34.87 + 5.83N_a; 9.79 + 251.86 P_a)$	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
$V_{25} = 36.03 + 57.33 P_a$	0.04	2223.43	2234.33	0.001
$V_{25} = 21.53 + 10.24N_a + 8.83 P_a$	0.25	2153.07	2167.60	<0.001
$V_{25} = 6.44 + 17.70N_a + 118.70 P_a - 51.98N_a P_a$	0.29	2141.92	2160.10	<0.001
$V_{25} = \min(22.13 + 10.46N_a; 75.85 + 19.52 P_a)$	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. \mathbb{F}_d and \mathbb{F}_e together) and savanna (\mathbb{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 \mathbb{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 \mathbb{F}_d or \mathbb{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 \mathbb{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 \mathbb{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 \mathbb{F}_d and \mathbb{F}_e . For V_{25} our model clearly suggests that savanna leaves with $N_a < 2.5 \text{ g m}^{-2}$ 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

Table 4 Comparisons of predictive models of area based maximum electron transport rate ($J_{25} = J_{\max}$ -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
$J_{25} = 64.15 + 64.28[P]_a$	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
$J_{25} = 25.94 + 32.89N_a + 99.60P_a - 101.93N_aP_a$	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
$J_{25} = 38.25 + 22.58N_a - 52.86P_a$	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

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 $\mu\text{mol CO}_2 \text{g}^{-1} \text{P s}^{-1}$ with the equivalent range being 246–539 $\mu\text{mol CO}_2 \text{g}^{-1} \text{P s}^{-1}$ for J_{25} (Electronic Supplementary Material, Table S2).

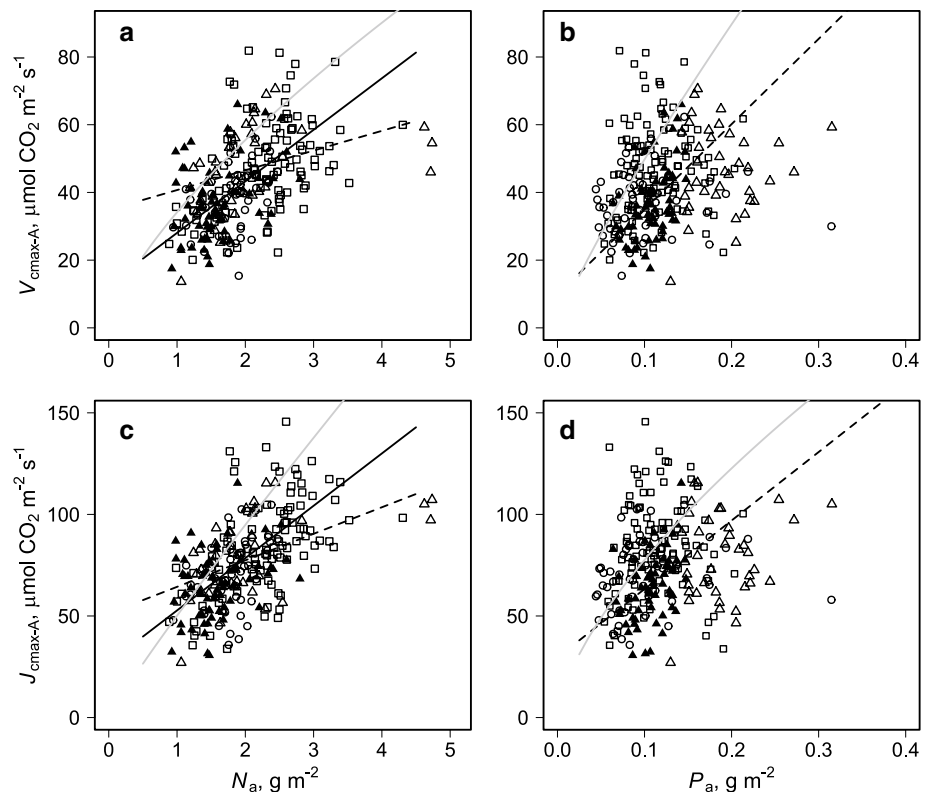
Also shown for all four parts of Fig. 5 are fitted relationships from the original application of the dual-limitation model of (Domingues et al. 2010) to a wide range of West African tree species and location, including those with a much drier climate (grey lines). In all cases the ‘West African’ slopes 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

Fig. 5 Area-based relationships between **a** estimated Rubisco activity standardized to 25 °C (V_{25}) and leaf N, **b** V_{25} and leaf P, **c** estimated electron transport capacity at 25 °C (J_{25}) and leaf N, **d** J_{25} and leaf P. Deciduous forest (squares), evergreen forest (circles), savanna (triangles). Filled savanna symbols show points modelled to be limited by P as per the model fit of Eq. 1 as detailed in Electronic Supplementary Material, Table 1. Also shown from this study are the model fits of Eq. 1 for forest (full lines) and savanna (dotted lines), along with a previous fit of the same model to a mixture of forest and savanna species sampled along a precipitation transect in West Africa (grey lines) as detailed in Domingues et al. (2010)



is because the best-fitting relationship between the photosynthetic parameters $V_{c(max)}$ and J_{max} for both evergreen and deciduous forest trees were 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 adaptations 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 AIC and/or 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

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 (Schrodt 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_a 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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