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Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests

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Summary

1. Regional above-ground biomass estimates for tropical moist forests remain highly inaccurate mostly because they are based on extrapolations from a few plots scattered across a limited range of soils and other environmental conditions. When such conditions impact biomass, the estimation is biased. The effect of soil types on biomass has especially yielded controversial results.

2. We investigated the relationship between above-ground biomass and soil type in undisturbed moist forests in the Central African Republic. We tested the effects of soil texture, as a surrogate for soil resources availability and physical constraints (soil depth and hydromorphy) on biomass. Forest inventory data were collected for trees ≥20 cm stem diameter in 2754 0.5 ha plots scattered over 4888 km^2. The plots contained 224 taxons, of which 209 were identified to species. Soil types were characterized from a 1:1 000 000 scale soil map. Species-specific values for wood density were extracted from the CIRAD's data base of wood technological properties.

3. We found that basal area and biomass differ in their responses to soil type, ranging from 17.8 m^2 ha^{-1} (217.5 t ha^{-1}) to 22.3 m^2 ha^{-1} (273.3 t ha^{-1}). While shallow and hydromorphic soils support forests with both low stem basal area and low biomass, forests on deep resource-poor soils are typically low in basal area but as high in biomass as forests on deep resource-rich soils. We demonstrated that the environmental filtering of slow growing dense-wooded species on resource-poor soils compensates for the low basal area, and we discuss whether this filtering effect is due to low fertility or to low water reserve.

4. *Synthesis*. We showed that soil physical conditions constrained the amount of biomass stored in tropical moist forests. Contrary to previous reports, our results suggest that biomass is similar on resource-poor and resource-rich soils. This finding highlights both the importance of taking into account soil characteristics and species wood density when trying to predict regional patterns of biomass. Our findings have implications for the evaluation of biomass stocks in tropical forests, in the context of the international negotiations on climate change.

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Introduction

Tropical forests play a major role in the global carbon cycle as they contain 45% of terrestrial vegetation stocks and their loss, through deforestation, contributes substantially to anthropogenic emissions of greenhouse gases (Intergovernmental Panel on Climate Change 2000). In the near future, countries with tropical forests could benefit from incentives designed to help reduce emissions from deforestation and degradation (REDD initiative, UN Framework Convention on Climate Change). To benefit from these incentives, they will need to demonstrate that they have reduced carbon emissions, which will require that they have detailed and accurate knowledge of the quantities of carbon stocks in standing forests and soils, and carbon fluxes that result from various land use activities and natural ecosystem processes.

Current estimates of above-ground biomass in tropical forests are highly inaccurate at large spatial scales (Houghton 2005) primarily because forest biomass stocks are difficult to quantify (Fearnside 1985; Brown, Gillespie & Lugo 1989; Phillips *et al.* 1998) and are usually estimated by extrapolating regional patterns from a limited number of plots (Brown *et al.* 1995; Houghton *et al.* 2001; Lewis *et al.* 2009). The extrapolation process raises a number of methodological and technical problems (Chave *et al.* 2004; Saatchi *et al.* 2007; Grainger 2008; Nasi *et al.* 2008). In particular, sampling designs seldom account for the environmental factors underlying biomass variations (Gibbs *et al.* 2007), e.g. soil fertility and topography, which also partly drive spatial patterns of deforestation (De Castilho *et al.* 2006; Paoli, Curran & Slik 2008). Extrapolating stocks and losses from deforestation while ignoring these environmental factors results in biases, which underscores the importance of understanding these relationships.

Only few studies investigated the relationship between soil fertility and biomass in tropical moist forests and they have yielded conflicting results. At the regional scale ($\geq 10^4$ km^2), above-ground biomass of Amazonian old-growth forests was found to be higher in wet regions with infertile soils (Malhi *et al.* 2006), while in Bornean forests, above-ground biomass was strongly positively correlated with soil fertility (Slik *et al.* 2010). At the local (< 1 km^2) and landscape scales (1–10^4 km^2), above-ground biomass in most accounts was reported to be higher on nutrient-rich clay soils than on nutrient-poor sandy soils (Laurance *et al.* 1999; De Castilho *et al.* 2006; Paoli, Curran & Slik 2008). Higher biomass on nutrient-rich soils has been suggested to result either from the filtering of emergent species containing a high fraction of the biomass, or from the capacity of trees to grow larger because of higher nutrient availability for investment in living material (Laurance *et al.* 1999). In contrast, some authors report that above-ground biomass is relatively insensitive to soil type and/or topography (synthesis in Vitousek & Sanford 1986; Clark & Clark 2000; DeWalt & Chave 2004). A possible explanation for these inconsistent findings is that many studies of forest biomass at local and landscape scales do not include species wood density in the allometric equations used to estimate biomass from measured tree dimensions (but see DeWalt & Chave 2004).

In addition to influencing biomass estimates, wood density is a fundamental trait related to the life-history strategies of tree species. For example, wood density correlates positively with a species' position along the continuum from fast-growing, short-lived pioneer species to slow-growing, long-lived late-successional species (Turner 2001; Muller-Landau 2004; Nascimento *et al.* 2005; van Gelder, Poorter & Sterck 2006).

Species with low wood density may be at a disadvantage on poor soils: on such soils indeed, inherently fast-growing species often fail to persist because of low resources availability, while on rich soils they may dominate given their competitive advantage (Grime *et al.* 1997; Poorter & Garnier 1999; Russo *et al.* 2005, 2008). Mean wood density consistently decreases with increasing soil fertility (Muller-Landau 2004; Ter Steege *et al.* 2006). Hence, ignoring wood density in biomass calculations may result in systematic underestimates of biomass on low fertility soils and overestimates on high-fertility soils (DeWalt & Chave 2004).

Here, we used landscape-scale tree surveys conducted by timber companies in moist semi-deciduous forests of the Central African Republic to determine how biomass varies across soil types. Firstly, we tested the effects of three soil types – deep resource-rich soils, deep resource-poor soils, and shallow or hydromorphic soils that physically constrain tree growth – on basal area and biomass estimates calculated using wood density data. We expected both basal area and biomass to be higher on deep resource-rich soils and lower on deep resource-poor soils and physically constrained soils. Secondly, we tested whether the differences found between soil types could be explained by species' differing life-history strategies, using wood density and vital rates – stem diameter growth and mortality rates – as proxies. We expected that the lower biomass stored on the deep resource-poor and physically constrained soils could be partly compensated for by a higher community-wide wood density than on the deep resource-rich soils, owing to a large amount of slow-growing and long-lived species in the community.

Finally, taking into account that wood density also affords greater resistance to water stress-induced xylem cavitation (Hacke *et al.* 2001), we discuss whether the soil resource effect revealed in this study might be a nutrient or a water reserve effect.

Materials and methods

STUDY AREA

The study area is located in southern Central African Republic (Fig. 1) where a humid tropical climate prevails with a mean annual rainfall of 1400–1700 mm and a 3- to 4-month dry season (Franquin *et al.* 1988, http://www.worldclim.org/, EFBC 2006), at altitudes of 400–800 m a.s.l. (Boulvert 1987 and Shuttle Radar Topography Mission, SRTM). The study area lays over various geological substrates: sandstone, dolerite, quartzite–schist association, gneiss and granite (Boulvert 1996). Boulvert (1996) recognized two landform units: (i) a sandstone plateau, with large interfluves dissected by few deep valleys and (ii) a 'Central African surface', with a succession of rolling hills or small plateaus dissected by many rivers. The region is home to mixed, moist, semi-deciduous and Guineo–Congolian rain forests (White 1983) characterized by the abundance of Ulmaceae, Sterculiaceae, Sapotaceae and Meliaceae families (Boulvert 1986).

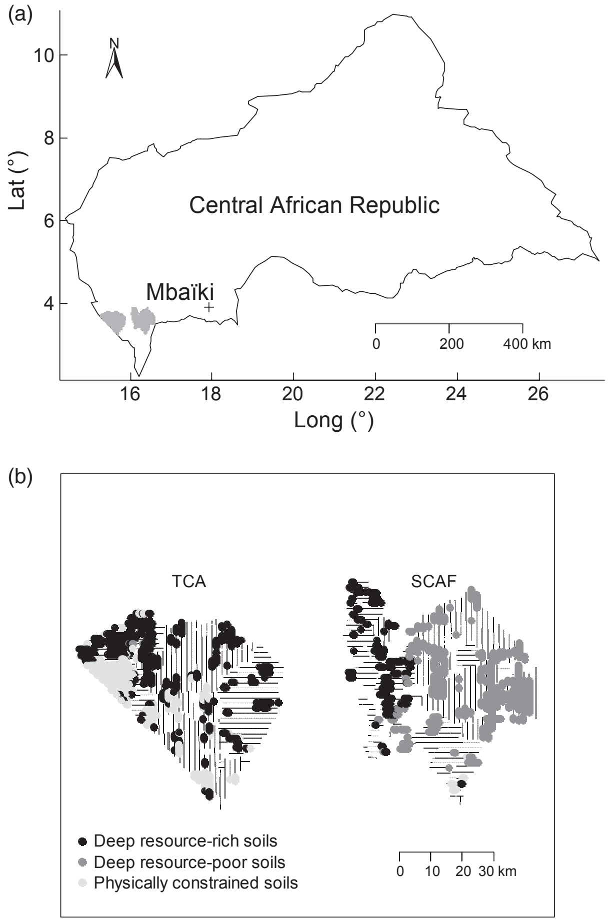

Fig. 1. Study area. (a) Location of the study sites in the Central African Republic (in grey) and of the Mbaïki Experimental Station. Latitude and longitude in the WGS84 reference coordinate system. (b) Sampling designs at each site consisted of continuous transects 25 m wide, separated by 2–3 km, and subdivided every 200 m into rectangular 0.5 ha plots (6453 plots in TCA and 6227 plots in SCAF). Dots correspond to the plots in undisturbed forests used for the analysis (1322 plots for TCA and 1432 for SCAF), and small grey points correspond to the other (unused) inventory plots. The colour of each dot (black, dark grey and light grey) corresponds to a soil type as described in the legend.

FLORISTIC DATA

We gathered data from two large-scale forest inventories conducted in 2005–06 by two logging companies: TCA (Thanry Centrafrique) and SCAF (Société Centrafricaine Forestière) covering 225 321 ha (3°14′–3°49′ N, 15°16′–15°52′ E) and 270 005 ha (3°15′–3°55′ N, 16°02′–16°35′ E), respectively and accounting for about 10% of the entire national moist forest area. The sampling design was systematic and consisted of continuous geo-referenced transects 25 m wide, 2–3 km apart and subdivided into rectangular 0.5 ha plots (Fig. 1). Sampling rates by TCA and SCAF corresponded to 1.5% and 1.4%, respectively. We used black and white (1:50 000 scale) aerial photographs combined with ground truthing to map vegetation types as moist forests, gallery forests, swamp forests and swamps, savanna woodlands and tree savannas, and to determine whether forests were undisturbed, degraded or regrowing. Plots located in moist undisturbed forests were then extracted from the data base and used for the study: 1322 TCA plots and 1432 SCAF plots (total: 2754 plots).

In each plot, all the trees with a d.b.h. ≥30 cm were measured and allocated into 10-cm-wide d.b.h. classes.

Trees 20–30 cm d.b.h. were recorded in a 0.125 ha subplot inside each plot. All trees were identified to species, where possible. In all, 209 taxons (out of 224) were identified to species in our set of 2754 plots, and about 8% of the trees were identified to the genus level or were left unidentified. Trees were identified by qualified teams assisted by experienced botanists as part of the French-funded PARPAF project (*Projet d'Appui à la Réalisation de Plans d'Aménagement Forestier*). Taxonomy was revised and homogenized to comply with the African Flowering Plants Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/) and the Angiosperm Phylogeny Group for orders and families (APG II 2003).

SOIL TYPE DATA

The soil typology was drawn from the 1:1 000 000 scale national soil map (Boulvert 1983). We used a Geographic Information System to assign each TCA and SCAF inventory plot one of eight soil types (Table S1 in Supporting Information) grouped into three major categories: (i) deep clay or clay loam (Luvic Phaeozems, Acrisols and Ferralsols/Nitisols), hereafter referred to as 'deep resource-rich soils'; (ii) deep sandy loam (Arenic Acrisols on plateaus and in valleys), hereafter referred to as 'deep resource-poor soils' and (iii) soils that are physically constrained either by the presence of highly concentrated ferruginous nodules and duricrust close to the surface (shallow clay loam: Skeletic Acrisols, Petroplinthic Acrisols) or by the presence of water (hydromorphic clay: Stagnosols), hereafter referred to as 'physically constrained soils'.

The difference between resource-rich and resource-poor among deep soils was based on soil texture as a surrogate of resources availability, with no *a priori* possibility to disentangle between nutrient and water availability. Indeed, clay or clay loam soils can be considered nutrient-rich, compared with sandy loam soils, due to higher cation exchange capacities and higher exchangeable bases, particularly under 10 cm depth from the soil surface (see details on soil hydromorphy, depth, texture and chemical fertility in Table S1). But clay or clay loam soils could also have a higher water reserve than deep sandy loam soils of equal depth. Despite being loamy or clayish, we *a priori* considered physically constrained soils to be both nutrient- and water-limited, due to the limited depth that could be used by roots.

Topography varies across soil types, with a clear contrast between Arenic Acrisols on plateaus (which occupy the summit of the 'sandstone plateau' landform of Boulvert 1996), typically flat, and all the other types, which are more heterogeneous. Within each soil type, except Arenic Acrisols on plateaus, all topographical positions were sampled by the inventory design. At our study scale, we measured a global substrate effect including the interaction between soils and local topography.

GROWTH AND MORTALITY RATES

We used data from permanent sample plots at the Mbaïki Experimental Station (3°90′N, 17°93′E, Fig. 1, hereafter 'Mbaïki') to calculate vital rates for species common to Mbaïki and the TCA or SCAF inventories (see calculation details in Table S5). The Mbaïki plots were established in 1982 to study the effects of silvicultural treatments on the dynamics of previously undisturbed forests (Picard & Gourlet-Fleury 2008). The Station maintains ten 4 ha permanent sample plots located mainly on Acrisols, in which all the trees ≥10 cm d.b.h. are measured annually. We assumed that species ranking with respect to vital rates was conserved across soil types, as demonstrated by Russo *et al.* (2005), and we used these rates to characterize species life-history strategies.

WOOD DENSITY DATA

CIRAD's database on wood properties (http://www.cirad.fr/ur/bois_tropicaux) was used to obtain individual wood density values for 1206 trees belonging to 256 African species found in continental moist forests (+ 29 taxons identified to the genus level). For each species s inventoried in the TCA and SCAF plots, we assigned the mean wood density value ($e[\rho_s]$, hereafter noted ρ_s to simplify notations) and variance ($v[\rho_s]$) calculated from matching trees found in the data base. When no information was available for the species, we assigned the genus, family, order or global mean value by following a set of rules intended to reduce sampling bias within various taxonomic levels (Tables S2 and S3). We used CIRAD's data base because the wood density measurements were all made with the same protocol (Table S2), thus guaranteeing consistent estimations of means and variances.

ESTIMATIONS OF ABOVE-GROUND BIOMASS

Above-ground biomass in each plot (AGBp) was estimated as the sum of the above-ground biomass of inventoried trees (AGBt), calculated with the pan-tropical allometric model for moist forests developed by Chave *et al.* (2005). Above-ground biomass in each plot thus cumulated uncertainties at two levels: (i) uncertainties at the tree level, linked to the allometric model error and to field measurements and/or sampling uncertainties of the variables used to predict AGBt: tree diameter – only diameter classes were known from the inventories – or specific wood density ρ_s and (ii) uncertainties at the plot level, linked to uncertainties about the number of trees inventoried in the 20–30 cm d.b.h. class. These uncertainties, which inflate the variance of AGBp, need to be taken into account when testing for AGBp differences between soil types (see 'Statistical analyses'). We detail the different stages of calculation of AGBp and its statistical moments (mean and variance) in Appendix S1.

Additionally, we estimated the mean wood density of each plot, WDp, as the sum of the species wood density of trees in plot p, weighted by their basal area:

$$\mathrm{WDp} = \sum_s G_s \times e[\rho_s] / \sum_s G_s$$

with G_s the cumulated basal area of all trees of species s in plot p.

STATISTICAL ANALYSES

The effect of soil type on basal area (Gp) and above-ground biomass (AGBp) was assessed by one-way Welch ANOVAS (Welch 1951) followed by *post hoc* Dunnett's modified Tukey–Kramer tests, to account for unequal variances. To handle the uncertainty associated with AGBp estimates, we used a parametric bootstrap procedure. We repeated the ANOVAS on 1000 sets of AGBp values (Table S4) sampled in a normal distribution with mean and variance defined by equations 6 and 7 in Appendix S1.

The effect of soil type on floristic composition was assessed by a constrained ordination analysis (Non-Symmetrical Correspondence Analysis on Instrumental Variable, NSCAIV, Couteron *et al.* 2003), which is less sensitive to rare species and more sensitive to abundant species than classical Canonical Correspondence Analysis (ter Braak 1986). We used NSCAIV to constrain the 'Plot × Species' matrix – where values corresponded to species basal area on each plot – by a 'Plot × Soil type' matrix. The initial analysis showed a marked effect of soil type, mainly driven by two abundant species (*Manilkara mabokeënsis* and *Terminalia superba*) that were excluded from the subsequent analyses because of their weight. Considering only species with a relative contribution to axis 1 ≥ 0.05%, we regressed species scores on the first NSCAIV axis against wood density and log-transformed vital rates to investigate the mechanisms of species sorting on different soil types. All statistical tests were performed with the R statistical software (R Development Core Team 2009). The 'Diversity' library (Pélissier & Couteron 2007, http://Pelissier.free.fr/Diversity.html) was used to perform the NSCAIV.

Results

EFFECT OF SOIL TYPE ON BASAL AREA AND ABOVE-GROUND BIOMASS

The mean AGBp values ranged between 217.5 t ha^{-1} (Stagnosols) and 273.3 t ha^{-1} (Luvic Phaeozems) for trees ≥20 cm d.b.h. We found that soil type had a marked effect both on plot basal area (Gp; Welch ANOVA: $W = 25.1$, $P < 0.001$) and above-ground biomass (AGBp; Welch ANOVA on mean values: $W = 12.1$, $P < 0.001$; $P(>W) < 0.001$ for 100% of the 1000 bootstrap replications), with highest Gp and AGBp values on deep resource-rich soils (Luvic Phaeozems), and lowest values on hydromorphic soils (Stagnosols) (Table 1 and Fig. 2a).

Post hoc comparisons revealed different Gp and AGBp patterns of variation according to soil type. Plot basal area values were the highest on deep resource-rich soils while they were the lowest on deep resource-poor and physically constrained (shallow or hydromorphic) soils ($P < 0.05$, Table 1). In contrast, AGBp was higher on both the deep resource-rich and resource-poor soils than on the physically constrained soils ($P < 0.05$; Table 1). When considering deep soils only, higher resources availability did not systematically result in higher biomass. Hence, while deep resource-poor soils (Arenic Acrisols) carry a low basal area, similar to that of physically constrained soils, they carry a high biomass, similar to that of deep resource-rich soils. These results were not challenged by uncertainties associated with AGBp estimates (Table S4).

Table 1. Soil types, number of plots and main structural characteristics of stands (trees ≥20 cm d.b.h.). Significant differences at the $\alpha = 0.05$ level among soil types are indicated by different lower case letters (Dunnett's modified Tukey–Kramer *post hoc* test)

	Deep resource-rich			Deep resource-poor		Physically constrained		
Soil type*	Luvic Phaeozems	Acrisols	Ferralsols or Nitisols	Arenic Acrisols (Valleys)	Arenic Acrisols (Plateaus)	Skeletic Acrisols	Petroplinthic Acrisols	Stagnosols
Number of plots	324	329	489	136	895	356	124	101
N (ha^{-1})	135 ± 5	138 ± 5	129 ± 4	133 ± 8	131 ± 3	123 ± 5	121 ± 7	123 ± 9
Gp (m^2 ha^{-1})	$22.3^{b} \pm 0.8$	$21.3^{b} \pm 0.8$	$21.4^{b} \pm 0.6$	$18.9^{a} \pm 1.0$	$18.3^{a} \pm 0.3$	$18.9^{a} \pm 0.6$	$18.5^{a} \pm 1.0$	$17.8^{a} \pm 1.4$
AGBp† (t ha^{-1})	$273.3^{c} \pm 10.5$	$258.2^{bc} \pm 10.2$	$250.8^{b} \pm 7.9$	$258.7^{bc} \pm 16.1$	$252.7^{b} \pm 5.1$	$227.9^{a} \pm 7.4$	$224.7^{a} \pm 12.7$	$217.5^{a} \pm 17.6$

*Soil types follow the WRB classification (2006) and were based on Boulvert (1983, 1996) descriptions (see Table S1 for details). N, number of trees ≥20 cm d.b.h.; Gp, basal area; AGBp, above-ground biomass. Total number of plots: 2754. Values for N, Gp and AGBp correspond to the mean ± $t_{(n-1,\ \alpha\ =\ 0.05)} \times \mathrm{SD}/\sqrt{n}$, scaled to 1 ha, with SD, standard deviation of the sample; and $t_{(n-1,\ \alpha\ =\ 0.05)}$, fractile of the Student distribution.

†The Welch ANOVA was first performed on the mean estimates of AGBp for each plot and was then repeated for 1000 samples of 2754 AGBp values (bootstrap, see the Materials and methods section). $e[\rho_s]$ and $v[\rho_s]$ were estimated from the CIRAD's database on species wood densities.

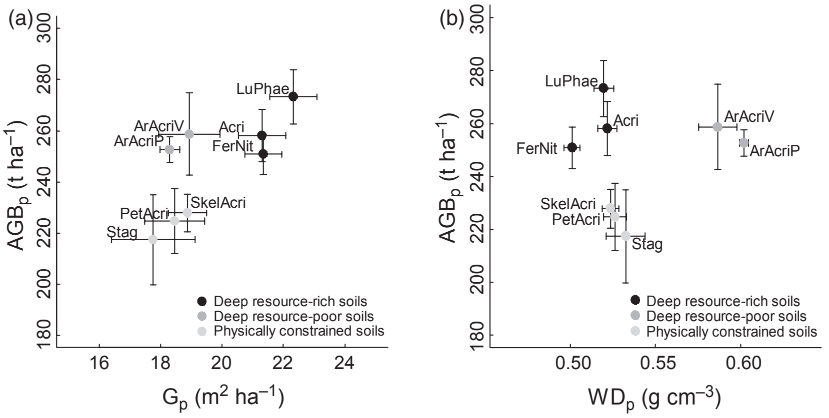

Fig. 2. Above-ground biomass (AGBp) against (a) basal area (Gp) and (b) mean wood density (WDp) for each soil type. LuPhae, Luvic Phaeozems; Acri, Acrisols; FerNit, Ferralsols/Nitisols; ArAcriV, Arenic Acrisols in valleys; ArAcriP, Arenic Acrisols on plateaus; SkelAcri, Skeletic Acrisols; PetAcri, Petroplinthic Acrisols; Stag, Stagnosols. Dots are mean values for AGBp, Gp and WDp by soil type. Error bars correspond to $\pm t_{(n-1,\ \alpha\ =\ 0.05)} \times \mathrm{SD}/\sqrt{n}$, where n = sample size, SD, standard deviation of the sample, and $t_{(n-1,\ \alpha\ =\ 0.05)}$, fractile of the Student distribution, assuming a normal distribution of errors for all variables.

The compensating effect observed on resource-poor soils results from trees tending to have a higher species wood density on these soils than on any other soil type (Fig. 2b, Welch ANOVA on mean WDp values: $W = 330.2$, $P < 0.001$). Disregarding variation in wood density across species by considering a mean value [$e(\rho_s) = 0.586$, see Table S2] would have resulted in overestimating AGBp by 12% (Stagnosols) to 20% (Ferralsols/Nitisols) on deep resource-rich and physically constrained soils, and slightly underestimating AGBp on deep resource-poor soils.

EFFECT OF SOIL TYPE ON FLORISTIC COMPOSITION AND SPECIES STRATEGY

Soil type greatly affected both the floristic and functional composition of tree communities, demonstrating that soil type filters species according to their life-history strategy. We explored the effect of soil type on floristic composition with a NSCAIV. The first ordination axis (NSCAIV1, 76.3% of explained variance) revealed a marked separation between deep resource-poor soils (Arenic Acrisols on plateaus and, to a lesser extent, in valleys) and all the other soil types (Fig. 3). This separation is mainly due to contrasting distribution patterns across soil types of: (i) species such as *Staudtia kamerunensis*, *Prioria oxyphylla*, *Entandrophragma cylindricum*, *Celtis mildbraedii*, *Pycnanthus angolensis*, *Lophira alata*, *Petersianthus macrocarpus*, *Blighia welwitschii* and *Irvingia excelsa* whose specific basal area (*Gs*) accounted for 26% and 20% of Gp on Arenic Acrisols on plateaus and in valleys, respectively, and for less than 14% on other soil types and (ii) species such as *Triplochiton scleroxylon*, *Ceiba pentandra*, *Mansonia altissima*, *Albizia adianthifolia*, *Ricinodendron heudelotii*, *Anonidium mannii*, *Celtis philippensis*, *Sterculia tragacantha* and *Duboscia macrocarpa* whose *Gs* accounted for only 8% and 9% of Gp

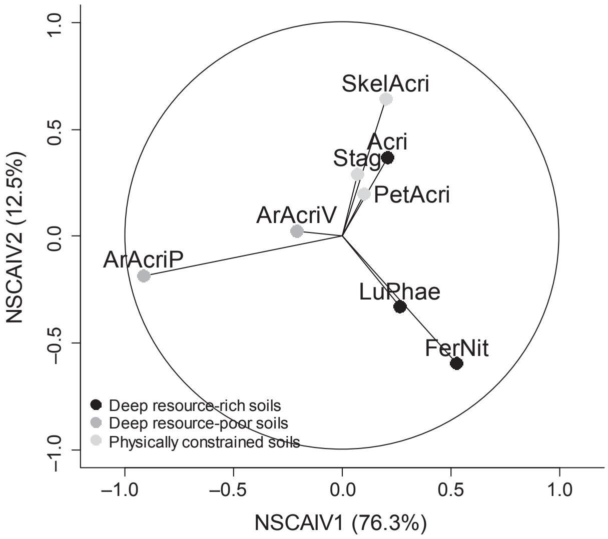

Fig. 3. Correlation circle of the Non-Symmetrical Correspondence Analysis on Instrumental Variable (NSCAIV) analysis (first two axes; percentage of explained variance between brackets) showing the marked opposition between deep nutrient-poor soils and the other soils along the first axis. The Plot × Species table, based on species basal area values, was regressed against the Plot × Soil types table (eight modalities). LuPhae, Luvic Phaeozems; Acri, Acrisols; FerNit, Ferralsols/Nitisols; ArAcriV, Arenic Acrisols in valleys; ArAcriP, Arenic Acrisols on plateaus; SkelAcri, Skeletic Acrisols; PetAcri, Petroplinthic Acrisols; Stag, Stagnosols. *Manilkara mabokeënsis* and *Terminalia superba* were omitted from the analysis.

on Arenic Acrisols on plateaus and in valleys, respectively, and for more than 19% of Gp on other soil types. This trend was further strengthened by the spatial pattern of two abundant species that we excluded from the NSCAIV analysis (see Materials and methods). These species clearly discriminated Arenic Acrisols (*Manilkara mabokeënsis*: *Gs* ≥9% of Gp on Arenic Acrisols and < 2% of Gp on all other soil types) from all the other soil types (*Terminalia superba*: *Gs* < 2% of Gp on Arenic Acrisols and ≥8% of Gp on other soil types).

The second ordination axis (NSCAIV2, 12.5% of explained variance) showed a gradient that opposed two deep resource-rich soil types (Luvic Phaeozems and Ferralsols/Nitisols) against the third resource-rich soil type (Acrisols) together with the physically constrained soil types. This gradient was mainly due to the distribution patterns of two species: *T. scleroxylon*, mainly found on the first two soil types (more than 4% of Gp) and *A. adianthifolia*, mainly found on the other soil types (more than 5% of Gp).

Species score on the NSCAIV1 represents species position across the soil gradient. We detected a strong negative linear relationship between species scores on this axis and wood density ($n = 79$ species, adjusted $R^2 = 0.235$, $P < 0.001$), and a positive linear relationship between species scores and the log-transformed maximum growth rate ($n = 48$ species; adjusted $R^2 = 0.115$, $P = 0.010$) (Fig. 4). No relationship was found between species scores and the log-transformed mortality rates ($n = 38$ species; adjusted $R^2 = 0.005$, $P = 0.281$). Thus, high wood density and low growth rate tended to be associated with deep resource-poor soils (low NSCAIV1 scores), while low wood density and high growth rate tended to be associated with the other soil types (high NSCAIV1 scores). In support of this finding, wood density value and growth rate in *M. mabokeënsis* and *T. superba* (Table S5) were consistent with their distribution across soil types.

Discussion

In this paper, we disentangled how the observed variation in basal area and above-ground biomass across undisturbed African moist forests is driven by soil type, and we evidenced the effects of soil type on species traits such as wood density.

AGBP VALUES IN THE STUDY AREA

The estimated values of AGBp ranged between 217.5 t ha^{-1} (Stagnosols) and 273.3 t ha^{-1} (Luvic Phaeozems) for trees ≥20 cm d.b.h., i.e. between 241.7 t ha^{-1} and 303.7 t ha^{-1} for trees ≥10 cm d.b.h., using a ratio of 0.90 (AGBp ≥20 cm/AGBp ≥10 cm) calculated from the three 4 ha control plots at Mbaïki. These values are consistent with published above-ground biomass estimates of African lowland moist forests: 267 t ha^{-1} (range 152–382, calculated from Gaston *et al.* 1998), 260 t ha^{-1} (range 160–430, Intergovernmental Panel on Climate Change 2006), 296.3 t ha^{-1} (semi-deciduous moist forests in Cameroon, FAO 2005), 216.3 t ha^{-1} (Baccini *et al.* 2008), encompassing both disturbed and undisturbed forests.

SOIL EFFECT ON AGBP

To the best of our knowledge, this is the first time that the relationship between biomass and soil type has been investigated in African moist forests on a landscape scale. As expected, above-ground biomass (AGBp), as Gp, was lower on physically constrained soils than on other soil types. Physically constrained soils (shallow soils and soils with permanent hydromorphy) have a huge impact on root system morphology (Humbel 1978; Gregory 2006) and prevent trees from reaching large diameters (Pendry & Proctor 1997; Jirka *et al.* 2007). At the other extreme, Luvic Phaeozems, which are among the most fertile of tropical soils (IUSS Working Group WRB 2006), carried the highest Gp and AGBp. A novel finding was that despite their lower basal area (Gp), AGBp values of forests growing on deep resource-poor soils were similar to those of forests on deep resource-rich soils.

Previous studies that reported greater above-ground biomass on clay soils than on sandy soils (Laurance *et al.* 1999; De Castilho *et al.* 2006; Paoli, Curran & Slik 2008), generally, but not systematically (De Castilho *et al.* 2006), attributed this difference to the greater nutrient availability of the former. Unfortunately, direct comparisons between studies are obscured by at least two elements: (i) the failure to consider wood densities in the detailed analysis relating AGBp to environmental variables, although most authors acknowledged a strong link between these variables and floristic composition. Including wood density in the calculations could have weakened the relationships evidenced; and (ii) our soil data could

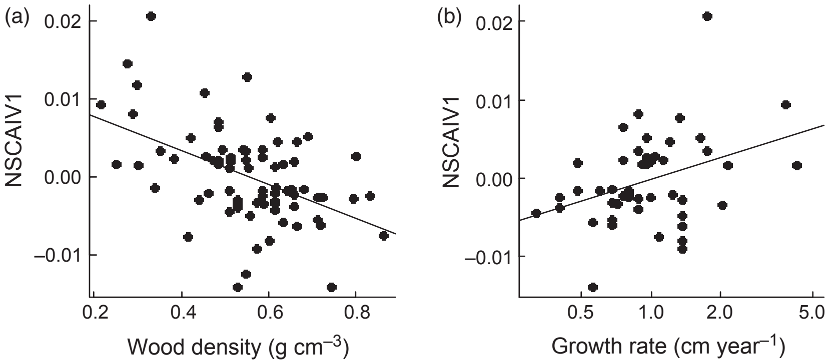

Fig. 4. Relationship between species scores on the first component of the Non-Symmetrical Correspondence Analysis on Instrumental Variable (NSCAIV1) and (a) species wood density (e[ρ_s], g cm^{-3}) calculated from the CIRAD's database; (b) annual growth rate [Log(ΔD), cm year^{-1}] from the Mbaïki database (with a logarithmic scale for the *x*-axis). *Manilkara mabokeënsis* and *Terminalia superba* were omitted from the NSCAIV analysis. Regression lines correspond to: (a) NSCAIV1 = −0.0224 × e[ρ_s] + 0.0124 (adjusted R^2 = 0.235, intercept and slope different from 0, $P < 0.001$); (b) NSCAIV1 = 0.0040 × Log(ΔD) – 0.0002 (adjusted R^2 = 0.115, intercept not different from zero, slope different from 0, $P = 0.010$). Only species with relative contributions to NSCAIV1 ≥0.05% were considered [79 species in (a)] and species owning more than 10 living trees ≥10 cm d.b.h. for ΔD calculations [48 species in (b)].

not be directly compared to those used in the above mentioned studies as we solely relied on broad soil types compared with the systematic chemical and physical soil properties analysed at the plot level in those studies. In addition, we worked at a larger geographical scale, with a data set that included a far larger number of plots on each soil type, probably encompassing a high degree of soil heterogeneity: local positive relationships between AGBp and soil properties could be masked by the landscape-level trends we found.

Finally, we must point out that our conclusions rely on the assumption that soil type has no major effect on the relationship between tree height and diameter. If nutrient and/or water limitation result in lower slenderness (H/D) coefficients, as it was shown in boreal forests (e.g. Wang, Titus & Lemay 1998), then our conclusion of a biomass being similar on deep sandy loam soils and deep clay or clay loam soils might be challenged. However, such effect remains unclear and, for example, fertilization or soil fertility can decrease slenderness (Almeida *et al.* 2010) or increase stem taper for a given diameter (Zhang, Borders & Bailey 2002), even if this latter effect can be difficult to disentangle from the stand density effect.

ENVIRONMENTAL FILTERING OF SPECIES STRATEGY

We showed that differences between soil types can be explained by differing species life-history strategies. As already noted for this study region (Rejou-Mechain *et al.* 2008) and elsewhere in the tropics (Ter Steege & Hammond 2001; Potts *et al.* 2002; Tuomisto, Ruokolainen & Yli-Halla 2003; Paoli, Curran & Zak 2006; Bohlman *et al.* 2008), soil conditions can have a strong influence on forest floristic composition. Here, we further showed that deep resource-poor soils favour dense-wooded species. This is coherent with previous findings in Neotropical forests (e.g. Muller-Landau 2004; Ter Steege *et al.* 2006), which related negatively mean wood density and soil fertility. As expected, this filtering effect compensates for the lower basal area on deep resource-poor soils, resulting in biomass values similar to those found on deep resource-rich soils. However, no such effect was observed on physically constrained soils, where low basal area is associated with low mean wood density values and low biomass.

We also found that species with slow growth rates at Mbaïki are associated with deep resource-poor soils, while species with fast growth rates typically grow on other soil types. This result is partly consistent with the demographic trade-off in soil-related habitat associations demonstrated in a Bornean rain forest (Russo *et al.* 2005, 2008). In that forest, species with slow growth and low mortality rates, were typical of sandy soils, while species with high growth and high mortality rates were more often associated with loam, clay loam and clay soils. Delcamp *et al.* (2008) further showed that species ranks according to growth rates were not modified by the level of disturbance, suggesting that slow-growing species remain slow-growing even if the level of resources (light in that case) increases. These results are consistent with the view of species with a conservative strategy being able to persist under stressful conditions related to low resources availability, but being outcompeted by fast-growing species where resources availability is higher (Grime 1977; Chapin 1980). Hence, when light availability increases (as in natural or human-induced gaps), fast-growing species are expected to outcompete slow-growing species where soil resources are not limited, due to their higher photosynthetic rates and lower allocation to defences. In contrast, the same fast-growing species might experience higher mortality rates where soil resources are limited due to the high nutrient and water costs of their physiological adaptations. Deep resource-poor soils could thus give an advantage to slow-growing species, and tend to favour species with high wood densities due to wood economics trade-offs (Muller-Landau 2004; Nascimento *et al.* 2005; Chave *et al.* 2009; Slik *et al.* 2010). To be fully supported, such an explanation would require the demonstration of a positive relationship between the soil resource gradient and mortality rate. Our results do not support such a relationship, but the data set we used to calculate species mortality rate was limited ($n = 38$ species) and rates were solely estimated on small populations (only 9 of the 38 species had more than 100 living trees at the beginning of the calculation period – Table S5). Such a data limitation could explain our failure to demonstrate a clear trend.

Unexpectedly, we did not find any evidence that physically constrained soils filter dense-wooded slow-growing species, despite a clear effect on limiting biomass accumulation. This suggests that, on these clay to clay loam soils, the level of resource is enough to allow growth and survival of light-wooded fast-growing species until they reach a medium diameter threshold. Above this threshold, nutrient and water costs might not be afforded any longer, due to the limited soil volume available to roots.

RESOURCE-POOR SOILS VS. RESOURCE-RICH SOILS: SOIL FERTILITY OR WATER RESERVE EFFECT?

Whether the effect of soil type we demonstrated results from low soil fertility or low water reserve is debatable. Indeed, high wood density characterizes slow-growing species that often dominate forests on nutrient-poor soils, but it also affords greater resistance to cavitation (Hacke *et al.* 2001). The filtering effect we observed on deep resource-poor soils could thus well result from water rather than from nutrient limitation. In Malaysia, for example, Yamada *et al.* (2005) found that tree species specialized to grow on sandy soil had deeper tap-roots than clay-rich-soil specialists, suggesting that seasonal water limitation could act as a driving filter on these soils.

Our results, including observations for the physically constrained soils, are coherent with both hypotheses: (i) Given that most of the root biomass is located within the first 50 cm of the soil (Canadell *et al.* 1996) where nutrients are concentrated, if nutrient limitation acted as the main driver of floristic composition, we would expect – and this is what we observed – light-wooded fast-growing species to dominate on both the deep and shallow clay to clay loam soils (Skeletic and Petroplinthic Acrisols have similar cation exchange capacities and exchangeable bases as deep clay loam Acrisols, see Table S1) while being outcompeted on sandy loam soils, (ii) Given that sandy loam soils have a lower water-holding capacity than clay and clay loam soils, if water limitation acted as the main driver of floristic composition, we would expect – and this is what we observed – species able to withstand water stress, i.e. with high wood density and probably well developed root systems, to survive preferentially on these soils and (iii) In the studied area, we also observed that evergreen tree species dominate the deep resource-poor soils, while deciduous species are more abundant on the other soil types (Gond *et al.* 2010 and unpublished results). Evergreen species, with long-lived leaves, tend to be favoured on nutrient-poor soils, while deciduous tree species better withstand seasonal drought (Givnish 2002). Given that species with long-lived leaves also tend to be dense-wooded (Ishida *et al.* 2008) and could thus afford both nutrient and water limitation, this may indicate that both factors actually act as driving filters in the area.

The roles played by water availability vs. soil fertility in biomass accumulation deserve further research. In their regional scale study of Amazonian old-growth forests, Malhi *et al.* (2006) suggested that biomass results from an interaction between high basal area, which is positively linked with the total amount of rainfall, and mean wood density, which tends to be higher on infertile soils. In the Amazonian case, the result of this interaction is a tendency towards higher biomass on infertile soils, whereas in Bornean forests, Slik *et al.* (2010) found a positive relationship between biomass and soil fertility; our results are intermediate. Thus, the balancing effects of water reserve (regulating basal area) and soil fertility (regulating mean wood density), are apparently not the same everywhere perhaps due to differing rainfall regimes (as suggested by Slik *et al.* 2010): indeed, many parts of Amazonia receive less rainfall and experience longer dry seasons than Borneo, which might limit biomass accumulation where soil fertility is high. Further work is needed to unravel these issues.

CONSEQUENCES FOR MONITORING AND ESTIMATING AFRICAN MOIST FORESTS BIOMASS

Our findings suggest that: (i) physical constraints, rather than soil texture, lower the amount of biomass stored in undisturbed moist forests of the Central African Republic and (ii) low basal areas on deep resource-poor soils are compensated for by high mean wood density, which results in a similar biomass to that found on deep resource-rich soils. Whether nutrients or water are the limiting resource that filter dense-wooded species on resource-poor soils, however, could not be clarified, and both might explain the soil effect on biomass.

Recovery from deforestation or degradation could be slower on deep resource-poor soils because they tend to favour slow-growing species with other conservative life-history strategies: particular attention should thus be paid to the conservation of these forests.

Today, the carbon estimates used for most African countries are based on a ‘biome-average approach’ which scales up point-based biomass harvest measurement data or forest inventory data to broad forest categories or biomes often with the use of remote sensing techniques (Gibbs *et al.* 2007; Baccini *et al.* 2008). These estimates disregard the environmental variation in each biome, such as related to elevation, soil type and land-use history. Our study clearly showed that soil type has a major impact on above-ground biomass in undisturbed forests and thus demonstrates the importance of designing national sampling schemes that take this factor into account when assessing carbon stocks.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Details of AGBt and AGBp calculations.

Table S1. Characteristics of the soils found in the study area.

Table S2. Mean species wood density and variance.

Table S3. Decision table for calculating mean species wood density and variance.

Table S4. Results of the 1000 repeated ANOVAS.

Table S5. Species coordinates on NSCAIV1 and vital rates.