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

Tomas Ferreira Domingues[1,2] · F.Yoko Ishida[3,4] · Ted R. Feldpausch[5,6] · John Grace[1] · Patrick Meir[1] · Gustavo Saiz[7,8] · Olivier Sene[9] · Franziska Schrodt[5,10,11] Bonaventure Sonké[9] · Herman Taedoumg[9] · Elmar M. Veenendaal[12] Simon Lewis[5,13] · Jon Lloyd[✉,4,14].

[1]School of GeoSciences, University of Edinburgh, UK.

[2]Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil

[3]Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil

[4]Centre for Tropical Environmental and Sustainability Sciences (TESS) and School of Marine and Tropical Biology, James Cook University, Cairns, Qld, Australia.

[5]School of Geography, University of Leeds, UK.

[6]College of Life and Environmental Sciences, University of Exeter, UK.

[7] Centre for Tropical Environmental and Sustainability Sciences (TESS) and School of Earth and Environmental Science, James Cook University, Cairns, Qld, Australia.

[8]Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research, Garmisch-Partenkirchen, Germany

[9]Department of Biology, University of Yaoundé, Cameroon

[10]Max Planck Institute for Biogeochemsitry, Jena, Germany

[11]iDiv, German Centre for Integrative Biodiversity Research Halle, Jena - Leipzig, Germany

[12]Centre for Ecosystem Studies, University of Wageningen, The Netherlands

[13]Department of Geography, University College London, UK

[14]Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

Running title: Photosynthesis at the forest-savanna boundary

✉**Corresponding author:** email jonathan.lloyd@imperial.ac.uk

36   **Abstract** Photosynthesis/nutrient relationships of proximally growing forest and savanna trees

37   were determined across several sites within an ecotonal region of Cameroon (Africa). Although

38   area-based foliar nitrogen concentrations were typically lower for savanna trees there was no

39   difference in area-based photosynthetic rates between tree characteristics of the two vegetation

40   formation types. Overall savanna trees appear to use N more efficiently than their forest

41   counterparts. On the other hand, area-based phosphorus concentrations were – on average -

42   slightly lower for forest trees and with a dependency of photosynthetic characteristics on foliar P

43   only evident for savanna trees.   Compared to many other tropical regions, soils of the study area

44   were notably high in P. Thus the generality of the results in relation other woody plants of the

45   terrestrial tropics remains unclear.

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49 **Introduction**

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51 Forests and savannas are the dominant vegetation types of tropical regions (Walter and Mueller-

52 Dombois 1971) but differ fundamentally in their structural characteristics and species

53 composition (Torello-Raventos et al. 2013). The tree species associated with forest *versus* savanna

54 differ in numerous physiological characteristics such as fire survivorship (Hoffmann et al. 2009;

55 Ratnam et al. 2011) and leaf traits (Hoffmann et al. 2005). We have, however, an incomplete

56 knowledge on how the species differ in photosynthesis characteristics, e.g. in relation to the

57 control of rates of photosynthesis by nutrient availability. Although tropical forests are more

58 productive and comprise larger carbon stocks than tropical savannas, forest species often have

59 lower maximum photosynthetic carbon assimilation rates per area of leaf (Domingues et al.

60 2010; Hoffmann et al. 2005). This is a finding similar to when the leaves of evergreen tropical

61 forests are compared with those of temperate deciduous forests (Kattge et al. 2009; Meir et al.

62 2002) but a mechanistic explanation for such differences is lacking.

63 Although it has been widely demonstrated that photosynthetic capacity depends on the

64 leaf nitrogen content (Evans 1989; Field and Mooney 1986), in the tropics, where soils are old

65 and weathered, P limitation may be more typical (Reich and Oleksyn 2004; Reich et al. 2009) and

66 with likely links to stand level productivity (Mercado et al. 2011; Quesada et al. 2012). On the

67 basis of several lines of evidence, it has, however, also been suggested that, in contrast to tropical

68 forests, savannas may be more likely to be limited by N than P (Lloyd et al. 2009).

69 Our earlier work from West Africa has demonstrated that both Rubisco activity and

70 electron transport activity of African savanna and forest trees can potentially be limited by either

71 N or P; this depending on their relative concentrations in the leaf tissue (Domingues et al. 2010).

72 But interpretations of forest/savanna differences in that paper were complicated by the savanna

73   measurements coming from a wide range of precipitation regimes with soil types that were

74   extremely diverse.

75   Moreover, because trees from more arid regions had higher photosynthetic capacities at

76   any given level of N and/or P than those from more mesic areas, no simple model emerged as

77   generally applicable to all species examined. As the results represent a transect spanning a large

78   climatic gradient, they may, while representative for species of the investigated forest and

79   savanna types have been systematically biased in relation to site specific climatic conditions.

80   Insight into the plasticity of photosynthetic traits among forest and savanna species occurring

81   under similar climatic conditions is therefore crucial to understand the role of leaf physiology

82   when forest changes into savanna or vice versa.

83   Here we report on work from a naturally occurring forest/savanna mosaic in Central

84   Cameroon where we investigate photosynthetic and associated foliar trait characteristics of trees

85   and shrubs for forest and savanna species growing *in close proximity* and thus the same climatic

86   regime for which some areas of savanna are currently transforming into forest. We aim to test

87   the hypotheses that under similar climatic conditions in a zone of transition:

88   a) Scaling between foliar nitrogen and phosphorus is different for forest and savanna

89   species;

90   b) Photosynthetic nutrient efficiencies of savanna species are greater than those of the

91   forest species;

92   c) Species growing in savannas show more indications of nitrogen limitation than forest

93   species (which would in turn, be more likely to be limited by phosphorus).

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Material and Methods

97   Study location

98   Measurements were made during the end of the 2007 wet season (October/December) at the

99   Mbam-Djerem National Park, central Cameroon (Fig. 1). The area encompasses a transitional

100   zone between the Guinea-Congo/Sudan formations (Maisels 2004; White 1983) where savannas

101   co-exist with tall canopy forest and gallery forest in a mosaic characterised by relatively sharp

102   boundaries (Mitchard et al. 2009). Mean annual precipitation is estimated at about 1.6 m a^{-1}

103   (Hijmans et al. 2005).

104   Study plots

105   Measurements were made in seven permanent one-hectare plots chosen to contain three

106   recognizable vegetation groupings on the basis of their structure and species composition,

107   classified by Torello-Raventos et al. (2013) as follows: (i) "long-grass savanna woodland" (three

108   plots denoted MDJ-02, MDJ-04 and MDJ-08, these all having a fractional grass cover of greater

109   than 0.1 and a height exceeding 1.0 m with woody strata fractional canopy cover (ς) between

110   0.25 and 0.50 and with an average height (H) between 6 and 12 m for trees with a diameter at

111   breast height (D) greater than 0.1 m); (ii) three plots within the broad "forest" groupings of

112   Torello-Raventos et al. (2013) (H > 12 m, ς > 0.5) and there being one "axylale-rich forest"

113   (MDJ-01) one "shrub-rich forest" (MDJ-03) and one "tall forest" (MDJ-07). Finally, we included

114   (iii) the "transitional forest" of Torello-Raventos et al. (2013) represented by a single plot MDJ-

115   05. This is an area which was once savanna, but which had recently been invaded by forest

116   species as described for our study area (Mitchard et al. 2011). For the interested reader,

117   photographs of this site as well as MDJ-04 (long grass savanna) and the forested MDJ-01 and

118   MDJ-03 are provided in Fig. 6 of Torello-Raventos et al. (2013).

119   Site characterisation

120   Biodiversity indices and measurements of plot structure were determined from measurements as

121   detailed in Torello-Raventos et al. (2013). Soil sampling and associated measurements were made

122   as described in Quesada et al. (2010) and Veenendaal et al. (2014).

123   Gas exchange characteristics

124   Data were obtained from 196 leaves fully exposed to the sun sampled from 69 individuals

125   representing 42 species of adult perennial C3 trees and shrubs (Appendix A). Within each plot

126   the quantitatively dominant species were selected, and measurements made for photosynthetic

127   capacity (A-C_i curves), leaf nutrients and leaf mass per unit area (M_a). Methodological details

128   follow Domingues et al. (2010), with a simple modification introduced for estimation of the two

129   key photosynthetic capacity parameters (V_{cmax}, the maximum rate of carboxylation and J_{max}, the

130   maximum rate of electron transport) optionally incorporating a mesophyll conductance term (g_m)

131   (Warren 2008) into the parameter estimation routine. The parameter g_m is difficult to estimate

132   from CO_2 response curves and the approach adopted in the present work followed two steps. A

133   curve fit based on CO_2 concentrations at the intercellular air spaces (C_i) as reported in

134   Domingues et al. (2010) was performed first to generate initial values of the photosynthetic

135   capacity parameters ($V_{cmax-Ci}$ and J_{max-Ci}). Next, a second curve fit was performed incorporating g_m

136   in order to calculate CO_2 concentrations at the sites of carboxylation (C_c) using the $V_{cmax-Ci}$ and

137   J_{max-Ci} values as a starting point for the iteration process. To make our data comparable, the

138   parameter fits for V_{cmax} and J_{max} were scaled to a reference temperature (25°C) as described in

139   Bernacchi et al. (2001).

140   Usually three replicates (leaves) were sampled from each individual plant sampled in this

141   study, and up to three, but sometimes one or two individuals of the same species were sampled

142   at a given plot (Appendix A). When possible measurements were taken directly from tree

143   branches, but often branches were detached from trees and smaller stems were then immediately

144   recut under water.

145   Statistical and modelling analysis

146   For statistical comparisons of leaf traits among plots, species averages within each plot were

147   computed after first taking averages from replicated samples of individual plants. Statistical

148   inferences on the relationships of photosynthetic capacity parameters and associated leaf traits

149   (nutrients and/or structure) were based on both simple and multiple linear regressions using

150   values derived from determinations on individual leaves. Data were $\log_{10}$ transformed before

151   standardized major axis (SMA) (Warton et al., 2006) analyses but not before the application of an

152   area version of a dual-limitation model of nitrogen and phosphorus introduced by Domingues

153   et al. (2010) and here employed on an area basis *viz*.

154
$$v_{\max} = \min \begin{Bmatrix} a_N + b_N[N]_a \\ a_P + b_P[P]_a \end{Bmatrix} \quad , \quad (1)$$

155   where $v_{\max}$ is either V_{cmax} or J_{ma}, a_N and a_P are intercepts and b_N and b_P are slopes empirically

156   derived from fitting the model to the data. Model comparisons were based on evaluations of

157   Akaike information criteria (AIC) and Bayesian information criteria (BIC). Bootstrapping

158   analysis (Chernick and LaBudde 2011) were applied in order to derive confidence intervals for

159   parameters originated from the application of the dual-limitation model (Eq. 1) All statistical

160   analysis was conducted using the statistical environment R (R Development Core Team 2011).

161

162   **Results**

163   Assignment of species to the forest or savanna guilds

164   As described in detail by Torello-Raventos et al. (2013), species found within the forest-savanna

165   ecotone can usually be classified as belonging to 'forest' or 'savanna' based on their observed

166 distribution, although a small degree of overlap inevitably occurs. This is illustrated in Fig. 2

167 where the distributions of tree/shrub species $(D > 0.1$ m) are represented using a Venn-Euler

168 diagram. Here, the number of plant species found in more than one vegetation type is

169 represented numerically and proportionally by the areas of intersection among the circles. There

170 were only 8 out of the 164 species observed in the seven study plots that occurred in both forest

171 and savanna - see also Table E1 of the Supplementary Information of Torello-Raventos et al.

172 (2013). The transitional forest (MDJ-05) did, however, contain many savanna species, and several

173 species occurring in neither nearby forest nor nearby savanna plots.

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175 Stand properties

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177 Consistent with Fig. 2 a larger variety of families, genera and species were found at the forest

178 sites (Table 1). Not surprisingly, the forest plots also had larger stem density and larger basal area

179 (Table 1). The transitional forest plot MDJ-05 had the highest stem density but that added to a

180 low total basal area (Table 1). That plot also showed a relatively large number of dead standing

181 savanna trees (data not shown).

182   The measured upper layer soil physical and chemical properties (0.0-0.3 m) also varied

183 substantially amongst plots but not consistently between the two main study vegetation types

184 (Table 1). For example, effective cation exchange capacity (the sum of exchangeable bases plus

185 aluminium) was highest at plot MDJ-01 (forest) and MDJ-08 (savanna) and with other plots for

186 both forest and savanna having only about one third of those values while total soil phosphorus

187 varied between 307 and 977 μg g^{-1} for the forest plots and 316 and 997 μg g^{-1} for the savanna

188 plots. One upper layer measured soil parameter found to have a significant difference (t-test

189 assuming unequal variances) between forest and savanna was the C:N ratio ($p = 0.02$), this being

190 higher for the savanna plots.

191   Leaf traits

192   A partitioning of the measured trait variation between plots, species, individual trees, and a

193   residual component (this representing the average variation between leaves within any given tree

194   plus any experimental error) is shown in Fig. 3. For leaf mass per unit area (M_a) and nitrogen per

195   unit area N_a, this shows that most of the variation not due to plot location was attributable to

196   species identity with the proportion of variation between trees of the same species and 'residual

197   variation' (i.e. attributable to within tree variability and experimental error) being relatively small.

198   By contrast, for P_a and the light/CO_2 saturated assimilation rate ($A_{max,a}$) most of this variation

199   was within species or within individual trees themselves (Fig. 3). In view of this inconsistent

200   pattern of variation among traits, we undertook all analyses on a 'leaf-wise' basis rather than

201   deriving individual tree means or some sort of (often cross-plot) species average value.

202   Despite often considerable overlap between leaf attributes found in forest versus

203   savanna, some differences are striking (Fig 4). For example, forest leaves typically had a lower

204   M_a, higher N_m, a lower P_a and a higher ratio of nitrogen to phosphorus (N:P). Also shown in Fig.

205   4 are the equivalent data for forest and savanna from the ZOT component of the West African

206   study of Domingues et al. (2010). This shows some interesting differences, the statistically

207   significant of which are evaluated – along with a comparison for the Cameroon forest species

208   with South American forest - in Table 2. Taken together, Table 2 and Fig. 4 show several intra-

209   and cross-continental differences.

210   Focussing first on the current study (Comparison 1) we find forest ($\mathbb{F}$) leaves to have a

211   higher N content than savanna ($\mathbb{S}$) leaves, and this is both on an area and a mass basis. The

212   effect of vegetation formation type ($\mathbb{V}$) on foliar phosphorus contents was, however, rather

213   small; though with significantly higher for $\mathbb{F}$ on an area basis. Despite the differences between $\mathbb{F}$

214   and $\mathbb{S}$ in both N_a and P_a (which we also point out were of opposite sign), there was no effect of

215    $\mathbb{V}$ on $A_{sat,a}$ (Table 2: Comparison 1).

216   Also in Table 2 (Comparison 2) we compare the significance of differences between

217   forest leaves from this study in Cameroon with the earlier study from West Africa. Noting that

218   the methodology was the same in the two locations, we find West African ZOT forest leaves to

219   have had significantly lower M_a, N_a and $A_{sat,a}$ than for Cameroon, but with about the same P and

220   N and A_{sat} on a mass basis.

221   The corresponding comparison for savanna also showed West African leaves to have a

222   lower M_a, but with their nitrogen concentration, and on a leaf mass basis, photosynthetic rates

223   basis no lower than for Cameroon. Nevertheless, because of the lower M_a in West Africa, $A_{sat,m}$

224   were higher and with this also being associated with higher P_m and N_m (Table 2).

225   Finally, to help put our study in a broader perspective we compared our Cameroon

226   forest data with that obtained from the forests of the Amazon Basin (Fyllas et al. 2009; Fyllas et

227   al. 2012). That study classified Amazonian sites into two soil fertility groups on the basis of their

228   soil chemical properties and demonstrated that 'low nutrient soil' forests have lower leaf N and P

229   on both an area and mass basis, and also with higher N:P ratios than those of our Cameroon

230   study area (Table 2). On the other hand, leaves from sites classified as 'high nutrient soil' by

231   Fyllas et al. (2009) were very similar in composition to our Cameroon sites on both a mass and

232   area basis. We therefore conclude that the African forest species sampled here are quite similar in

233   their nitrogen and phosphorus concentrations to trees occurring on the more fertile soils of the

234   Amazon Basin. As M_a are, on average, similar, this is true on both an area and mass basis and

235   with African forests studied here differing from Amazon Basin forests on lower nutrient status

236   soils mostly in terms of a higher leaf phosphorus status.

237

238   Bivariate relationships

239

240   Concentrating again on the Cameroon data, Figure 5 shows the associations between $A_{sat,a}$, M_a,

241   N_a and P_a where - noting that all savanna species were deciduous – see (Schrodt et al. 2014) we

242   have differentiated forest species according to their leaf habit (evergreen *vs.* deciduous).

243   Working, at the same sites in Cameroon as well as in West Africa, Schrodt et al. (2014) found

244   this division justified on the basis of a multivariate analysis of a range of leaf traits (cation and

245   carbon contents as well as M_a, N_m and P_m).

246   Although the relationship between $A_{max,a}$ and M_a was not significant for either of the

247   forest habit types, we found that for the deciduous savanna species (S_d), there was a statistically

248   significant positive relationship (p=0.038) with a (common) SMA slope of 0.13 µmol CO_2 g^{-1}

249   DW s^{-1} but with a clear difference in intercept as compared to the two forest types (Fig. 5a). That

250   is to say, for any given M_a savanna species (S_d) tend to have a lower $A_{sat,a}$ than either of the forest

251   habit types. When examined as a function of N_a, all three habitat groupings showed statistically

252   significant relationships ($p < 0.10$) with S_d having a photosynthetic rate about 2.5 µmol CO_2 m^{-2}

253   s^{-1} greater than the forest species at any given N_a (common slope of 5.90 µmol CO_2 g^{-1} N s^{-1})

254   Relationships between $A_{sat,a}$ and P_a were significant only for S_d (slope = 74 µmol CO_2 g^{-1} P s^{-1}; $p <$

255   0.05) and with data for the forest evergreen leaves (F_e) even suggesting a negative relationship -

256   albeit a non-significant one (Fig. 5c). The N_a: P_a relationship was statistically significant for both

257   deciduous types, with a clear difference in elevation with S_d typically having a P_a about 0.04 g m^{-2}

258   greater than their deciduous forest counterparts (F_d) at any given N_a (Fig. 5d).

259   For all four bivariate relationships investigated there were no clear indications of trees

260   sampled from transitional vegetation being distinct from those of either the (non-transitional)

261   forest or savanna vegetation types. Overall, we may conclude from Fig. 5 that the strongest

262   relationship is between $A_{sat,a}$ and N_a and with the deciduous savanna species emerging as being

263   markedly different from both forest species types, in particular, exhibiting a substantially higher

264   mean $A_{sat,a}$ for any given N_a. In addition, unlike the forest species, there is also a dependence of

265   savanna species $A_{sat,a}$ on P_a. At any given N_a there was more P in the savanna leaves (Fig 5d).

266   Variations in Rubisco and electron transport capacities in relation to N and P

267   Although one would ideally like to model variations in both V_{cmax} and J_{max} in terms of the partial

268   pressure of CO_2 in the chloroplast (C_c) this requires some reliable measure of the leaf "internal"

269   conductance (g_m). Nevertheless, for the study here, both V_{cmax} and J_{max} ended up being estimated

270   directly from the A-C_i curve with the associated kinetic constants for $g_m = \infty$ applied (Von

271   Caemmerer 2000). We made this decision on the basis of a) there being no significant

272   relationship between our curve-fitting derived estimates of g_m and traits previously considered to

273   co-vary with it (*viz*: M_a or $\delta^{13}C$; (Niinemets 1999); b) there being no consistent differences in

274   apparent g_m between vegetation types and c) there was little systematic difference observed

275   between C_c and C_i (intercellular spaces) based estimates of these photosynthetic parameters (Fig.

276   S1).

277   For these C_i analyses of the nutrient dependencies of V_{cmax} and J_{max} we also included data from

278   the West African transect ZOT in Ghana (Domingues et al. 2010) so as to increase both the

279   sample size and the variation of N and P observed.

280   Details of area-based photosynthesis-nutrient relationships as found for simple OLS

281   linear models and the more complex dual-limitation model of Eq. (1) are shown in Table 3. For

282   F_e the best fit according to the Akaike's Information Criterion (*AIC*) was the simple linear model

283   wherein V_{25} is a simple function of N_a (r^2=0.17, p=0.002) and with the Bayes Information

284   Criterion (*BIC*) – similar to the *AIC* but with more severe penalties for extra terms – giving the

285   same rank. Of the linear models a simple dependence of V_{25} on N_a also gave the best fit

286   according to the *BIC*, (r^2=0.21, p=0.001) but the alternative dual-limitation model of nitrogen

287   and phosphorus (Domingues et al. 2010) being marginally better according to the *AIC* (r^2=0.23,

288   p=0.001). Note, however, that in this model the P_a term is negative, suggesting an inhibitory

289   effect of phosphorus on V_{25}. Overall, the results for the two forest types were similar: so when

290   combined there was, not surprisingly, an increase in the correlation coefficient values for the N_a

291   based models with the *AIC* suggesting the dual-limitation model ($r^2 = 0.29$) to be marginally

292   superior to the simple N_a based linear model which was unambiguously favoured when

293   considering the *BIC*. Note that in none of the forest cases was there any indication for a role for

294   P_a as a modulator of V_{25} when considered on its own ($r^2 \lesssim 0.01$), and with P_a having only a

295   marginal influence when considered in conjunction with N_a.

296   In contrast, for S_d it was found that P_a was nearly as good a predictor as N_a when

297   considered on its own ($r^2 = 0.18$ *vs.* 0.19) and with the linear model fits including both terms

298   being significantly better when either N_a or P_a were considered on their own. Overall, the dual-

299   limitation model was, nevertheless, found superior to the OLS models according to both the

300   *AIC* and *BIC* (r^2=0.30, $p < 0.001$). Although a simple combination of the forest and savanna data

301   suggest that the dual-limitation model is not the best when looking for a common (cross-biome)

302   relationship– in this case it being surpassed by a model containing linear functions of N_a and P_a

303   and their interaction term N_a and P_a – a simple analyses of *AIC/BIC* and/or the residual sum of

304   squares (*RSS*) according to a procedure outlined in Lloyd et al. (1989) also shows that this

305   combined (forest + savanna) model provides an inferior fit compared to when forest (*i.e.* F_d and

306   F_e together) and savanna (S_d) are considered separately ($p < 0.001$). That is to say, although for

307   the forest species V_{25} showed a simple dependency upon N_a, for S_d an additional role for P_a is

308   clearly implicated.

309   A similar picture emerges when models for J_{25} are sought with little evidence of a role for

310   P_a as a modulating factor for either F_d or F_e and with N_a effects apparently much more important

311   for these two forest types (Table 4). As for V_{25} there is, however, a clear indication of a role for

312   P for S_d, and with the dual-limitation model giving the best fit. Likewise, when all data are

313   combined, then comparisons of either *AIC, BIC* or *RSS* with the individual models shows that in

314   any analyses of their J_{25} nutrient dependencies, forest and savanna species need to be considered

315   separately.

316   Fitting separate relationships for both forest and savanna, the resulting goodness of

317   model fit is shown for both V_{25} and J_{25} in Fig. 6. This shows that in all cases, model predictions

318   involved a much smaller degree of variation than suggested by the observations. An examination

319   of model residuals in terms of the predictor variables N_a and P_a along with a range of other

320   potentially confounding covariates such as M_a and area-based cations (see Figs S2 and S3) did not

321   however, suggest reasons for concern in terms of any trait specific systematic bias for either V_{25}

322   or $J_{25.}$

323   For both V_{25} and J_{25} the observed relationships with N_a and P_a are shown in Fig. 7. Here

324   for forest we have shown the fitted lines for the modelled simple linear N_a dependencies for

325   both V_{25} and J_{25} but with the   dual-limitation model predictions presented for S_d. This

326   differentiation has been made on the basis of a bootstrapping analysis (Chernick and LaBudde

327   2011) of the savanna dual-limitation model results which showed that for both V_{25} and J_{25} the

328   (apparently negative) V_{25} and P_a term was not significantly different from zero (see Table S1 in

329   supplementary material). For V_{25} our model suggests that savanna leaves with $N_a < 2.5$ g m^{-2}

330   have a higher carboxylation capacity than forest leaves (Fig. 7a)

331   Consistent with the simple linear $V_{25} = fN_a$ model being applied for the forest species,

332   no fitted lines are shown for the forest species for the P_a relationships of Figs 6b and 6d. In both

333   cases, the bootstrapping analysis did, however, show the savanna co-limitation model P_a slope to

334   be significant with a 0.95 confidence interval for V_{25} of 190 - 375 µmol CO_2 g^{-1} P s^{-1} with the

335   equivalent range being 246 - 539 µmol CO_2 g^{-1} P s^{-1} for J_{25}.

336   Also shown for all four panels of Fig. 7 are fitted relationships from the original

337   application of the dual-limitation model of (Domingues et al. 2010) to a wide range of West

338   African tree species and location, including with a much drier climate (grey lines). In all cases the

339   "West African" slopes are much steeper than found here for Cameroon, where the analysis has

340   been confined to two forest-savanna transition zones and with differences at high N_a and P_a

341   being particularly marked.

342

343

Discussion

345

346   The question of whether the productivity of tropical forests and woodlands is controlled by the

347   availability of nitrogen or phosphorus has long been under debate (Alvarez-Clare et al. 2013;

348   Sollins 1998; Vitousek et al. 2010). Tropical soils are highly diverse and they are generally (but

349   not always) old, highly weathered and low in cation exchange capacity (Jordan and Herrera 1981;

350   Peh et al. 2011; Proctor 1987; Quesada et al. 2011; Silver 1994; Uehara and Gilman 1981; Wright

351   et al. 2011; Young 1980). Many authors have hypothesised that growth over much of the tropics,

352   in contrast to the temperate zone, is controlled by the availability of phosphorus rather than

353   nitrogen, and there have been a number of experimental studies designed to test that hypothesis

354   (Burslem et al. 1995; Gunatilleke et al. 1997; Mirmanto et al. 1999; Newbery et al. 2002;

355   Palmiotto et al. 2004). The results have been equivocal, partly because (with few exceptions, see

356   for example Tanner et al. (1998) and Alvarez-Clare et al. (2013)) the experiments have been

357   conducted on seedlings which are still in the processes of establishing, and partly because there

358   appears to be inherent variation in the behaviour of different species, perhaps reflecting a varied

359   evolutionary history and different selection pressures during the Late Glacial Maximum when

360   tropical forests retreated into refugia (Anhuf et al. 2006; Prentice et al. 2011). In the present

361   work we were able to evaluate the relative importance of N and P in the control of

362   photosynthesis of a sample of many species of mature trees in two contrasting types of

363   vegetation which were growing under identical climatic conditions in Central Africa

364   The pattern of variation in the photosynthetic data showed that the area-based nitrogen

365   content of leaves, N_a, was strongly a species-specific attribute, whilst for phosphorus it was more

366   the case that P_a varied within individuals of the same species (Fig. 3). Using as our individual unit

367   of variation the individual leaf (rather than the tree or species), the best-fitting relationship

368   between the photosynthetic parameters $V_{c(max)}$ and J_{max} for both evergreen and deciduous forest

369   trees was a simple linear relationship with N_a, and there was no relationship at all when a linear

370   model with phosphorus content was tested. In contrast, the savanna species (all of which were

371   deciduous) showed significant relationships with P_a as well as with N_a – albeit with a different

372   nitrogen dependence to that found for the forest species. For the savanna species the best model

373   was the dual-limitation model which may be considered as one application of Liebig's Law of

374   the Minimum, whereby photosynthesis is controlled not by the total amount of nutrients

375   available, but by the one most limiting to carbon uptake. One might speculate that $V_{c(max)}$ would

376   be more limited by N because of the importance of nitrogen in ribulose-1,5 bisphosphate

377   carboxylase/oxygenase (Rubisco) whilst J_{max} would be more limited by P, because of the

378   importance of phosphorus intermediates in energy flow during photosynthesis (Morcuende et al.

379   2007). But this is not so in our data, presumably because carboxylation and electron transport are

380   so tightly coupled *in vivo* (see also Bloomfield et al. (2014))

381   With leaves intercepting light on a per-unit area basis and spurious correlations possible

382   when two unrelated area-based entities are transformed to a mass basis – the so called 'lulu

383   effect' (Lloyd et al. 2013) - we see for the current paper no practical reason to analyse our

384   photosynthesis-nutrient dependencies on per-unit mass basis (see also Osnas et al. (2013).

385   Nevertheless, for the purposes of illustration our area-based analysis is repeated on a mass basis

386   as part of the Electronic Supplementary Material. This shows - in addition to the inevitable

387   higher correlations associated with a 'common-element' correlation (Lloyd et al. 2013) – that for

388   the forest species it is more often than not the more complex models involving not only both

389   N_m and P_m, but also their interaction that have the lowest *AIC* and/or *BIC* (Tables S2 and S3).

390   This is as opposed to the simple forest species linear nitrogen dependency for both V_{25} and J_{25}

391   for the area-based fits. Overall there results are consistent with the assertion that in multivariate

392   cases a simple area-to-mass conversion can easily give rise to variables not actually associated

393   with the dependent variable appearing to be functionally linked .(Lloyd et al. 2013). We also note

394   that whilst the area-based models showed little bias in their residuals when examined as a

395   function of M_a. N:P and a range of area based leaf-nutrient measures (Figs S2 and S3), this was

396   not the case for the mass-based models for which there was a bias towards positive residuals at

397   low M_a(Figs S4 and S5).

398   With our earlier analyses using the formulation of Eqn. 1 having actually focussed on

399   mass-based model fits (Domingues et al. 2010), this then raises the obvious question to what

400   extent are some previous conclusions of Domingues et al. (2010) regarding the relative roles on

401   N and P still valid? In answer, with only minor modifications they still hold. For example, in that

402   paper we also showed that area-based fits of the min-min model implied a role for both N and P

403   as alternate limiting factors for photosynthesis (in addition to the mass based models) and with

404   area-based comparisons with simple linear models also showing the min-min model to have the

405   lowest *AIC*. Indeed, the analysis here should be best considered a refinement of the work of

406   Domingues et al. (2010), probing further into the nature of the apparent different

407   nutrient/photosynthesis relationships identified for species associated with the different rainfall

408   environments first identified there. Within Domingues et al. (2010) we also discussed at length

409   possible reasons for forest trees having an apparent less efficient use of N: with these focussing

410   on including increased allocation of N to non-photosynthetic compounds when conditions

411   favouring a longer leaf longevity are also combined with a more variable light environment.

412   That when growing under the same climatic conditions we have now found forest trees

413   photosynthesis to be less sensitive to variations in P_a than for savanna species (at least at the

414   foliar concentrations apparent in this study which were relatively high: see Table 2) requires,

415   however, further explanation and biome history may be important here, For example any forest

416   refugia in Africa at the LGM (Anhuf et al. 2006) would have been most likely to have occurred

417   where both precipitation regime and soil conditions remained most favourable for forest tree

418   function. So, with deeper tropical soils of a high water holding capacity also typically being of a

419   low phosphorus status due to their long history of extreme weathering (Quesada et al. 2010),

420   specific adaptions to a chronically low P_a for forest trees seem likely, for example in the

421 replacement of phospholipids by galactolipids and sulfolipids under condition of low P-supply

422 (Lambers et al. 2012; Tjellström et al. 2008; Zhang et al. 2014). The question remains, however,

423 as to the extent to which the original parameterisation of Domingues et al. (2010), or the new

424 forest parameterisation developed here, validly apply to tropical forest trees growing on low-P

425 availability soils, such as those which cover much of the eastern Amazon Basin (Quesada et al.

426 2011), especially as already investigated as part of the modelling studies of Mercado et al. (2011)

427 and Fyllas et al. (2014). Trees on such soils do, nevertheless, typically have a foliage of a much

428 lower P_a than encountered here (Table 2) and so it will only be with further dedicated

429 measurements under the full spectrum of P_a:N_a variability and across a range of different growth

430 forms that we will be able to ascertain the generality (or most likely otherwise) of any

431 photosynthesis-nutrient relationships developed.

432   Most likely the dual-limitation model applies because for some specific locations and/or

433 for some particular times of the year, phosphorus is rate-limiting whilst for other times/places it

434 is nitrogen which constrains photosynthetic productivity. As for the Amazon Basin forest case

435 discussed above, these regional variations, arising mostly from soil variations – but also clearly

436 depending on vegetation formation type - will give rise to variations in the rates of

437 photosynthesis, and these are presumably important when parameterizing global vegetation

438 models - for example Sitch et al. (2008) and Piao et al. (2013) – placing great importance on the

439 development of realistic models of ecosystem N and P cycling that include soil biogeochemical

440 processes in a realistic manner (Fisher et al. 2010; Goll et al. 2012; Ostle et al. 2009; Thomas et

441 al. 2013; Xu et al. 2012; Yang et al. 2013).

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444   **Acknowledgments**

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	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_2O)	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, $\mu g\ g^{-1}$	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)							
M_a, $g\ m^{-2}$	80±31	97±26	109±21	113±41	136±23	127±26	135±32
V_{25}, $\mu mol\ m^{-2}\ s^{-1}$	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
J_{25}, $\mu mol\ m^{-2}\ s^{-1}$	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
N_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
P_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
$\delta^{13}C$, ‰	-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

Table 1. Soil and vegetation properties of the study plots. 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.

Location	Vegetation Formation Type	M_a (g m^{-2})	N_a (g m^{-2})	P_a (g m^{-2})	$A_{sat,a}$ (μmol m^{-2} s^{-1})	N_m (mg g^{-1})	P_m (mg g^{-1})	N:P (g g^{-1})	$A_{sat,m}$ (μmol g^{-1} 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	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**	0.11ns	8.6***	24.7ns	1.37***	18.6*	0.105ns
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***	1.73ns	0.14ns	9.8ns	18.5***	1.68***	12.7ns	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	95ns	2.09ns	0.11ns	ND	21.6**	1.11ns	19.4*	ND

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). Asterisks denote the result of a Kruskal-Wallace test of significance (*p<0.05, ** p <0.01,*** p <0.001). 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})

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
$V_{25} = 7.71 + 19.37N_a + 143.95P_a - 78.49N_aP_a$	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 & Deciduous)				
$V_{25} = 18.61 + 12.03N_a$	0.27	1208.24	**1217.39**	<0.001
$V_{25} = 38.95 + 46.60P_a$	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
$V_{25} = 11.02 + 16.96N_a + 64.75P_a - 41.37N_aP_a$	0.27	1210.75	1226.00	<0.001
$V_{25} = \min(12.83 + 15.22N_a; 57.43 - 34.33P_a)$	**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
$V_{25} = 6.44 + 17.70N_a + 118.70P_a - 51.98N_aP_a$	**0.29**	**2141.92**	**2160.10**	<0.001
$V_{25} = \min(22.13 + 10.46N_a; 75.85 + 19.52P_a)$	0.25	2154.39	2173.56	<0.001

Table 3. Comparisons of predictive models of area based maximum carboxylation capacity (V_{cmax}-area 25 °C; µmol m^{-2} s^{-1}) based on leaf nitrogen and/or phosphorus content. Coefficients in black are significantly different from zero ($p < 0.01$); coefficients in red are not significantly different from zero ($p > 0.05$) and; coefficients in green are marginally different from zero ($0.01 > p > 0.05$): N_a = nitrogen per unit leaf area (g m^{-2}); P_a = phosphorus per unit leaf area (g m^{-2}).

	r^2	AIC	BIC	p
Forest Evergreen				
$J_{25,a} = 32.69 + 21.14N_a$	**0.18**	**426.88**	**432.68**	0.001
$J_{25,a} = 64.15 + 64.28[P]_a$	0.02	436.24	442.03	0.181
$J_{25,a} = 32.66 + 20.68N_a + 8.58P_a$	0.16	428.85	436.58	0.005
$J_{25,a} = 28.78 + 22.89N_a + 48.23P_a - 21.78N_aP_a$	0.15	430.81	440.47	0.015
$J_{25,a} = \min(32.69 + 21.14N_a; 78.99 + 64.40P_a)$	0.16	429.88	440.54	0.028
Forest Deciduous				
$J_{25,a} = 40.42 + 19.60N_a$	0.24	946.15	**954.12**	<0.001
$J_{25,a} = 83.76 - 9.89P_a$	-0.01	975.38	983.34	0.888
$J_{25,a} = 49.03 + 21.89N_a - 121.73P_a$	0.25	944.48	955.10	<0.001
$J_{25,a} = 25.94 + 32.89N_a + 99.60P_a - 101.93N_aP_a$	0.26	945.34	958.61	<0.001
$J_{25,a} = \min(30.05 + 24.93N_a; 105.64 - 55.54P_a)$	**0.26**	**945.12**	959.39	<0.001
Forest (Evergreen & Deciduous)				
$J_{25,a} = 35.21 + 21.30N_a$	0.29	1376.58	**1385.73**	<0.001
$J_{25,a} = 73.34 + 62.94P_a$	0.01	1428.19	1437.34	0.172
$J_{25,a} = 38.25 + 22.58N_a - 52.86P_a$	0.29	1376.94	1389.14	<0.001
$J_{25,a} = 15.48 + 34.54N_a + 164.81P_a - 109.80N_aP_a$	0.29	1376.58	1391.83	<0.001
$J_{25,a} = \min(26.97 + 25.76N_a; 105.46 - 59.78 P_a)$	**0.30**	**1374.66**	1390.91	<0.001
Savanna (Deciduous)				
$J_{25,a} = 45.60 + 14.01N_a$	0.23	861.59	869.44	<0.001
$J_{25,a} = 46.59 + 170.38P_a$	0.18	868.26	876.11	<0.001
$J_{25,a} = 40.56 + 10.27N_a + 83.73P_a$	0.25	859.78	870.24	<0.001
$J_{25,a} = 21.18 + 21.91N_a + 178.51P_a - 53.96N_aP_a$	0.26	859.05	872.12	<0.001
$J_{25,a} = \min(51.28 + 13.06N_a; 29.55 + 337.17P_a)$	**0.29**	**855.17**	**869.25**	<0.001
Forest and Savanna (Deciduous and Evergreen)				
$J_{25,a} = 38.23 + 19.42N_a$	0.30	2431.46	2442.36	<0.001
$J_{25,a} = 68.53 + 68.45P_a$	0.02	2528.29	2539.19	0.017
$J_{25,a} = 40.06 + 20.09N_a - 26.70P_a$	0.30	2432.37	2446.90	<0.001
$J_{25,a} = 15.87 + 32.06N_a + 149.52P_a - 83.38N_aP_a$	**0.33**	**2421.91**	**2440.09**	<0.001
$J_{25,a} = \min(29.42 + 24.36N_a; 97.57 + 6.46P_a)$	0.33	2422.10	2441.28	<0.001

Table 4. Comparisons of predictive models of area based maximum electron transport rate (J_{max}-area 25 °C; µmol m^{-2} s^{-1}) based on leaf nitrogen and/or phosphorus content. Coefficients in black are significantly different from zero ($p < 0.01$); coefficients in red are not significantly different from zero ($p > 0.05$) and; coefficients in green are marginally different from zero ($0.01 > p > 0.05$): N_a = nitrogen per unit leaf area (g m^{-2}); P_a = phosphorus per unit leaf area (g m^{-2}).
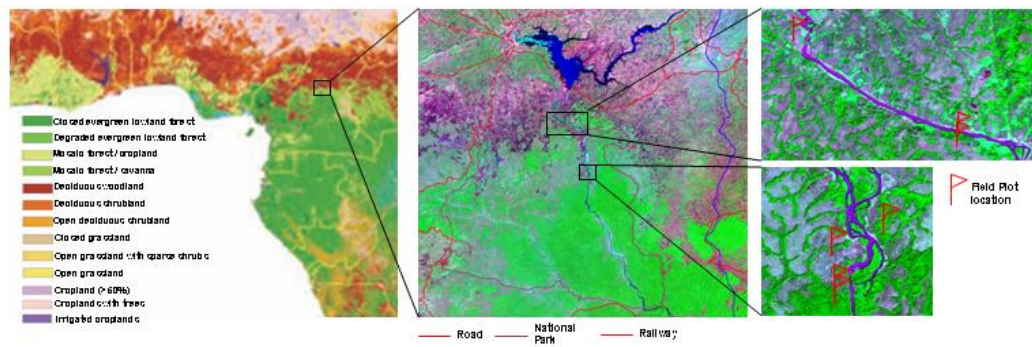
Fig. 1 A section of a vegetation map of Africa taken from Mayaux et al. (2004), showing the location of the study area within Cameroon (left panel) with field plot locations within the forest/savanna mosaic shown (centre and right hand panels). The latter come from the satellite imagery analysis of Mitchard et al. (2009) for which forest areas are typically green with savanna areas blue.
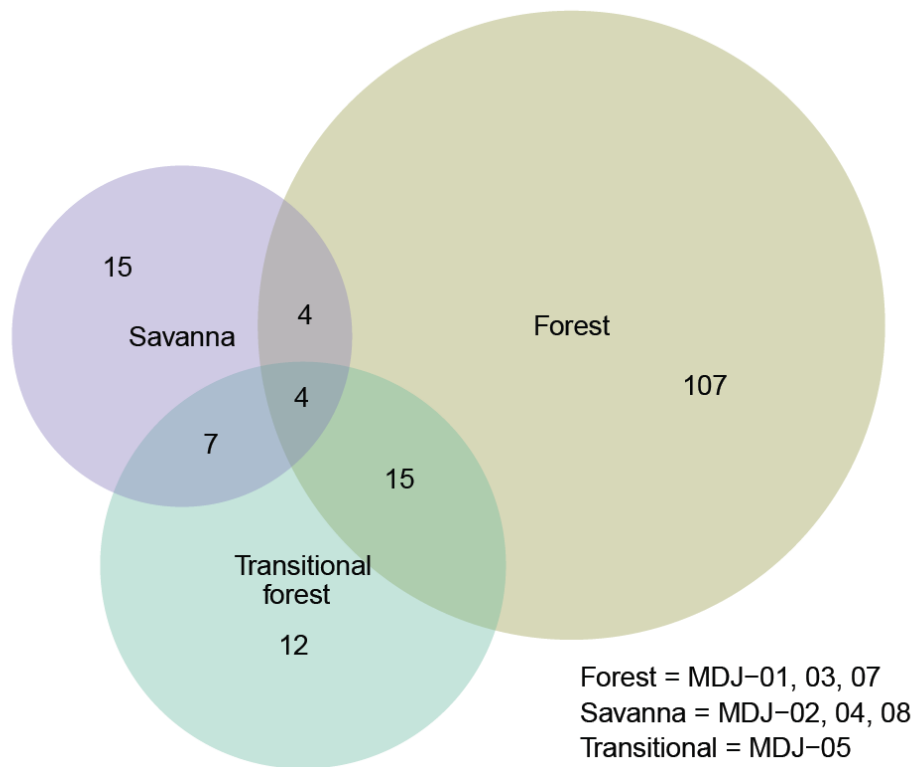
Fig. 2 Venn-Euler diagram showing the abundance of tree species across sample plots considered as "forest", "savanna" and "transitional forest" according to the classification of Torello-Raventos et al. (2013). Numbers refer to number of individual species.
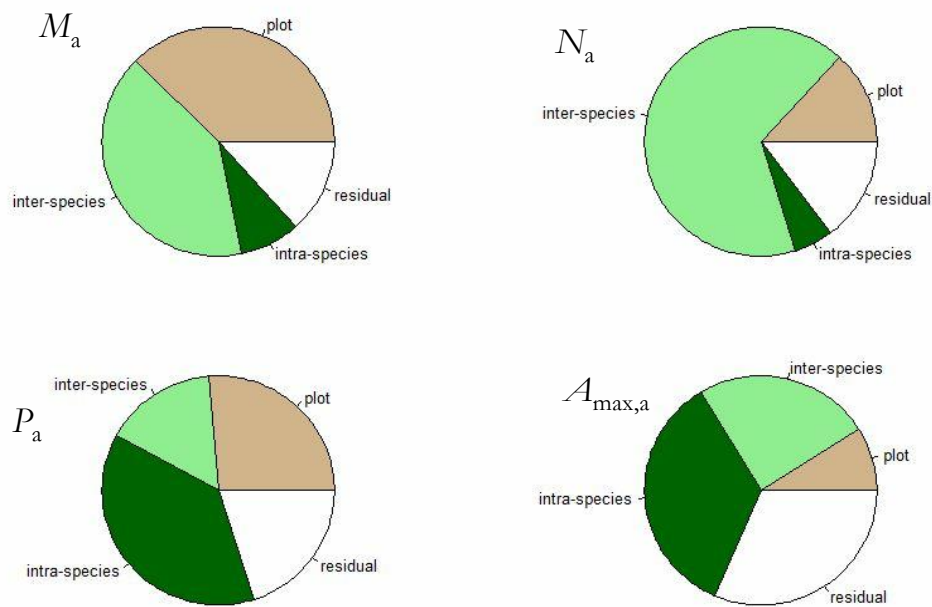
Fig. 3 Partition of the total variance between plots, species, individual trees. The residual term includes between-leaf variation and experimental error: M_a = leaf mass per unit area; N_a = nitrogen per unit leaf area; P_a = phosphorus per unit leaf area; $A_{max(a)}$ = Net CO_2 assimilation rate per unit leaf area at saturating light and $[CO_2]$.
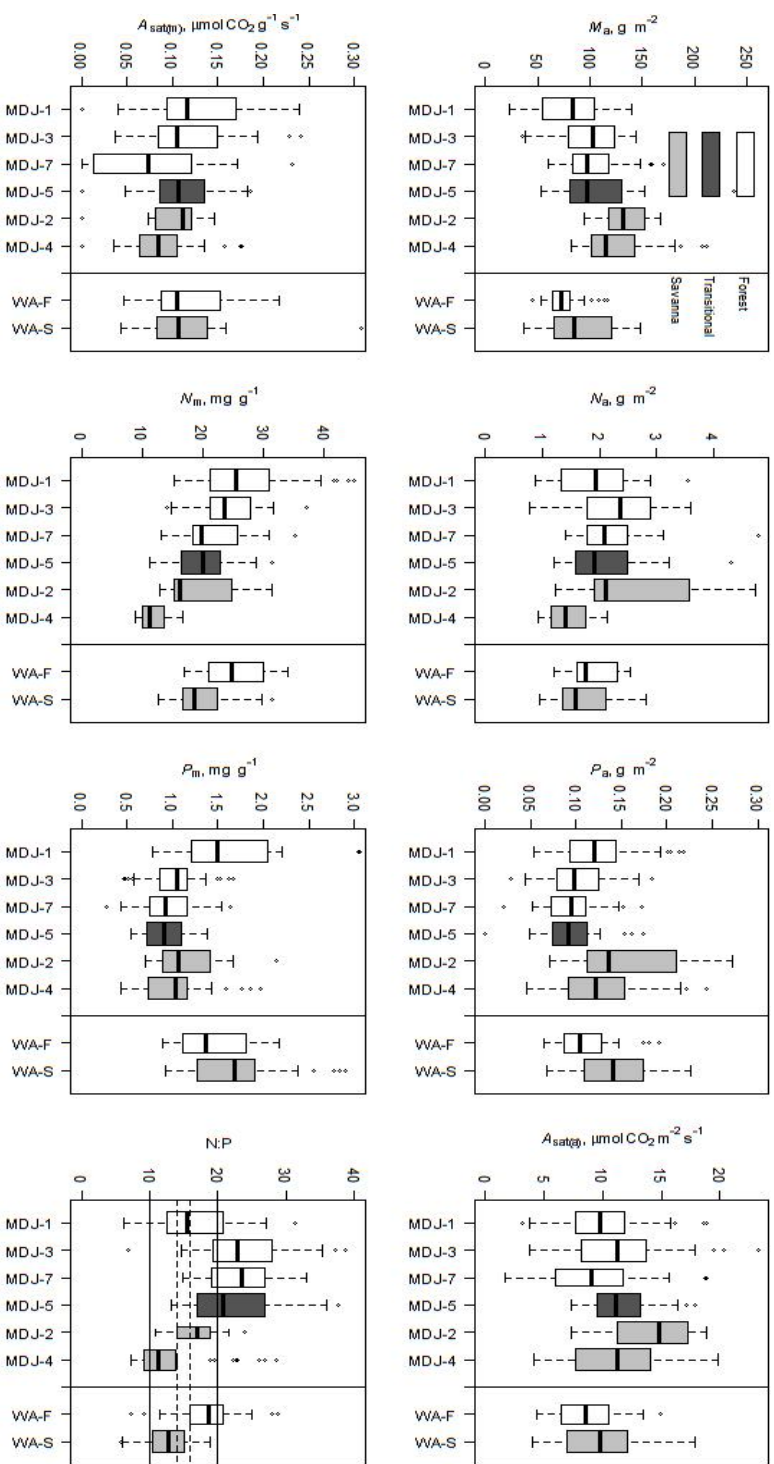
Fig. 4 Statistical comparison of leaf attributes of forest (white bars), savanna (light grey) and transitional forest (dark grey) in sampled in central Cameroon. Also shown (right of vertical line) are forest and data from a previous study in West Africa (Domingues et al. 2010) designated as "WA-F" and "WA_S" respectively. 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}).
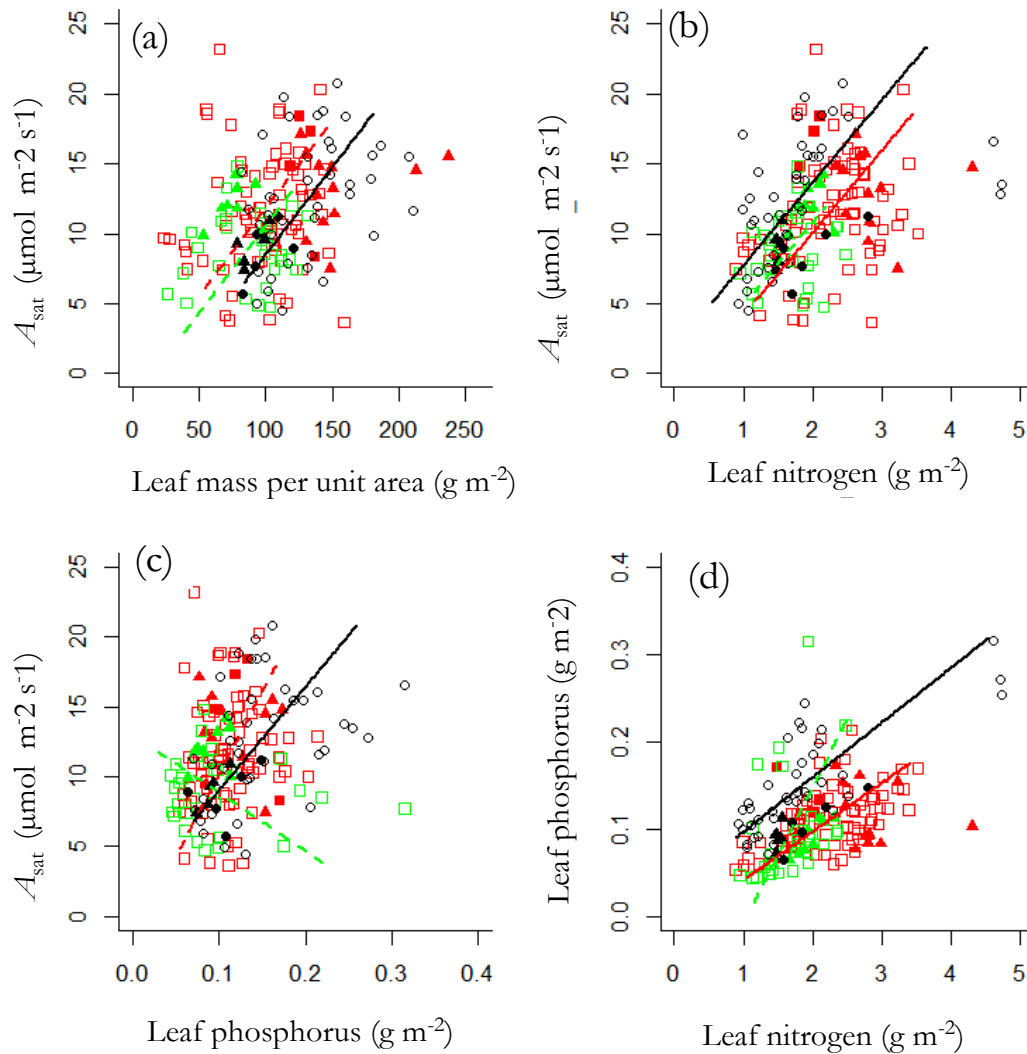
Fig. 5 Bivariate plots of observed relationships between area based measures of light saturated photosynthetic rate (A_{sat}), nitrogen and phosphorus. Symbols are deciduous forest (red), evergreen forest (green) and savanna (black) with filled symbols indicating taken the transitional forest (MDJ-05). Lines shown are for standard major axis (SMA) regression fits. Solid lines: ordinary least squares regression (OLS) fit significant at $p < 0.05$; dashed lines (OLS) regression significant at $p > 0.05$).
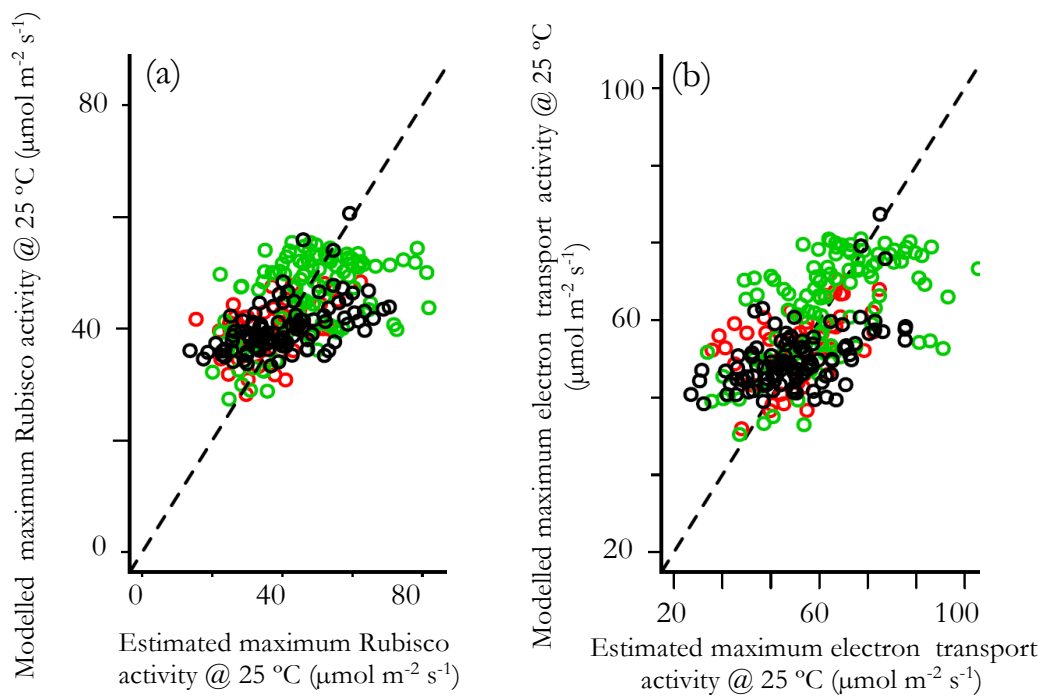
Fig. 6 Model predictions of estimated Rubisco activity standardised to 25 °C (V_{25}) and (b) estimated electron transport capacity @ 25 °C according to Eq. 2.
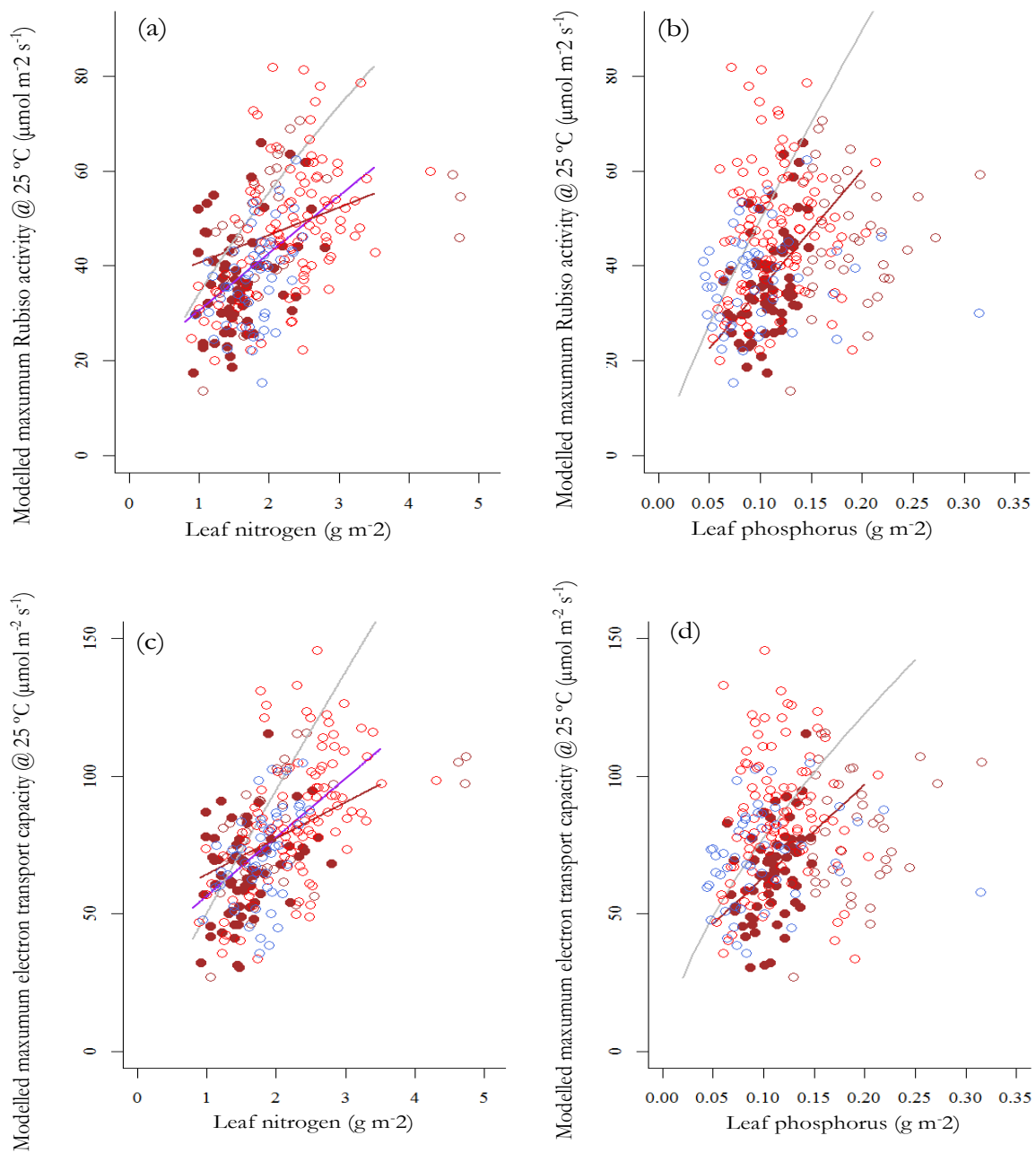
Fig. 7 Area-based relationships between (a) estimated Rubisco activity standardised to 25 °C (V_{25}) and leaf nitrogen; (b) V_{25} and leaf phopshorus ; (c) estimated electron transport capacity @ 25 °C (J_{25}) and leaf nitrogen; (J_{25}) and leaf phopshorus. Symbols are: deciduous forest (red), evergreen forest (green) and savanna (brown). Filled savanna symbols show points modelled to be limited by phosphorus as per the model fit of Eq. 2 as detailed in Supporting Information Table 1. Also shown from this study are the model fits of Eq. 2 for forest (purple) and savanna (brown), 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) as detailed in Domingues et al. (2010).