

Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon

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Abstract

We present tree community diversity, species composition, basal area and aboveground biomass of three forest types in the Dja Biosphere Reserve, in South-East Cameroon, part of the contiguous tropical forest of the Congo Basin. A total of fourteen, 1 ha, plots were established in heterogeneous *terra firme* forests (TFF), *Gilbertiodendron dewevrei* forests (GDF) and periodically flooded forests (PFF). A total of 281 tree species with diameter ≥ 10 cm were recorded. The Shannon diversity index was significantly higher in TFF (5.7 ± 0.28) and PFF (5.6 ± 0.23) than in GDF (2.29 ± 0.48) (ANOVA, $F_{2,11} = 139.75$, $P < 0.001$). While tree density did not differ between forest types ($F_{2,11} = 3.50$, $P = 0.06$), basal area differed significantly ($F_{2,11} = 7.38$, $P = 0.009$), as did aboveground biomass ($F_{2,11} = 17.95$, $P < 0.001$). Mean AGB values were respectively, 596.1 ± 62.24 , 401.67 ± 58.06 and 383.14 ± 61.91 Mg ha⁻¹ in GDF, TFF and PFF. Variation in the abundance of trees with large diameter was the main reason for these differences. Few dominant species made the greatest contribution to the AGB. *G. dewevrei*, accounted for 83% of AGB in GDF, *Pentaclethra macrophylla* for 9.9% in TFF and *Uapaca heudelotii* for 10.6% in PFF. The importance of preserving *G. dewevrei* forest in the context of 'Reducing Emissions from Deforestation and forest Degradation' (REDD) policies is discussed.

Key words: aboveground biomass, cameroon, carbon, diversity, *Gilbertiodendron dewevrei*, rainforest

Résumé

Nous présentons la diversité des communautés d'arbres, la composition des guildes, la surface terrière et la biomasse aérienne de trois types forestiers de la Réserve de Biosphère du Dja, dans le sud-est du Cameroun, qui fait partie de la forêt tropicale contigüe du Bassin du Congo. Nous avons établi un total de 14 parcelles, d'un hectare chacune, dans des forêts hétérogènes sur *terra firma* (FTF), dans des forêts à *Gilbertiodendron dewevrei* (FGD) et dans des forêts périodiquement inondées (FPI). Nous avons relevé au total la présence de 281 espèces d'arbres d'un diamètre ≥ 10 cm. L'index de diversité de Shannon était significativement plus élevé dans les FTF (5.7 ± 0.28) et les FPI (5.6 ± 0.23) que dans les FGD (2.29 ± 0.48) (ANOVA, $F_{2,11} = 139.75$, $P < 0.001$). Alors que la densité des arbres ne différait pas significativement entre les types forestiers ($F_{2,11} = 3.50$; $P = 0.06$), la surface terrière différait de façon significative ($F_{2,11} = 7.38$; $P = 0.009$), tout comme la biomasse aérienne ($F_{2,11} = 17.95$; $P < 0.001$). Les valeurs de la biomasse étaient respectivement de $596,1 \pm 62,24$, $401,67 \pm 58,06$ et $383,14 \pm 61,91$ Mg ha⁻¹ dans les FGD, FTF et FPI. Une variation de l'abondance d'arbres de grand diamètre était la principale raison de ces différences. Quelques espèces dominantes constituaient la plus forte contribution à la biomasse aérienne. *G. dewevrei* comptait pour 83% de la biomasse aérienne dans les FGD, *Pentaclethra macrophylla* pour 9,9% dans les FTF, et *Uapaca heudelotii* pour 10,6% dans les FPI. L'on discute de l'importance qu'il y a de préserver la forêt à *Gilbertiodendron dewevrei* dans le cadre des politiques REDD (Réduction des émissions résultant du déboisement et de la dégradation forestière).

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Introduction

Accurately quantifying the role of tropical forests in the global carbon cycle is one of the key requirements to improving our understanding of current patterns of terrestrial carbon storage and exchange (Baker *et al.*, 2004a; Lewis, 2006; Denman *et al.*, 2007; Lewis *et al.*, 2009a; Lewis *et al.*, 2009b). This is important because humans emitted 8.7 Pg C yr⁻¹ from fossil fuel use and 1.2 Pg C yr⁻¹ from land-use change in 2008, yet only approximately 3.9 Pg C yr⁻¹ was added to the atmosphere, with the rest being absorbed by the oceans (2.3 Pg yr⁻¹) and terrestrial biosphere (4.7 Pg yr⁻¹) (Le Quére *et al.*, 2009). Tropical forests are implicated in both the emissions from land-use change, which are predominantly attributed to tropical deforestation (Van Der Werf *et al.*, 2009), and absorbing a significant fraction of the carbon added to the atmosphere (1.3 Pg C yr⁻¹) over recent decades (Lewis *et al.*, 2009a). However, the estimates of both of these fluxes of carbon are critically dependent upon accurate estimates of the biomass and carbon storage in heterogeneous tropical forests (Lewis, 2006).

There are several sources of uncertainty in determining the biomass of a given area of forest. First, many areas are actually composed of structurally and floristically differing forests which each needs to be sampled. Secondly, there are difficulties in utilizing models to convert tree diameter measurements to aboveground biomass (AGB) estimates (Chave *et al.*, 2005), because tropical forests are often comprised of hundreds of different tree species; therefore it is not practically possible to use species-specific regression models, as in the temperate zone (Brown & Schroeder, 1999; Fays, 2008). Instead, generic mixed species tree biomass regression models must be used. Moreover, published regression models are based on a relatively small number of directly harvested trees and include very few large diameter trees, thus do not necessarily well represent these larger trees that contain much of the forest biomass. Hence, different models applied to the same forest may yield different AGB estimates, often driven by the number of large trees, which imposes large uncertainty on stand level biomass estimates (Brown, 1997; Clark & Clark, 2000; Houghton *et al.*, 2001; Chave *et al.*, 2005). Thirdly, different species have different densities of wood, which also needs to be taken into account when assessing biomass (Chave *et al.*, 2009).

There is great variation in biomass estimates for different tropical forests (170.3–689.7 Mg ha⁻¹) (Brown & Lugo,

1984; Clark *et al.*, 2001; Zheng *et al.*, 2006). The wide differences in biomass estimates may result from variations in tree species and stand structures within mature forest types on different soils or landform units, altitudes or regions (Baker *et al.*, 2004a; Chave *et al.*, 2005; Zheng *et al.*, 2006). Also, relatively little is known about the temporal variability of forest biomass in the tropics (Phillips *et al.*, 2008; Lewis *et al.*, 2009a). In the same way, the variation of biomass amongst various types of tropical forest, such as between seasonally flooded and nearby upland areas, is poorly quantified, particularly in Africa. For example, in a recent study reporting biomass values from across Africa, none came from seasonally flooded forest (Lewis *et al.*, 2009a).

The aims of this study were to compare forest structure, species composition, aboveground biomass and allocation patterns in three types of forest (upland *terra firme*, periodically flooded forest and monodominant *Gilbertiodendron dewevrei* forest) in the Dja Biosphere Reserve, an area poorly understood in terms of biomass and carbon storage. The results obtained should improve both the quantity and quality of aboveground biomass estimates from central Africa and contribute to a better understanding of the role of tropical forest biome within the global carbon cycle.

Materials and methods

Study sites

The Dja Biosphere Reserve is an area of 526,000 ha in South-east Cameroon located between latitudes 2°50'–3°30' N and longitudes 12°20'–13°40' E. The reserve was established in 1950 as one of the largest protected rain forest areas in Africa (McGinley, 2008). About two-thirds of the reserve perimeter is demarcated by the Dja River, forming a natural boundary. The Dja Reserve is covered primarily by three broad types of forest: mixed species *terra firme* forest, monodominant forest dominated by *Gilbertiodendron dewevrei* and periodically flooded forest (Sonké, 2005). The forests have been classified as moist evergreen tropical forests (Letouzey, 1985). Relief maps show many shallow valleys. Average altitude is approximately 600 m. Precambrian crystalline metamorphic rocks, comprising schists, gneisses and quartzite (McGinley, 2008) are overlain by soils that are red ferrallitic, porous, sometimes more or less humus-bearing with areas that are hydro-morphic because of the proximity of the groundwater (Gartlan, 1989). There are no significant differences in the

physical or chemical soil characteristics between the two upland forest types, the mixed and monodominant forests (Peh, 2009). Four seasons alternate during the year including two dry and two moist seasons, with approximately 1512 mm of rainfall per year (average from 1979 to 2008), with 3 months having rainfall <100 mm (December, January and February). Mean annual temperature is 24.3°C, with mean monthly minimum temperatures of 23.4°C and mean monthly maximum temperatures of 26.5°C (Peh, 2009). The Dja Reserve has never been logged and still contains a complete fauna, including elephants and lowland gorillas (Williamson & Usongo, 1995).

Data collection

Data were collected in fourteen plots of 1 ha each. Five plots were established in *G. dewevrei* forest (GDF), five in upland *terra firme* forest (TFF) and four others in periodically flooded forest (PFF) (Fig. 1). Sample sites were selected on the presence of *G. dewevrei* forest which is patchily distributed throughout the Reserve. *Terra firme*, and periodically flooded forests were selected as close as possible to *G. dewevrei* forest to minimize potential differences related to soil or topography which may increase with distance. Each plot was selected such that the entire area was within a homogeneous forest type. Plots established were squares of 100 m × 100 m within which all the trees with a diameter at breast height (dbh) ≥10 cm were identified and measured using standard forestry methods (Dallmeier, Kabel & Rice, 1992; White & Edwards,

2001; Baker *et al.*, 2004a; Lewis *et al.*, 2009a). Herbarium specimens were collected for each plant to confirm the field identification by using existing floras and herbarium specimens at the National Herbarium of Cameroon and National Botanical Garden of Belgium.

Data analysis

Vegetation

Diversity was determined by using the *Shannon Index*: $ISH = -\sum p_i \log_2(p_i)$ where p_i is the frequency of species I (N_i/N), N_i the number of individuals of species i and N the number of individuals of all the species.

Biomass estimation

Biomass was estimated using allometric regression models to convert stem diameter measurements from the inventory data to an estimate of AGB (Chave *et al.*, 2005; De Wasseige *et al.*, 2009; Lewis *et al.*, 2009a; Stegen *et al.*, 2009). We use the moist forest equation derived by Chave *et al.* (2005), as it utilizes the largest dataset available (2410 trees, ≥5 cm diameter, directly harvested in 27 study sites across the tropics):

$$AGB = \rho \times \exp[-1.499 + 2.148 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3],$$

where D = dbh, and ρ = wood mass density.

Wood mass density is defined as the oven dry weight divided by the fresh volume (Fearnside, 1997). Wood mass

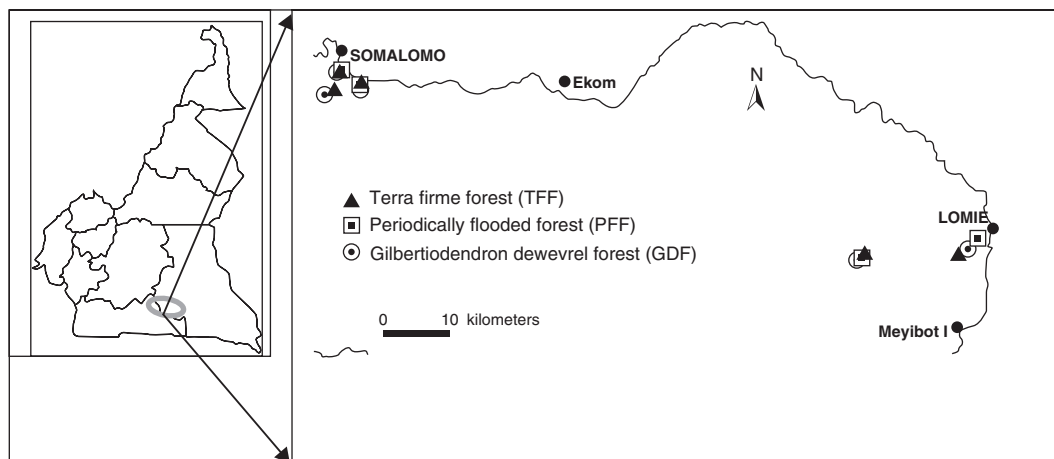


Fig 1 Location of sampling sites within the Dja Biosphere Reserve

density data were compiled from published sources (Anonymous, 1986; Brown, 1997; Wood density database <http://worldagroforestry.org/sea/Products/AFDbases/WD/Index.htm>), with those reported as calculated at 12% moisture content were corrected using a calibration equation (Reyes, Brown & Chapman, 1992; Brown, 1997; Baker *et al.*, 2004b):

$$\rho = 0.0134 + 0.800x,$$

Where x = wood mass density at 12%.

In the absence of species-level wood mass density, a mean density from the genera or family (if no genera-level wood density values were available) was used. The overall mean wood density obtained in this study was applied to completely unidentified stems, and stems identified to family but which no wood density information was available (Baker *et al.*, 2004a).

AGB values can also be expressed in terms of carbon by assuming a carbon content of 50%, so carbon stock can be calculated simply by dividing the AGB values by two (Brown, 1997; Houghton *et al.*, 2001; Baker *et al.*, 2004b; Chave *et al.*, 2005; Lewis *et al.*, 2009a).

Analysis

The differences between forest types for each variable were evaluated using analysis of variance (ANOVA) after verification of the assumptions of normality and equal variances. Newman–Keuls test was performed for *post hoc* comparison of differences amongst the forest types. Means \pm one standard deviations are presented. All analyses were conducted using STATISTICA 6 (StatSoft France, Maisons - Alfort, France).

Results

Forest diversity and guild composition

Overall, 281 species were identified in the three forest types, with 207 species in TFF (5 ha), 193 species in PFF (4 ha) and 121 species in GDF (5 ha). In addition, 0.84% of stems were unidentified and 4.81% identified to the level of the genera. Caesalpiniaceae, Euphorbiaceae, Annonaceae, Meliaceae and Olacaceae were the commonest families considering the 14 plots combined. Euphorbiaceae was the most diversified family with 40 species, followed by Rubiaceae, Caesalpiniaceae and Annonaceae with 21, 17 and 16 species, respectively.

The average number of species per plot differed significantly between habitat types (one-way ANOVA, $F_{2,11} = 30.94$, $P < 0.001$). Average Shannon index was highest in TFF (5.70 ± 0.28), marginally lower in PFF (5.56 ± 0.23), and significantly lower in GDF (2.29 ± 0.48) (Newman–Keuls, $df = 11$, $P < 0.001$) (Table 1), indicating higher species diversity in PFF and TFF than in GDF.

Ranks of the most important species differed among forest type and with the index used (relative stem density or relative basal area) (Table 2). Based on stem density, *G. dewevrei* had the most important contribution in the monodominant forest, and *Carapa procera* DC was among the most abundant species in all types of forest. Five other species were among the most abundant in two types of forests (*Plagiostyles africana* (Müll. Arg.) Prain, *Polyalthia suaveolens* Engl. & Diels, *Pentaclethra macrophylla* Benth.,

Table 1 Diversity index and aboveground biomass (AGB) of GDF (monodominant forests dominated by *Gilbertiodendron dewevrei*); PFF (periodically flooded forests); TFF (*terra firme* forests). BA: basal area; N: density; RS: species richness; ISH: Shannon's index

Plot/types of Forest	BA (m ² /ha)	N (tree/ha)	RS	ISH	AGB (Mg ha ⁻¹)
GDF1	36.5	310	38	2.12	583.4
GDF2	31.5	297	37	1.89	503.5
GDF3	42.0	375	41	1.85	672.6
GDF4	37.8	408	56	2.67	594.6
GDF5	39.7	370	51	2.93	626.2
Mean	37.5	352.0	44.6	2.29	596.1
Standard deviation	3.9	46.8	8.4	0.48	62.2
PFF1	24.1	450	97	5.66	310.0
PFF2	35.1	589	111	5.83	459.1
PFF3	27.7	422	93	5.46	369.8
PFF4	29.0	338	75	5.3	397.7
Mean	29.0	449.7	94.0	5.56	384.1
Standard deviation	5.6	104.3	14.8	0.23	61.9
TFF1	29.0	443	108	5.87	356.5
TFF2	28.7	388	101	5.86	379.8
TFF3	29.6	471	96	5.58	370.2
TFF4	34.4	453	78	5.25	501.5
TFF5	30.7	547	106	5.92	400.3
Mean	30.5	460.4	97.8	5.70	401.7
Standard deviation	2.3	57.4	12.0	0.28	58.0

Table 2 Ranks of 10 most important tree species in the three types of forest. Ranks are based on relative density and relative basal area

Monodominant forests (GDF)		Periodically flooded forest (PFF)		Terra Firme forests (TFF)		
Relative density rank						
1	<i>Gilbertiodendron dewevrei</i> (De Wild.) Léonard	70.74	<i>Uapaca guineensis</i> Müll. Arg.	5.73	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	5.26
2	<i>Carapa procera</i> DC.	1.48	<i>Uapaca paludosa</i> Aubrév. & Léandri	5.00	<i>Carapa procera</i> DC.	4.74
3	<i>Plagiostyles africana</i> (Müll.Arg.) Prain	1.36	<i>Rinorea oblongifolia</i> C. Marquand	3.78	<i>Santiria trimera</i> (Oliv.) Aubrév.	4.43
4	<i>Angylocalyx pynaertii</i> De Wild.	1.25	<i>Dialium pachyphyllum</i> Harms	3.50	<i>Polyalthia suaveolens</i> Engl. & Diels	3.95
5	<i>Polyalthia suaveolens</i> Engl. & Diels	1.14	<i>Strombosiopsis tetandra</i> Engl.	3.45	<i>Heisteria trillesiana</i> Pierre	3.43
6	<i>Irvingia gabonensis</i> (Aurey-Lecomte ex O'Rorke) Baill.	1.08	<i>Carapa procera</i> DC.	2.95	<i>Pentaclethra macrophylla</i> Benth.	3.43
7	<i>Tessmannia africana</i> Harms	1.08	<i>Pentaclethra macrophylla</i> Benth.	2.67	<i>Anonidium mannii</i> (Oliv.) Engl. &	3.21
8	<i>Strombosia pustulata</i> Oliv.	1.02	<i>Heisteria trillesiana</i> Pierre	2.56	<i>Centroplacus glaucinus</i> Pierre	2.91
9	<i>Centroplacus glaucinus</i> Pierre	0.97	<i>Santiria trimera</i> (Oliv.) Aubrév.	2.56	<i>Plagiostyles africana</i> (Müll.Arg.)	2.78
10	<i>Dialium pachyphyllum</i> Harms	0.97	<i>Hylodendron gabunense</i> Taub.	2.33	<i>Tabernaemontana crassa</i> Benth.	2.39
Relative basal area rank						
1	<i>Gilbertiodendron dewevrei</i> (De Wild.) Léonard	81.13	<i>Uapaca heudelotii</i> Baill.	8.64	<i>Pentaclethra macrophylla</i> Benth.	7.09
2	<i>Pentaclethra macrophylla</i> Benth.	1.54	<i>Uapaca paludosa</i> Aubrév. & Léandri	8.39	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	6.42
3	<i>Parinari excelsa</i> Sabine	0.89	<i>Strombosiopsis tetandra</i> Engl.	5.41	<i>Heisteria trillesiana</i> Pierre	5.75
4	<i>Tessmannia africana</i> Harms	0.89	<i>Irvingia grandifolia</i> Engl.	4.85	<i>Uapaca paludosa</i> Aubrév. & Léandri	4.12
5	<i>Carapa procera</i> DC.	0.85	<i>Pentaclethra macrophylla</i> Benth.	4.08	<i>Carapa procera</i> DC.	2.78
6	<i>Desbordesia glaucescens</i> Tiegh.	0.81	<i>Heisteria trillesiana</i> Pierre	3.22	<i>Polyalthia suaveolens</i> Engl. & Diels	2.49
7	<i>Pachyelasma tessmannii</i> Harms	0.62	<i>Panda oleosa</i> Pierre	3.04	<i>Celtis tessmannii</i> De Wild.	2.47
8	<i>Erythrophleum suaveolens</i> (Guil. & Perr.) Brenan	0.59	<i>Uapaca guineensis</i> Müll. Arg.	3	<i>Santiria trimera</i> (Oliv.) Aubrév.	2.27
9	<i>Celtis tessmannii</i> De Wild.	0.58	<i>Hylodendron gabunense</i> Taub.	2.5	<i>Guarea cedrata</i> (A.Chev.) Pellegr.	2.01
10	<i>Irvingia gabonensis</i> (Aurey-Lecomte ex O'Rorke) Baill.	0.57	<i>Carapa procera</i> DC.	2.47	<i>Pachyelasma tessmannii</i> Harms	1.95

Heisteria trillesiana Pierre and *Santiria trimera* (Oliv.) Aubrév.).

Based on relative basal area, *Pentaclethra macrophylla* and *Carapa procera* were among the ten most dominant species in all three types of forest, whereas *Pachyelasma tessmannii* Harms, *Celtis tessmannii* De Wild., *Uapaca paludosa* Aubrév. & Léandri and *Heisteria trillesiana* Pierre dominated in two of the forest types.

Forest structure

Size-class frequency distributions indicated an approximately exponential structure for the three types of forests (Fig. 2). Overall, 5861 stems were recorded in the fourteen plots. Mean stem density (Table 1) was 460.4 ± 57.5 trees ha^{-1} in the TFF, 449.7 ± 104.3 trees ha^{-1} in PFF and 352.0 ± 46.8 trees ha^{-1} in GDF. The differences

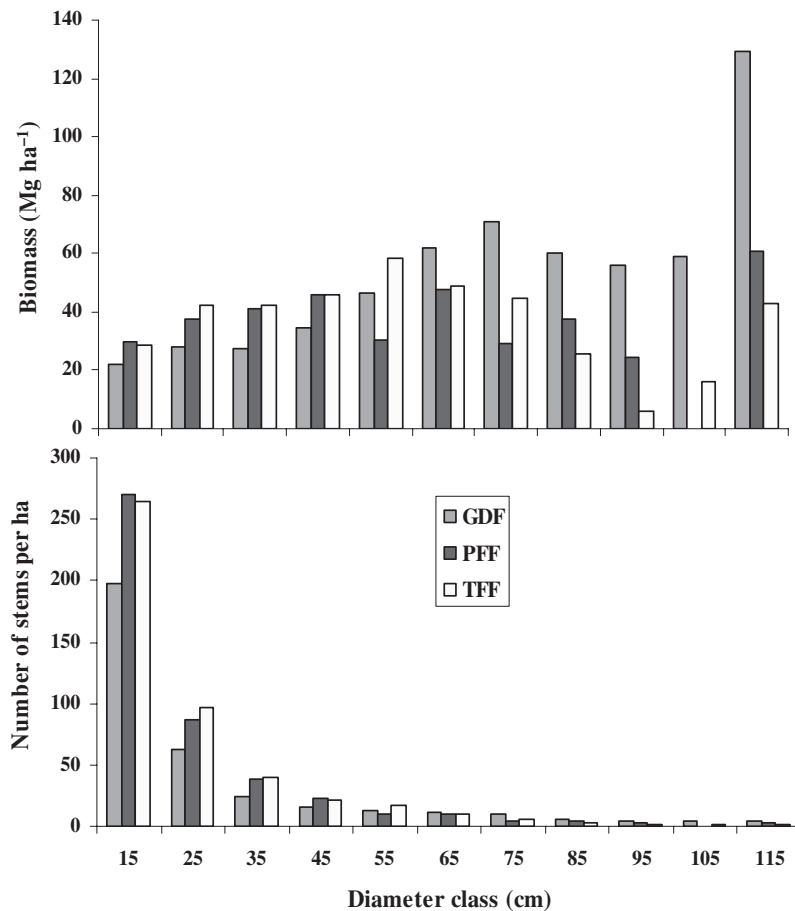


Fig 2 Variation of density (bottom) and biomass (top) (Mg/ha) with diameter class (cm) and with types of forest

were not statistically significant (ANOVA, $F_{2,11} = 3.50$, $P = 0.06$).

The average basal areas per plot differed significantly between forest types (one-way ANOVA, $F_{2,11} = 7.38$, $P = 0.009$). The value was highest in GDF ($30.5 \pm 2.3 \text{ m}^2 \text{ ha}^{-1}$). However, the difference between TFF ($30.5 \pm 2.3 \text{ m}^2 \text{ ha}^{-1}$) and PFF ($29.0 \pm 5.6 \text{ m}^2 \text{ ha}^{-1}$) was not significant (Newman–Keuls, $df = 11$, $P = 0.52$).

Aboveground biomass estimation

The average wood mass density of a stem in this study was $0.60 \pm 0.15 \text{ g cm}^{-3}$. Most of the species had a density between 0.50 and 0.79 g cm^{-3} . Eight species had a density higher than 0.79 g cm^{-3} and 41 species lower than 0.50 g cm^{-3} . The percentage of stems in central density interval varied from 83.3% (TFF) to 94.6% (GDF) (Fig. 3).

The total AGB estimate varied widely among the four-teen plots, from 310.0 to 672.6 Mg ha^{-1} . Mean biomass

for each forest type were, respectively, 596.1 ± 62.2 , 401.7 ± 58.0 and $384.1 \pm 61.9 \text{ Mg ha}^{-1}$ for GDF, TFF and PFF (Table 1). These values varied significantly between the types of forest (ANOVA, $F_{2,11} = 17.95$, $P < 0.001$). GDF biomass was significantly higher than the biomass of the two other vegetation types (Newman–Keuls, $df = 11$, $P < 0.001$).

Most AGB was found in trees with large diameters in all three types of forest (Fig. 2). Individuals with diameter $\geq 55 \text{ cm}$ accounted for 81.2% of the biomass in GDF, 59.8% in PFF and 60.5% in TFF.

Tree biomass allocation by different species

The top ten species with the most AGB contributed, respectively, to 91.1%, 52.4% and 42.2% of GDF, PFF and TFF biomass (Table 3). These results indicate that a few dominant species made the greatest contribution to the AGB in the studied rain forest. The AGB of *G. dewevrei*, the

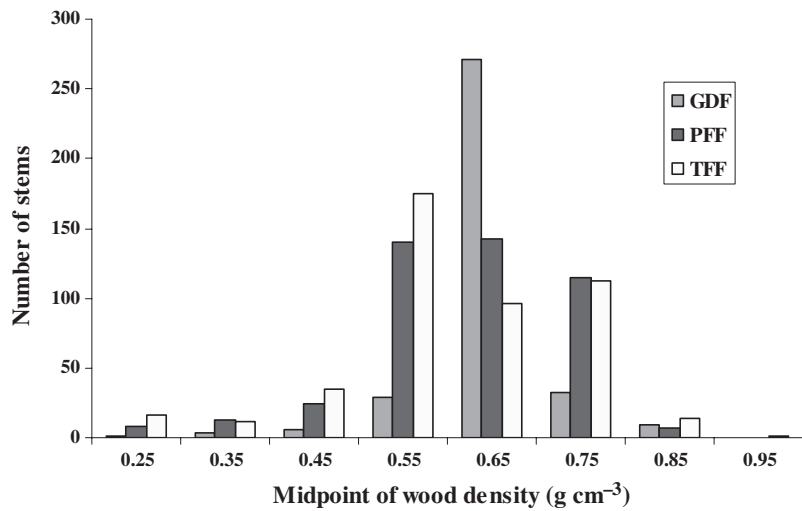


Fig 3 Number of stems by wood density classes

Table 3 The ten species with the relative highest AGB (%) in the three types of forest

Monodominant forests (GDF)		Periodically flooded forest (PFF)		Terra Firme forests (TFF)		
1	<i>Gilbertiodendron dewevrei</i> (De Wild.) Léonard	83.21	<i>Uapaca heudelotii</i> Baill	10.62	<i>Pentaclethra macrophylla</i> Benth	9.89
2	<i>Pentaclethra macrophylla</i> Benth	1.82	<i>Irvingia grandifolia</i> Engl	8.73	<i>Heisteria trillesiana</i> Pierre	7.19
3	<i>Tessmannia africana</i> Harms	1.07	<i>Uapaca paludosa</i> Aubrév. & Léandri	8.69	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	5.72
4	<i>Parinari excelsa</i> Sabine	0.93	<i>Strombosiopsis tetandra</i> Engl	5.19	<i>Uapaca paludosa</i> Aubrév. & Léandri	4.48
5	<i>Desbordesia glaucescens</i> Tiegh	0.86	<i>Pentaclethra macrophylla</i> Benth	5.17	<i>Pachyelasma tessmannii</i> Harms	3.21
6	<i>Pachyelasma tessmannii</i> Harms	0.84	<i>Heisteria trillesiana</i> Pierre	3.72	<i>Klainedoxa gabonensis</i> Pierre	2.92
7	<i>Erythrophleum suaveolens</i> (Guil. & Perr.) Brenan	0.75	<i>Panda oleosa</i> Pierre	2.90	<i>Irvingia grandifolia</i> Engl	2.38
8	<i>Carapa procera</i> DC	0.69	<i>Hylodendron gabunense</i> Taub	2.80	<i>Celtis tessmannii</i> De Wild	2.35
9	<i>Celtis tessmannii</i> De Wild	0.50	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	2.29	<i>Polyalthia suaveolens</i> Engl. & Diels	2.05
10	<i>Irvingia gabonensis</i> (Aurey-Lecomte ex O'Rorke) Baill	0.47	<i>Desbordesia glaucescens</i> Tiegh	2.27	<i>Carapa procera</i> DC	2.00

most abundant species in the monodominant forest accounted for 83.2% of the total AGB in GDF. In PFF and TFF, *Uapaca heudelotii* Baill. (10.6%) and *Pentaclethra macrophylla* (9.9%) had, respectively, the highest values of AGB. The latter species was also important in PFF (5.2%). While the individuals of *U. heudelotii* and *P. macrophylla* were relatively infrequent (Table 2), they contributed to a large proportion of the stand biomass because of their large average size.

Discussion

Vegetation

Tropical forests are known to be among the most diverse plant communities worldwide (Parmentier *et al.*, 2007). Nevertheless, the occurrence of patches of forest dominated by one or few species has been noted in several surveys of tropical vegetation (Connell & Lowman, 1989; Hart, Hart

& Murphy, 1989; Peters, 1997; Sonké, 2005; Peh, 2009; Kouob, 2009).

The high and close values of Shannon index in *terra firme* forests and periodically flooded forests indicate a high diversity, whereas a low diversity was observed in the *G. dewevrei* forests confirming their floristic homogeneity (Connell & Lowman, 1989). A similar pattern was observed by Hart, Hart & Murphy (1989) in Ituri forest (Democratic Republic of Congo): in monodominant stands of this forest, *G. dewevrei* accounted for 88% of the total basal area, and diversity indexes were three times lower than in mixed forest.

In spite of differences in structure, the three forest types share common species (e.g. *Pentaclethra macrophylla*). This observation supports the view that monodominant forests are not distinct associations with characteristic species (Hart, Hart & Murphy, 1989; Peh, 2009; Kouob, 2009). Many of the species co-occurring with *G. dewevrei* are also found in the other two forest types.

The greater species diversity in TFF has tended not to be explained by substrate differences (Hart, Hart & Murphy, 1989; Peh, 2009) or greater predation on seeds or juveniles (Hart, 1995; Gross *et al.*, 2000). The presence of ectomycorrhizae (Torti & Coley, 1999; McGuire, 2007) could play a role, but according to Torti, Coley & Kursar (2001), the dominance of *G. dewevrei* is not the result of one trait or mechanism. It is hypothesized to be the result of a number of different traits in adult trees that significantly modify understory environment, making it difficult for other species to regenerate there. Lower light levels and deep litter in the monodominant forest could inhibit the establishment of seedlings of a number of species. By contrast, Hart, Hart & Murphy (1989) consider that monodominant forest may indicate areas that have not experienced large-scale disturbance events for long periods. More recent reviews of the literature suggest that both traits and lack of disturbance may be needed for certain species to attain monodominance (Peh, 2009).

Aboveground biomass (AGB)

Average wood mass density obtained in this study (0.60 g cm^{-3}) is close to the one recorded by Brown (1997) for FAO data concerning tropical Africa species (0.58 g cm^{-3}). The greatest number of individuals, ranged between 0.50 and 0.79 g cm^{-3} , is similar to results obtained by Chave *et al.* (2003) in Panama. The range of

wood mass density found is similar to that from a recent study of 79 plots from across Africa (Lewis *et al.*, 2009a).

The AGB values obtained in this study vary amongst the three types of forest. The difference in the density of large trees appears to be the proximate cause of this variation. The high values of AGB (596 Mg ha^{-1}) obtained in the monodominant forest resulted from the fact that the *G. dewevrei* constitutes more than 80% of the number of large individuals and represents 83.2% of the total AGB. Note that the highest AGB forests had the lowest diversity levels and *vice versa*.

Our AGB value of 402 Mg ha^{-1} for TFF is not significantly different from other values from other tropical forests. This is similar to the 404 Mg ha^{-1} average from 79 closed canopy forest plots from across Africa by Lewis *et al.* (2009a), and within the range of values from Central Amazon forest of Brazil, which ranged between 231 and 492 Mg ha^{-1} (mean 356 Mg ha^{-1}) from $65 \times 1 \text{ ha}$ plots (Laurance *et al.*, 1999). Similarly, in the French Guiana, on $22 \times 1 \text{ ha}$ plots had from 230 to 416 Mg ha^{-1} (mean 323 Mg ha^{-1}) were obtained (Chave, Riera & Dubois, 2001) and are close to the 410 Mg ha^{-1} obtained by Zheng *et al.* (2006) in tropical rain forest of China. The mean AGB of monodominant forest 596 Mg ha^{-1} is higher than most estimates from other locations but is similar to that from another GDF in Eastern Democratic Republic of Congo, at 542 Mg ha^{-1} (Chave *et al.*, 2008).

In several tropical forests, results showed that AGB is strongly correlated with the number of individuals $\geq 70 \text{ cm}$ in diameter that contribute to more than 30% of AGB (Brown, Gillespie & Lugo, 1989; Brown & Lugo, 1992; Clark & Clark, 2000; Chave *et al.*, 2003). Similar results were obtained during this study with individuals belonging to this class contributing 48.5% of total AGB. Of course, as a significant fraction of AGB is stored in very large trees ($\geq 70 \text{ cm}$), the choice of allometric equation based on diameters for this size class can greatly influence AGB estimates (Clark & Clark, 2000; Dewalt & Chave, 2004; Chave *et al.*, 2005; Lewis *et al.*, 2009a).

Importance of African forests in the carbon cycle

Forests store $\sim 212 \text{ Pg}$ carbon in their biomass, more than any other terrestrial ecosystem (Dixon *et al.*, 1994; Clark, 2002). Tropical deforestation is estimated to have released 1.6 billion of tones of carbon per year during the 1990s, approximately 20% of total annual carbon emissions in the 1990s (Denman *et al.*, 2007). In Africa,

deforestation is 0.1–0.3 Pg C yr⁻¹ and 0.1 Pg C yr⁻¹ from harvesting wood (Ciais *et al.*, 2009), while fossil fuel use was 0.26 Pg C yr⁻¹ over the period 2000–2005 (Canadell, Raupach & Houghton, 2009). In addition, African forests absorbed 0.3 Pg C yr⁻¹, most likely through fertilization by more carbon dioxide in the atmosphere causing increased photosynthesis and plant growth (Lewis *et al.*, 2009a). Clearing tropical forest therefore not only adds carbon to the atmosphere, but additionally removes an important carbon sink which is currently sequestering CO₂ (Lescuyer & Locatelli, 1999). The data presented here can help improve these estimates via the new carbon storage estimates for fourteen more locations in central Africa. Recently, the importance of including carbon emissions from tropical deforestation, and preserving forest as carbon stores and sinks, in climate change policy has grown. Political acceptance and implementation of policies aimed at reducing emissions from deforestation and degradation, known as REDD, in turn requires accurate estimate of biomass carbon stocks (Gibbs *et al.*, 2007). The data presented here can assist in these efforts. In particular, the high carbon storage value of *G. dewevrei* forests suggests that they should be priority forest types in terms of protection from deforestation.

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