Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa

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ABSTRACT

The development of tree allometric equations is crucial to accurate forest carbon assessment. However, very few allometric equations exist for sub-Saharan Africa and as a result generalized allometric equations, often established for forests in other continents, are used by default. The objectives of this study were (1) to propose a sampling methodology and calculation procedures to assess biomass for tropical tree species of contrasted tree shapes in Africa, (2) to identify factors affecting within and between trees wood density, (3) to propose an allometric model that integrates these factors and (4) to evaluate the reliability of using generalized allometric equations in this type of forests. Models were developed to predict wood density and phytomass of the trees based on the harvesting of 42 trees from 16 species, representing three guild status in the wet evergreen forest of Boi Tano in Ghana. Results indicated that the wood density was highly influenced by the tree species, guild status, size of the tree and pith to bark distance. Dry mass of a tree was influenced by diameter at breast height, crown diameter and wood density. The wood density depends on the position of the wood within the tree and the guild status considered. The use of generalized allometric models in literature is limited by the specific climate zone, the consideration of tree height and species specific wood density. In considering those factors, using generalized allometric equations could result in an error of 3%. Further research should better consider the bigger trees and the influence of the topography and ecosystem history.

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1. Introduction

Accurate estimation of forest biomass is crucial for commercial uses (e.g., fuel wood and fibre), national development planning, as well as for scientific studies of ecosystem productivity, carbon (C) and nutrient flows and for assessing the contribution of changes in forest lands to the global C cycle (Basuki et al., 2009). Particularly in the latter context, the estimation of the above-ground biomass with a sufficient accuracy to assess the variations in C stored in the forest is becoming increasingly important (Ketterings et al., 2001; Chave et al., 2004).

Variability of biomass could be explained by several factors. Climate, topography, soil fertility, water supply, wood density, distribution of tree species, tree functional types and forest disturbances have impact on forest variability (Sicard et al., 2006; Fearnside, 1997; Luizão et al., 2004; Slik et al., 2008). For a determined tree species, tree mass is influenced by the size of the tree, its architecture, form (Birot and Caillez, 1970), health (e.g. hollow trees) (Fearnside, 1997), social status and variation of the wood density (Patino et al., 2009).

Wood density is a key variable for the estimation of tree mass. Within individual trees, wood density differs among branches, trunk and roots and can also vary radially within the trunk as wood is added at the periphery during growth. In a tropical forest plantation in Venezuela, Espinoza (2004) reported an increase in wood density from pith to bark, a decrease from the stump to half of the total tree height and then an increase towards the top of the stem for *Gmelina arborea*. Amorim (1991) and De Castro

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et al. (1993) reported pith to bark radial decrease of the wood density at breast height of 1.3 m for trees in tropical forests. In addition, De Macedo (1991) and Higuchi and de Carvalho (1994) indicated higher basic density at the breast height than at the top of the commercial bole. Fearnside (1997) found different wood densities in the different tree organs and reported that a better estimation of the proportion of heartwood, sapwood and bark would improve biomass estimation. Different tree species showed different radial variations in temperate forests (Woodcock and Shier, 2002). These authors reported that radial increases associated with low values of specific gravity are an early successional characteristic and radial decreases associated with high value of wood density with late succession. The difference in wood density and its radial trends reflect growth strategy and biomechanical considerations. However, there is no available report of wood density variations within tree in the natural forest of sub-Saharan Africa.

Changes in wood density are directly associated with structural variations at the molecular, cellular and organ levels. These structural differences are strongly correlated with a tree's mechanical properties (Gartner and Meinzer, 2005), water transport efficiency and safety factors for buckling and bending (Pittermann et al., 2006; van Gelder et al., 2006), photosynthesis and rates of carbon dioxide exchange (Ishida et al., 2008) and perhaps resistance to pathogens and herbivores (Rowe and Speck, 2005). Different species from different taxonomic, phylogenetic and architectural groups show convergence of these functional characteristics in response to the environment (Meinzer, 2003).

Estimation of biomass in a given forest consists in carrying out an inventory of the vegetation in sampled plots, application of appropriate allometric equations, and up-scaling to estimate biomass C stocks at the stand level (Chave et al., 2004). Key point of this method is the allometric equations (Návar, 2009). Despite their apparent simplicity, they have to be fitted carefully using the latest regression techniques available (Parresol, 1999; Wirth et al., 2004). Inappropriate application of allometric equations developed for a particular forest type to a different forest type may lead to considerable bias in C stocks estimations. For example, application of an allometric equation developed for a tropical moist forest (Brown, 1997) when applied to a tropical wet forest (Clark and Clark, 2000) over estimated aboveground biomass by 79% (Clark et al., 2001).

Measurements to develop allometric equations could be achieved by direct and indirect methods. Direct methods measure the biomass directly by weighing trees in the field while indirect methods involve the estimate of difficult to measure parameter, like stem volume and tree mass, from easy to measure tree parameter, like diameter at breast height and tree height (Peltier et al., 2007). Weighing trees in the field is undoubtedly the most accurate method of estimating aboveground tree dry mass but it is extremely time consuming and is generally limited to small areas and small-sized trees (Parresol, 1999). For the development of an allometric equation, samples of various tree components or organs at different points of the tree are taken, bulk density determined and together with volume, used to estimate dry mass of the component. Dry mass of the various components are summed up to obtain total tree dry mass (phytomass). This is then related to easy to measure parameter of the tree to develop allometric equations.

The allometric equations are then used to estimate the tree biomass over large areas. Most allometric equations concerning tropical forests have been developed for the tropical forests of South America and Asia (Brown, 1997; Baker et al., 2004; Chave et al., 2005). Moreover, there is a lack of such equations for the tropical humid forests of Africa hence equations developed for other regions are as consequence used by default. Moreover, reliability of

such equations has never been tested. Some authors concluded that species-specific allometric relationships are not needed to generate reliable estimates for forest C stocks (Gibbs et al., 2007), while others showed that species-specific allometric equation will improve biomass estimation (Ketterings et al., 2001; Pilli et al., 2006). Site variables have been shown to improve the performance of equations in both tropical and temperate even-aged forests (Saint-André et al., 2005).

Big trees represent important proportion of the forest biomass (Martinelli et al., 1994), hence data for generic allometric equations are skewed towards big trees. However, many forest disturbances affect mostly small trees (Villela et al., 2006). Currently, validity of established generalized equations excludes their use to all trees in a stand. For instance, the generalized equations provided by Brown (1997) and Chave et al. (2005) are valid for trees up to a diameter at breast height (d_{bh}) of 148 and 152 cm, respectively. The tropical forest consists of a variety of tree species per unit area; more than 300 tree species per hectare could be found in a tropical forest (Gibbs et al., 2007). In assessing the forest C stocks and biomass change it is necessary to consider the different ranges of trees species, their distribution and the variation of wood density. Fearnside (1997) reported that the best situation is to match both density and volume information identified to species level.

The main aim of this study was therefore to analyze the wood density and phytomass variations within and among trees and to develop an allometric model to estimate tree biomass in the wet evergreen forests of Ghana. The specific objectives were (i) to propose a sampling methodology and calculation procedures to assess phytomass of tropical rainforest tree species of contrasted tree shape (ii) to identify factors that affect wood density between and within trees of contrasted functional type, (iii) to propose two allometric models; one that integrates the most significant variables and another that considers convenient variables for field measurement and (iv) to evaluate the reliability of using generalized allometric equations in the evergreen forest type. In order to reach these objectives, two main steps were considered. The first step consists in analyzing the sources of variation in wood density while the second step focuses on the factors influencing the variation of phytomass.

2. Materials and method

2.1. Study site

This study was carried out in Boi Tano Reserve Forest (5°20′–5°36′N and 2°34′–2°50′W), located in the Enchi Forest District of the Western Region of Ghana. The forest reserve has a total area of 122 km² and is classified as wet-evergreen forest type (Hall and Swaine, 1976). The climate is characterised by a bimodal rainfall distribution and the mean annual precipitation is 1750 mm (Hall and Swaine, 1981), and 2155 mm (FAO, 2005). The Forest Reserve transverse the lower Tano basin and consists of a series of hills. The soils are mostly oxisols (Hawthorne and Abu Juam, 1995). The forest falls in the Cynometra - Lophira - Terriatia association vegetation classification (Taylor, 1960), the tropical rainforest ecological zone (FAO, 2001), the Koppen equatorial monsoon climatic zone and the moist climate zone (FAO/Agrhymet Network & ESRI). Very little is known about the history of the Boi Tano Forest Reserve before its first concession in 1947. There was timber exploitation before its selection and demarcation in 1967 as forest reserve, but the area did not appear to have come under intensive selective logging and clearing for farming because of the low soil fertility and the hilly terrain. The Forest Reserve is currently being logged by Samartex Timber and Plywood Limited.

2.2. Tree sampling

Selection of trees for destructive measurement was based on three criteria. Selection of the big trees ($d_{bh} \geq 50$ cm) was dictated by the trees earmarked by the company for harvesting according to the Ghanaian forestry law. The stipulated felling limit is 50 cm d_{bh}. The medium sized trees (20 cm $\leq d_{bh} < 50$ cm) were selected from the trees affected by the logging operations. Severely damaged trees were avoided. Whereas the smaller trees ($d_{bh} < 20$ cm) were randomly selected from the forest stand. The selected trees reflected three Guild classes, namely Non Pioneer Light Demander species (NPLD), Pioneer species (P) and Shade Bearer species (SB) (Hawthorne, 1995), with the number of trees within the guilds being 22, 11 and 9, respectively. The total number of sampled trees was therefore 42. The number of species within the NPLD, P and SB was 5, 4 and 7 respectively, given a total of 16 species. The species were identified with the aid of experts in tree identification and botanical books specific for the forests of Ghana (Hawthorne, 1999; Hawthorne and Gyakari, 2006). The 16 tree species represent 1.56% of the total number of tree species in that forest. Diameter at breast height, d_{bh}, ranged from 2.6 to 180 cm, height from 1.5 to 61 m, crown diameter from 1.5 to 98 m and stem volume from 0.01 to 112 m^3 (Table 1). Twenty of the trees were within the d_{bh} class of less than 50 cm, 15 within the 50 to 99 cm diameter class, five within the 100 to 149 cm diameter class and two with diameter greater than 150 cm.

The sampled trees were felled with a chainsaw according to conventional logging practices leaving a stump of up to about 2.0 m height, depending on tree size. The measurements carried out on the felled trees were d_{bh}, total height (H), crown diameter (CD), buttress height (H_b) and length (L_b). In the absence of buttress, the d_{bh} was measured with a calliper at 1.3 meters height while in the presence of buttress the d_{bh} was measured at the end of the buttress. Tree height, CD, L_b and H_b were measured with a measuring tape.

2.3. Pytomass estimation of small-sized trees

The small-sized trees ($d_{bh} < 20$ cm) were felled close to the ground and stratified into trunk, branches and foliage. The fresh mass of the trunk (M_t), branches (M_b) and foliage (M_l) were weighed using a spring balance. Samples were taken from each of the three organs for the determination of dry to fresh mass ratio (Fig. 1). The leaf samples were dried at 65 °C for 48 h, while the wood samples were dried at 105 °C to constant mass. The fresh and the dry mass of the samples were measured with an electronic balance. From the ratio of fresh to dry mass and the total fresh mass of a component, dry mass of the component was determined. The total above ground phytomass of a tree (AGB) was calculated by summing the dry mass of the various components.

2.4. Phytomas estimation of big-sized trees

Diameter measurements for big-sized trees ($d_{bh} \geq 20$ cm) were carried out at 1.0 and 2.0 m intervals, starting from the base, for branch and trunk, respectively. The measurements were used to calculate the respective branch and trunk volume. Schematic representation of the sectioning is given in Fig. 1. Dry mass of the buttresses, stump, trunk and the big branches (diameter >10 cm) were determined from volume and wood density measurements. For the small branches, three branches were randomly selected from each tree and the dry mass determined. The dry mass was then related to the basal diameter to develop allometric equation. The best fitting models between the branch basal diameter (BD) and the dry mass of the branches (M_{br}) were performed for each guild status.
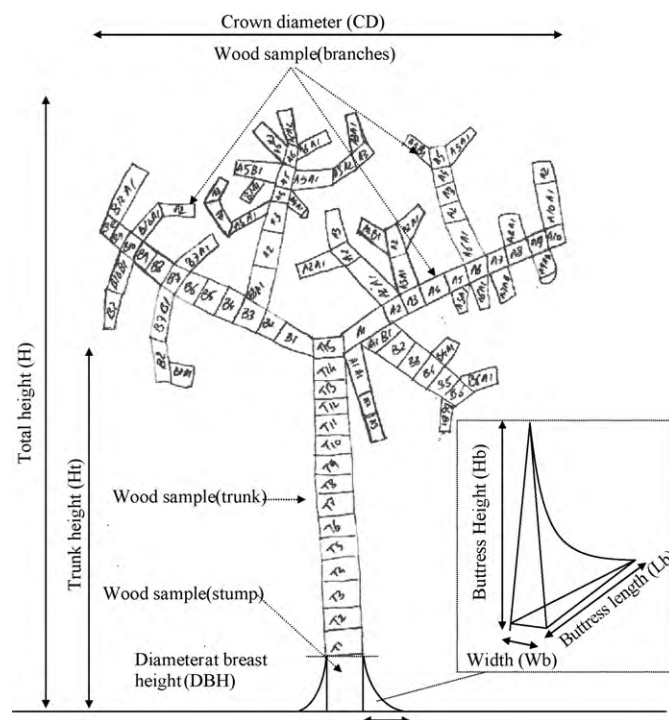

Fig. 1. Schematic of partition procedure for mass determination of the trees. The diagram represents the location of tree measurements within each tree. The sections T1 [.] Tn represents the different trunk sections while B1 [.] Bn represents the branch sections. While the diameter of the trunk was measured at two meter intervals, the branch diameter was measured at one meter intervals. The wood samples were collected at the base and middle of the trunk and from three branches. The buttresses were represented by a sort of pyramid whose hypotenuse followed a quarter circle.

Large trees often have many buttresses. The volume of each buttress q was estimated by measuring the height of the buttress (H_b), the width (W_b), and the length (L_b) (Fig. 1).

$$V_q = \left(\frac{4 \times (L_b \times H_b) - (\pi \times H_b \times L_b)}{4} \right) \times \frac{W_b}{3} \tag{1}$$

The stump (V_r) was considered as a cylinder with the cut end being the diameter (D_{cut}). Together with height of the stump (H_{cut}), the volume was calculated. The volume of sections (V_s) of the trunk and big branches was determined by Smalians formula as;

$$V_s = \frac{\pi \times L_s}{8} \times \left(D_1^2 + D_2^2 \right) \tag{2}$$

where L_s is the length of the section, D_1 and D_2 are the diameters of the smaller and larger end of the section, respectively.

The volume of the trunk and big branches was determined by the summation of the sections of the respective organs. The wood density for each section was obtained using the model presented in Equation (5). Mass of the buttresses, stump, trunk and big branches was determined by multiplying the volume of the section by the respective wood density. The aboveground biomass (AGB) is here defined as:

$$\begin{aligned} AGB = \sum_{q=0}^{m} (V_q \times WD_q) + V_r \times WD_r \\ + \sum_{s=1}^{n} (V_s \times WD_s) + \sum_{l=1}^{o} M_{brl} \end{aligned} \tag{3}$$

where V_q, V_r and V_s are volume and WD_q, WD_r, and WD_s are wood density for buttress, stump and trunk and big branches, respectively.

Table 1
Characteristics of the selected trees.

Guild types	Botanical Names	Common names	Frequency		Tree ID	d_{bh} (cm)	H (m)	CD (m)	Mean WD (Mg m^{-3})	Volume (m^3)	Mass in tree components (Mg)					BCEF	BEF
			%all DBH	%DBH > 50cm							Branches	Leaves	Trunk	Buttress	Total		
NPLD	Heritiera utilis	Nyankom	0.27	8.00	1	7.3	5.1	3.7	0.58	0.03	0.02	0	-	-	0.02	0.64	-
					2	12.4	12	5	0.62	0.11	0.02	0	0.05	-	0.07	0.64	1.42
					3	31	22	9	0.61	1.34	0.1	0.01	0.71	0.02	0.83	0.62	1.17
					4	32.5	27.5	7.1	0.61	1.12	0.07	0.01	0.61	0.01	0.7	0.62	1.14
					5	48.1	35.6	7.9	0.61	3.83	0.24	0.01	2.07	0.01	2.33	0.61	1.13
					6	56.5	35.1	8	0.6	5.43	0.85	0.03	2.28	0.14	3.31	0.61	1.45
					7	62	40.4	11.1	0.6	6.84	0.68	0.04	3.28	0.15	4.15	0.61	1.26
					8	71.9	42.3	20	0.6	9.84	1.34	0.05	4.43	0.11	5.93	0.6	1.34
					9	83	39.4	15.9	0.6	11.89	2.2	0.09	4.83	0.04	7.16	0.6	1.48
					10	100	50.5	19.1	0.58	31.71	8.71	0.11	8.39	1.4	18.61	0.59	2.22
					11	105	50.5	19.2	0.58	35.36	8.81	0.13	11.18	0.65	20.76	0.59	1.86
					12	6.5	8.1	1.5	0.78	0.01	0.01	0	-	-	0.01	0.85	-
	Tieghemella heckelii	Makore	0.01	0.80	13	12	17	4.7	0.78	0.15	0.12	0.01	-	-	0.13	0.86	-
					14	73.5	45	11.1	0.66	11.08	1.27	0.04	5.91	0.14	7.36	0.66	1.25
					15	80.5	50.7	13	0.66	12.25	1.54	0.05	6.45	0.09	8.13	0.66	1.26
					16	93	45	17	0.66	17.79	3.66	0.06	7.8	0.21	11.73	0.66	1.5
					17	180	61	41	0.62	112.81	27.28	0.74	35.07	7.16	70.24	0.62	2
	Piptadeniastrum africanum	Dahoma	0.11	3.6	18	70	39.7	10.5	0.58	10.98	2.97	0.06	3.29	0.07	6.39	0.58	1.94
					19	89	50	18.8	0.57	15.72	3.69	0.05	5.16	0.16	9.06	0.58	1.75
					20	90	50.2	16	0.57	22.34	5.73	0.38	6.23	0.74	13.08	0.59	2.1
	Aubrevillea kerstingii	Dahomanua	0.02	-	21	65	32.5	9	0.62	4.79	1.52	0.02	1.45	-	2.99	0.62	2.06
	Afzelia bella	Papao-nua	0.02	-	22	83.6	40	13.5	0.67	14.57	3.17	0.03	6	0.58	9.79	0.67	1.63
P.	Cecropia peltata	Odwuma	<0.001	-	23	7.8	2.3	2.5	0.17	0.07	0	0	0.01	-	0.01	0.18	1.31
					24	20.5	21.2	6.2	0.23	0.44	0.03	0	0.07	-	0.11	0.24	1.55
					25	29.3	22.5	8.9	0.27	1.11	0.13	0.01	0.16	-	0.31	0.28	1.87
					26	35.5	12	7.3	0.26	1.39	0.12	0.02	0.25	-	0.38	0.28	1.53
	Ceiba pentandra	Onyina	<0.001	<0.001	27	132	45	16	0.54	28.55	1.53	0.04	13.37	0.44	15.39	0.54	1.15
					28	170	51	27.1	0.26	64.84	3.2	0.1	11.87	1.88	17.05	0.26	1.44
	Nauclea diderrichii	Kusia	0.01	0.58	29	2.6	4.9	8.4	0.76	0	0	0	-	-	0	0.86	-
					30	94.6	50.5	12	0.5	17.19	1.06	0.02	7.49	0.06	8.64	0.5	1.15
					31	110	58.8	14.1	0.4	28.71	3.47	0.06	7.9	0.07	11.49	0.4	1.45
					32	112	40	13.2	0.47	22.74	3.41	0.1	7.19	0.13	10.82	0.48	1.5
	Daniellia thurifera	Sopi	0.02	0.38	33	9	9.3	8	0.42	0.11	0.05	0.01	-	-	0.05	0.47	-
SB	Guarea cedrata	Kwabohoro	0.04	0.19	34	12.8	13	3.1	0.62	0.12	0.08	0.01	-	-	0.08	0.69	-
					35	71.5	45.5	14	0.5	10.12	0.65	0.02	4.3	0.13	5.1	0.5	1.19
	Strombosia glaucescens	Afena	< 0.001	-	36	7.6	11.3	3.9	0.66	0.07	0.05	0.01	-	-	0.05	0.74	-
					37	26.5	26	12.2	0.73	1.09	0.2	0.01	0.58	0	0.8	0.74	1.37
	Garcinia epunctata	Nsokonua	0.23	-	38	7.1	5.7	3.8	0.65	0.08	0.05	0.01	-	-	0.06	0.73	-
	Drypetes chevalieri	Katreka	<0.001	-	39	13.2	15.7	5	0.65	0.22	0.15	0.02	-	-	0.16	0.73	-
	Cola nitida	Bese	0.37	0.38	40	23.6	23.4	6.3	0.56	0.68	0.09	0.01	0.28	0	0.39	0.57	1.36
	Nesogordonia papaverifera	Danta	<0.001	-	41	24.3	30.2	6.5	0.69	0.73	0.12	0.01	0.36	0.02	0.51	0.7	1.41
	Dialium aubrevilliei	Dua bankye	0.46	4.23	42	98	43.7	98	0.65	18.49	2.55	0.05	9.07	0.4	12.07	0.65	1.33

P: Pioneer, NPLD: Non Pioneer Light Demander, SB: Shade bearer, d_{bh}: diameter at breast height, H: height, CD: crown diameter, WD: wood density, Volume: the total volume including small branches, BEF: individual biomass expansion factor (conversion of the trunk biomass to the total biomass), BCEF: individual biomass conversion and expansion factor (conversion of the trunk volume to the total biomass); The frequency of tree species were measured on a 16 ha inventory for tree stems above 2 cm of d_{bh} in the same forest but in a different block (Henry et al. unpublished).

2.5. Wood density

The felled trees were stratified into four tree compartments or organs namely; (1) stump with buttress (2) trunk (3) big branches, with basal diameter greater than 10 cm, and (4) small branches with basal diameter smaller than 10 cm. Sampled disks were extracted from the stump, trunk and branches with chainsaw machine. The distance from the base of the tree to where the disk samples were collected was measured. Three disk samples were collected from the branches, while one disk sample was collected from both the stump and trunk. The sampled disks were taken to the laboratory where rectangular sub-samples of $2.0 \, cm \times 2.0 \, cm \times 10 \, cm$ were extracted from each sample at 2.0 cm intervals from the pith to the periphery. For accuracy, the rectangular wood samples were re-measured with a digital calliper at three points along the length for the width and breadth and at two points for the length, for fresh volume calculations. The rectangular wood samples, which numbered 811, were oven-dried at 105 °C to constant mass and the dry mass determined with an electronic balance. The wood samples for *Daniellia thurifera* got rotten during transportation, hence were excluded from further analysis. The volume and the dry mass measurements were used to calculate wood density as:

$$WD_k = \frac{M_{wk}}{V_{wk}} \tag{4}$$

where M_{wk} is the dry mass of the wood sample k (g), V_{wk} is the green volume (cm^3) and WD is the basic wood density (g cm^{-3}).

2.6. Data analysis

2.6.1. Wood density

The wood density was analysed to reflect the inter- and intra-variability according to the following factors: tree species (SP), Guild status (GS), a surrogate of tree volume (Dim=DBH$^2 \times$ H), tree height (H), crown diameter (CD), radial and vertical positions, tree social status and compartment (stump, trunk and branch). The term social status describes the instantaneous position of the tree in its very local environment and is expressed in this study as the ratio of CD to H (SO1), and H to DBH (SO2) (Moravie et al., 1999). The vertical position of the samples in the tree was expressed in relative height (H_r), which is expressed as the ratio of that height position to total tree height, while the radial position corresponded to the distance from the pith to the periphery. A first statistical descrip-

tion and test of comparison was carried out using Friedman ANOVA test followed by Tukey HSD test.

The wood density was modelled using the following formula:

$$WD_{ijklmno} = \delta + \alpha_i + \beta_j + \gamma_k + \beta_j(\gamma_k) + \mu_l + \theta_m + \rho_n + \lambda_o + \delta_o$$
$$+ \lambda_o \times \mu_l + \lambda_o \times \theta_m + \gamma_k \times \mu_l + \gamma_k \times \lambda_o + \delta_o \times \lambda_o$$
$$+ \lambda_o \times \mu_l + \varepsilon_{ijklmno} \tag{5}$$

where α_i, $i = 1,2.44$ - corresponds to the tree (categorical variable), β_j, $j = 1,2,.13$ - corresponds to the tree species (categorical), γ_k, $k =$ non Pioneer Light Demander, Pioneer and Shade Bearer - corresponds to the guild status (categorical), μl, corresponds to the size of the tree (Dim, continuous), θ_m, $m =$ stump, trunk and branch - corresponds to the location within the trunk (categorical variable), ρ_n corresponds to the relative height (H_r, continuous), λ_o corresponds to the distance from the pith (continuous), δ_p corresponds to the social status (So1 and 2, continuous) and $\varepsilon_{ijklmno}$, corresponds to the residual term.

The influence of each of the factors in the model was tested using MIXED procedure in the SAS software (SAS® Institute Inc., Cary, NC, USA, 2004). Some of the parameters were considered as fixed effects and others as random effects (Appendix A). All measurements from the same individual tree were considered as repeated measurements. There were no wood density samples for some tree components of three individuals; hence those individuals were excluded from the analysed dataset. Thus the analysis was performed on 788 wood samples from 39 trees of 13 species. A total of 114 models were run allowing the testing of several combinations of the effects (Appendix A). The model selection was achieved using Akaike Information Criterion (AIC) criteria which represents a good balance between model adjustment and number of parameters (Burnham and Anderson, 2002).

2.6.2. Choice of a functional form for the allometric equation

Relationship between tree characteristics and mass of the tree components was fitted using the procedure NLP of SAS software. Linear (with additive error), nonlinear (with additive error) and nonlinear (with multiplicative error) models were tested using one to three inputs leading to nine basic models (Table 2). All possible combinations of variables were tested. Primary variables of DBH, H, CD and WD, surrogates of tree cross sectional area (DBH^2 and CD^2) and surrogates of tree phytomass (DBH$^2 \times H \times$ WD and CD$^2 \times H \times$ WD) were used. A total of 960 models were tested to

Table 2
Selected models for estimating tree biomass: The selected inputs were: the diameter at breast height (d_{bh}), tree height (H), the wood density (WD), the basal area (BA) and the crown diameter (CD).

Models	Group	Model	Model inputs			Model parameters				Model performances				
			X	W	Z	a	b	c	d	Sigma2	k	RMSE	AIC	ΔAIC
$Y = a \times X^b \times W^c \times Z^d$	ALL	6	d_{bh}	CD	WD	0.03	8.61E-02	0.03	0.04	0.01	0.10	1750	611	0
$Y = a + b \times X + c \times W$		2	d_{bh}^2xHxWD	CD		3.47E-03	0.17		0.01	0.10	2496	617	6	
$Y = a + b \times X \times W$		7	d_{bh}^2xH	WD		3.47E-03			0.02	0.10	2344	624	13	
$Y = a \times X^b$		4	d_{bh}^2xHxWD		0.01	6.67E-02			0.01	0.06	2880	628	16	
$Y = a + b \times X + c \times W$	NPLD	2	d_{bh}^2xHxWD	CD		-9.38	3.47E-03	0.27		0.00	0.13	621	343	0
$Y = a \times X^b \times W^c$		5	d_{bh}^2xHxWD	CD	0.01	5.76E-02	0.03		0.00	0.12	1308	368	24	
$Y = a \times X^b \times W^c \times Z^d$	P	6	d_{bh}	H	CD	0.00	1.37E-01	0.03	-0.92	0.49	0.06	72	137	0
$Y = a + b \times X$		1	d_{bh}^2xWD			-4.99	8.61E-02			0.00	0.14	1182	140	3
$Y = a + b \times X \times W + c \times X \times Z$		8	d_{bh}	H	CD	6.94E-03	0.04		0.00	0.19	4021	144	6	
$Y = a \times X^b$		4	d_{bh}^2xHxWD		0.02	5.97E-02			0.00	0.06	629	147	10	
$Y = a \times X^b \times W^c \times Z^d$	SB	6	d_{bh}	CD	WD	0.03	9.10E-02	0.02	0.05	358	-	1112	90	0
$Y = a + b \times X + c \times W$		2	d_{bh}^2xHxWD	CD		2.78E-03	0.53		0.08	0.05	2496	103	13	
$Y = a + b \times X$		1	d_{bh}^2xHxWD		48.87	2.78E-03			0.17	0.05	34	107	16	
$Y = a \times X^b$		4	d_{bh}^2xWD			0.05	4.86E-02			0.10	0.04	90	109	19

Model 1: $Y = a + b \times X$, 2: $Y = a + b \times X + c \times W$, 3: $Y = a + b \times X + c \times W + d \times Z$, 4: $Y = a \times X^b$, 5: $Y = a \times X^b \times W^c$, 6: $Y = a \times X^b \times W^c \times Z^d$, 7: $Y = a + b \times X \times W$, 8: $Y = a + b \times X \times W + c \times X \times Z$, and 9: $Y = a + b \times X \times (c \times W + d \times Z)$; The results from model 3 were equivalent to model 2, and model 9 were equivalent to model 8. Sigma2 and k were the parameters used to model the variance (Variance = sigma2 × (dbh)$\hat{}$(2 × k)) and consider the heteroscedasticity RMSE: root mean square error, AIC: Akaike Information Criterion.

fit phytomass of the tree, leaves, branches and trunks using DBH, height, wood density, basal area and crown diameter as predictive variables. The best and easy to implement models (i.e. when only the DBH or the DBH and WD were available) were selected (The selected inputs were: the diameter at breast height (DBH), tree height (H), the wood density (WD), the basal area (BA) and the crown diameter (CD).

Model 1: $Y = a + b \times X$, 2: $Y = a + b \times X + c \times W$, 3: $Y = a + b \times X + c \times W + d \times Z$, 4: $Y = a \times Xb$, 5: $Y = a \times Xb \times Wc$, 6: $Y = a \times Xb \times Wc + Zd$, 7: $Y = a + b \times X \times W$, 8: $Y = a + b \times X \times W + c \times X \times Z$, and 9: $Y = a + b \times X \times (c \times W + d \times Z)$

The results from model 3 were equivalent to model 2, and model 9 were equivalent to model 8. Sigma2 and K were the parameters used to model the variance (Variance = sigma2 × (DBH)$(2 \times k)$) and consider the heteroscedasticity RMSE: root mean square error, AIC: Akaike Information Criterion (Table 3).

2.6.3. Validity of generalized allometric models

In order to test the validity of the generalized allometric equations, the estimations using equations from literature were compared with those of this study. The statistical test consisted in a student test for the intercept equal to zero and slope of the regressions equal to unity (cf. Adu-Bredu et al., 2008). The bias of the model was calculated as the mean of the residual, with the ideal value being zero. The model efficiency (ef) was calculated following Mayer and Butler (1993).

$$ef = 1 - \frac{\sum(y - \hat{y})^2}{\sum(y - \bar{y})^2} \qquad (6)$$

where y is the measured value, $\hat{y}$ and is the predicted value and $\bar{y}$ is the mean of all the measured values. Equations developed for forests in both wet and moist climatic zones were used for comparison (Table 4).

3. Results

3.1. Wood density

The wood density ranged from 0.11 to 1.01 g cm^{-3}, with an average value of 0.59 ± 0.00484 (SD) g cm^{-3} (Table 5). The wood density was significantly influenced by the guild status ($p < 0.001$, DF = 609): The pioneers (P) species had the lowest wood density value of 0.42 ± 0.012 (SD) g cm^{-3}, followed in an increasing order by Non-Pioneer Light Demanders (NPLD) and Shade bearers (SB), with mean values of 0.63 ± 0.00388 g cm^{-3} and 0.64 ± 0.0107 g cm^{-3}, respectively. However, the difference in wood density between NPLD and SB was not significant ($p = 0.303$, DF = 641). Within a guild, the wood density varied among tree species (Table 5). For example, the lowest wood density for the pioneer group was observed for *Cecropia peltata* (0.25 ± 0.0156 g cm^{-3}) while the highest was for *Ceiba pentandra* (0.48 ± 1.92 10^{-2} g cm^{-3}). With regard to the NPLD and the SB, the lowest wood densities were observed for *Piptadeniastrum africanum* (0.59 ± 0.00703 g cm^{-3}) and *Guarea cedrata* (0.53 ± 0.0122 g cm^{-3}), while the highest were observed for *Afzelia bella* (0.69 ± 0.0157 g m^{-3}) and *Drypetes chevalieri* (0.92 ± 0.0258 g cm^{-3}), respectively. Moreover, wood density varied significantly within a guild type and some species from the SB group (*Guarea cedrata*) presented lower values than all the tree species from the *NPLD* group ($p < 0.0001$, DF = 553).

From the 114 models that were tested, the best parameters for the prediction of wood density included tree species, guild status, pith to bark distance and tree size (Appendix A).

$$WD = \text{Intercept} + b_1 \times \text{Dist} + b_2 \times \text{Dim} + b_3 \times \text{PFT} + b_4$$
$$\times \text{Dim(PFT)} + b_5 \times \text{SP(PFT)} + b_1 \times \frac{\text{mean(Dist)}}{\text{SD(Dist)}} \times \text{SD(WD)}$$
$$+ b_2 \times \frac{\text{mean(Dim)}}{\text{SD(Dim)}} \times \text{SD(WD)} + b_4 \times \frac{\text{Mean(Dim)}}{\text{SD(Dim)}}$$
$$\times \text{SD(WD)} \qquad (7)$$

There was a decrease in wood density from pith to bark (Fig. 2a). The rate of decrease was not significantly different among guild types ($p < 0.05$), but the intercept value of 0.427, 0.643, 0.645 for P, NPLD and SB, respectively was significantly different. For instance, for a tree of d_{bh} 200 cm the wood density would be 10% lower in outer wood than in inner wood. Wood density variation with tree size was significantly different among the guild types ($p < 0.0001$) (Fig. 2b). The wood density increased with tree size by 0.1% per cubic meter for P species, and by 0.01 and 0.03% for NPLD and SB species, respectively. Moreover, for a P species with a volume of about 190 m^3 the wood density was found to be 38% greater

Table 3
Selected models for estimating biomass of tree components.

Models	Component	Guild status	a	b	c	sigma	k	AIC	RMSE
$Y = a \times d_{bh}\hat{}(b) \times CD\hat{}(c)$	Branches	ALL	0.02	2.06	1.00	0.00	3.14	504	2654
		NPLD	0.00	3.75	−0.47	0.00	2.48	308	1378
		P	0.03	1.81	1.04	0.00	3.39	120	840
		SB	0.25	1.48	0.76	0.00	3.34	63	166
$Y = a \times d_{bh}\hat{}(b \times CD\hat{}(c)$	Leaves	ALL	0.01	1.62	0.79	0.00	2.98	296	140
		NPLD	0.00	2.00	0.65	0.00	2.11	201	76
		P	0.04	1.05	0.86	0.00	1.67	74	726
		SB	0.12	1.82	−0.94	5.21	–	30	6
$Y = a \times d_{bh}\hat{}(b) \times WD\hat{}(c)$	Trunk	ALL	0.19	2.20	0.17	0.05	1.99	536	2778
		NPLD	0.21	2.29	0.04	0.10	1.83	313	1263
		P	0.03	3.58	−1.63	0.00	2.90	133	3176
		SB	0.19	2.02	0.57	0.00	2.20	67	1396
$Y = a \times d_{bh}\hat{}(b)$	Total	ALL	0.30	2.31		0.05	2.11	647	5322
		NPLD	0.11	2.58		0.05	1.02	345	1080
		P		1.95		0.09	0.94	168	688
		SB		1.99		0.98	0.73	115	445
$Y = a \times d_{bh}\hat{b} \times H\hat{}c$	Total	ALL	0.17	1.97	0.55	0.05	2.09	644	5324
$Y = a + b \times (d_{bh}\hat{2} \times H)$		NPLD		0.03		0.02	2.08	344	1846
$Y = a + b \times d_{bh} + c \times H$		P	−30.75	4.24	4.73	0.00	3.82	153	4415
$Y = a + b \times d_{bh}\hat{2} \times H$		SB	47.21	0.03		0.03	2.04	114	230

Table 4
Comparison with other tree allometric equations found in the literature.

References	Brown et al. (1989)				Brown (1997)		Chave et al. (2005)						IPCC (2006)	Pearson et al. (2005) only Cecropia undefined	This study	
Climate zone Variables	Wet DBH	Wet DBH, H	Moist DBH	Moist DBH, H	Wet DBH	Moist DBH	Wet DBH, H and WD (literature)	Wet DBH, H and WD (this study)	Wet DBH and WD (this study)	Moist DBH, H and WD (literature)	Moist DBH, H and WD (this study)	Moist DBH and WD (this study)	Moist DBH	DBH	DBH, CD and WD	DBH, H or CD, WD and GS
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
Mean (observed values)	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	6.82	0.20	6.82	6.82
Mean (simulated values)	3.34	4.50	5.77	7.87	3.60	5.98	4.89	5.02	3.86	7.66	7.03	6.51	9.40	0.21	6.66	7.05
Mean Errors	−3.47	−2.31	−1.04	1.06	−3.21	−0.83	−1.93	−1.80	−2.95	0.85	0.22	−0.31	2.59	0.01	−0.16	0.24
Mean Absolute Errors (MAE)	3.50	2.59	2.20	2.06	3.28	2.17	2.34	1.82	2.97	2.25	1.12	1.41	2.83	0.03	1.38	1.36
Modelling Efficiency	0.44	0.67	0.73	0.84	0.49	0.75	0.74	0.80	0.58	0.81	0.97	0.90	0.59	0.97	0.95	0.93
RMSE	8.69	6.67	6.01	4.68	8.32	5.85	5.96	5.16	7.58	5.13	2.10	3.71	7.45	0.03	2.64	3.18
MAE/Mean (%)	51%	38%	32%	30%	48%	32%	34%	27%	44%	33%	16%	21%	42%	13%	20%	20%
Linear Regression																
R^2	0.84	0.84	0.78	0.85	0.78	0.78	0.90	0.96	0.91	0.91	0.97	0.93	0.81	0.84	0.95	0.93
Slope	2.31 ***	1.66 ***	1.33 **	0.93 NS	2.13 ***	1.28 *	1.63 ***	1.59 ***	2.2 ***	0.92 NS	1.08 *	1.24 ***	0.69 ***	1.04 NS	0.97 NS	1.04 NS
Intercept	−0.92 NS	−0.68 NS	−0.84 NS	−0.52 NS	−0.85 NS	−0.92 NS	−1.15 NS	−1.18 **	−1.69 *	−0.2 NS	−0.75 *	−1.23 *	0.37 ***	−0.02 NS	0.33 NS	−0.54 NS
Bias	32.63 ***	22.94 ***	5.3 **	1.77 NS	28.48 ***	32.63 ***	32.51 ***	83.11 ***	79.67 ***	1.36 NS	3.74 *	10.49 ***	23.97 ***	0.24 NS	0.35 NS	0.58 NS
Deviation	−51%	−−34%	−15%	16%	−47%	−12%	−28%	−26%	−43%	12%	3%	−5%	38%	5%	−2%	3%

* p(H0: Fobs > Fth = 0) < 0.05. ** p(H0: Fobs > Fth = 0) < 0.01. *** P(H0: Fobs > Fth = 0) < 0.001; NS means non significant. The inputs were: the diameter at breast height (d_{bh}), tree height (H), the wood density (WD), the basal area (BA) and the crown diameter (CD). Sigma2 and K were the parameters used to model the variance. RMSE means root mean square error. The selected equations from this study were: All functional types: $Y = 0.49 \times dbh^{2.04} \times CD^{0.47} + WD^{1.02}$; NPLD; $Y = −9.38 + 0.05 \times dbh^2 \times H \times WD + 5.89 \times CD$; P: $Y = 0.04 \times dbh^{2.77} \times H^{0.47} + CD − 0.92$; SB: $Y = 0.41 \times dbh^{2.11} \times CD^{0.36} + WD^{0.79}$.
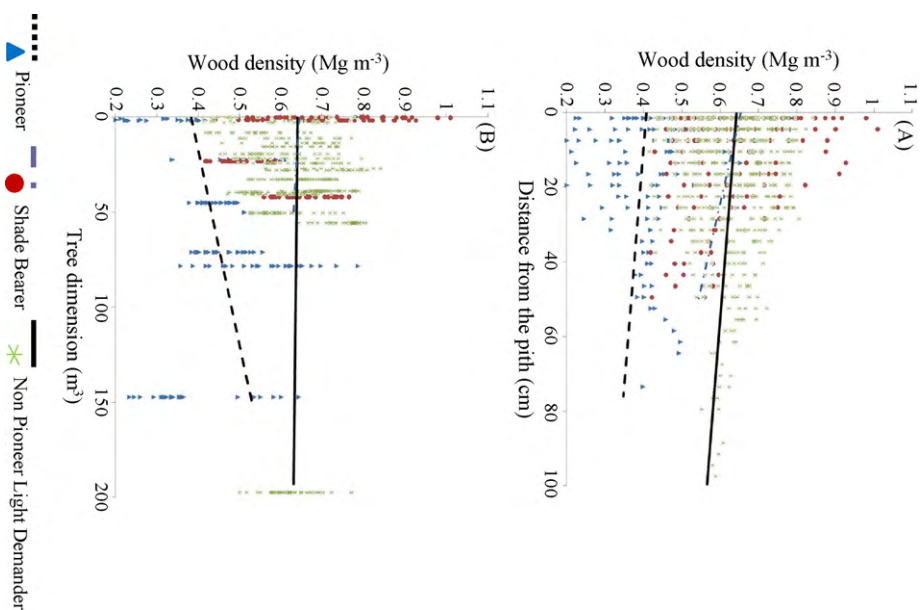

Fig. 2. Influence of radial distance from the earth and volume on wood density. Top: variation according to the pith to bark distance; (b) below: variation according to the dimension of the tree ($d_{bh}^2 \times$ Height).

than a tree with a volume of 1.0 m³. The model could explain 62% of the variability of the wood density (RMSE = 0.08, n = 788). The model did not consider effects such as the social position. However, there were some form of relationship between the ratio of height to d_{bh} (SO2) and wood density ($p < 0.05$). The SO2 was negatively related to wood density for pioneer trees, null for shade bearers and positive for NPLD.

3.2. Tree biomass

Three allometric equations were developed (Fig. 3) for the branches of NPLD, P and SB. Foliage accounted for 10.3% of the total dry mass. Shade bearers had lower foliage mass than NPLD ($p < 0.05$, DF = 74), while that of P was not significantly different from SB and NPLD ($p = 0.506$, DF = 104). Wood accounted for bulk of the mass, with NPLD having significantly higher wood mass than P and SB (<0.05, DF = 103). While the woody compartment showed a significant relationship with the basal diameter ($R^2 = 0.809$, RSS = 1.63E + 09), the foliage mass was less significant ($R^2 = 0.348$, RSS = 1.15E + 07).

The mass of the trunk and the branches dominated the total mass of the trees. The proportion of the masses of the trunk, branch, buttress and foliage was 69, 27, 3.0 and 1.0%, respectively (Fig. 4a). The distribution of the plant mass into the different organs was influenced by the size of the trees. However, it was not very evident in the P and SB trees because not all the diameter classes were well represented. Within the NPLD group, (Fig. 4b), buttress was absent for small trees, while the buttress represented 7% of the total for

Table 5
Wood densities of the different tree species included into the analysis of the wood density.

Guild status	Wood density (Mg m⁻³)					Mean from the literature (Mg m⁻³)			
	Tree species	n	Mean (SE)	Min	Max	Mean	Min	Max	References
Non Pioneer	*Aubrevillea kertingii*	16	0.65 ±1.99E−02	0.46	0.74	a,b	–	–	–	–
Light Demander	*Piptadeniastrum africanum*	93	0.59 ±7.03E−03	0.45	0.74	c	0.60	0.55	0.65	1,2,3,9,10,13,14,16,18
	Tieghemella Hecklii	165	0.65 ±5.22E−03	0.5	0.79	b	0.55	0.51	0.58	1,2,13, 19, 6, 9, 15, 10,11,16,
	Heritiera utilis	211	0.62 ±6.98E−03	0.41	0.84	b	0.54	–	–	13
	Afzelia bella	26	0.69 ±1.57E−02	0.57	0.81	a	0.64	–	–	1
	Average	511	0.63 ±3.88E−03	0.41	0.84	a				
Significance					***	a				
Pioneer	*Cecropia peltata*	38	0.25 ±1.56E−02	0.11	0.42	b	0.32	–	–	2
	Ceiba pentandra	56	0.48 ±1.92E−02	0.23	0.79	a	0.28	0.24	0.35	1,2,3,4,5,6,7,8, 9,10,11,12,13,14
	Nauclea diderrichii	52	0.46 ±1.03E−02	0.38	0.78	a	0.66	0.32	0.78	1,2,3,9,13,14,15,17
	Average	157	0.42 ±1.17E−02	0.11	0.79	b				
Significance					***					
Shade Bearer	*Strombosia glaucescens*	30	0.73 ±1.71E−02	0.53	0.93	c	0.77	0.74	0.80	2,13
	Cola nitida	14	0.53 ±8.75E−03	0.44	0.57	e	–	–	–	–
	Nesogordonia papaverifera	12	0.68 ±1.32E−02	0.62	0.78	c,d	0.64	0.48	0.66	1,2,3,9,10,13,14,15,17,
	Guarea cedrata	43	0.53 ±1.22E−02	0.42	0.92	e	0.53	0.46	0.77	1,2,3,9,10, 11,13,14,15,16,
	Drypetes chevalieri	6	0.92 ±2.58E−02	0.85	1.01	a	–	–	–	–
	Garcinia epunctata	6	0.81 ±1.70E−02	0.74	0.85	b	0.79	0.78	0.82	2,9,13
	Dialium aubrevilliei	32	0.66 ±1.03E−02	0.56	0.77	d	–	–	–	–
	Average	143	0.64 ±1.07E−02	0.42	1.01	a	–	–	–	–
	Average	811	0.59 ±4.84E−03	0.11	1.01	***	***	0.60	0.58	0.67

The mean wood density found in the literature was obtained by averaging the wood density values reported in the documents: 1: (Sallenave 1955), 2: (Brown, 1997), 3: (A.T.I.B.S. 1982), 4: (CTFT, 1989), 5: (Compendium 2009), 6: (Flynn Jr. and Holder 2001), 7: (Gyimah-Buadi 1999), 8: (Hidayat and Simpson 1994), 9: (Howard 1951), 10: (Kryn and Fobes 1959), 11: (Kukachka 1970), 12: (Reyes, Brown et al. 1992), 13: (Sylla and Picard 2007), 14: (Tree Talk 2005), 15: (ICRAF 2009), 16: (Lavers 1983), 17: (Rijsdijk and Laming 1994), 18: (Soerjanegara and Lemmens 1994), 19: (Chudnoff 1984). * p(H0: Fobs > Fth = 0) < 0.05, ** p(H0: Fobs > Fth = 0) < 0.01. ± standard error. The number of wood sample collected in this study differs between tree species and individuals. The original data and the references are reported in Appendix B.

trees greater than 100 cm d_{bh}. The percentage of the foliage mass was approximately constant for all tree sizes, while the proportion of trunk mass tended to decrease with tree size, and that of the branches tended to increase but not significant ($p < 0.05$).

3.3. Allometric equation

3.3.1. Model fitting

The best models among the 960 tested equations (lower AIC) are presented in Table 2. Model 6 was found to be the most appropriate for all the tree species. However, the ranking differed among guild status. The best model for NPLD was Model 8 and 2 (same AIC), while the best model for P and SB was Model 6. However, the difference between Models 8 and 6 for NPLD was not significantly

different. The best model for NPLD and SB considered the variables d_{bh}, CD and WD while the best model for P did not consider the wood density.

3.3.2. Comparison with existing allometric equations

Fitting the dataset into existing equations from other source yielded results significantly different from those developed in this study, except for Equations 4, 10 and 14 (Table 4). All the equations developed for the wet climatic zone under estimated the tree phytomass (Fig. 5), the deviation of which ranged from −26 to 51%. All the equations were significantly biased ($p < 0.0001$). In addition, the mean absolute error was important and ranged from 27 to 51% of the mean. By including tree height and wood density into the equations, the deviation decreased by 17 and 7%, respectively. The
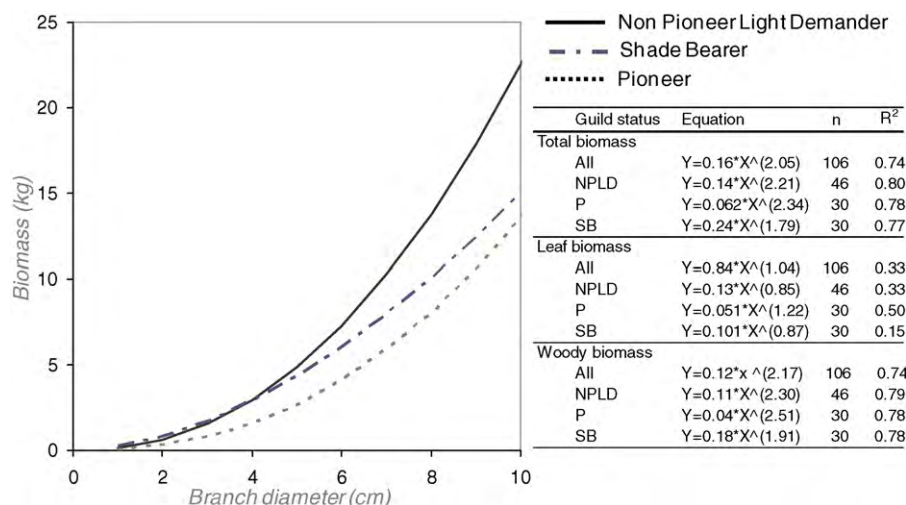

Fig. 3. Branch allometric equations. The branch allometric equations were performed for each guild status. The power model was identified as the best predictive model for branches and branch diameter is the best practical model input.
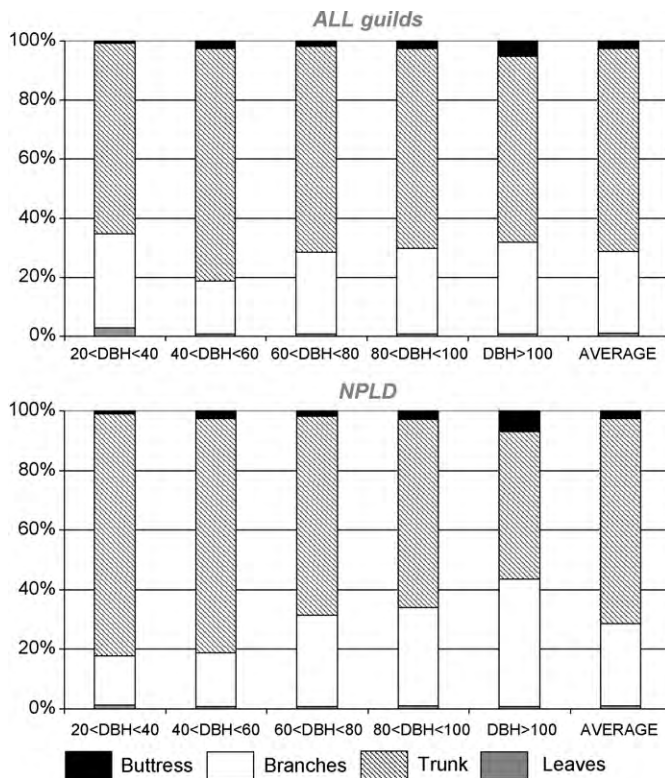
Fig. 4. Contribution of the various tree component to individual total phytomass according to DBH class. The distribution of phytomass is for all the guild types, and then only for Non Pioneer Light Demander (NPLD). This is because some tree diameter classes were missing for the Shade bearer and Pioneer trees. The proportion of phytomass in the different tree components vary according to the size of the tree.
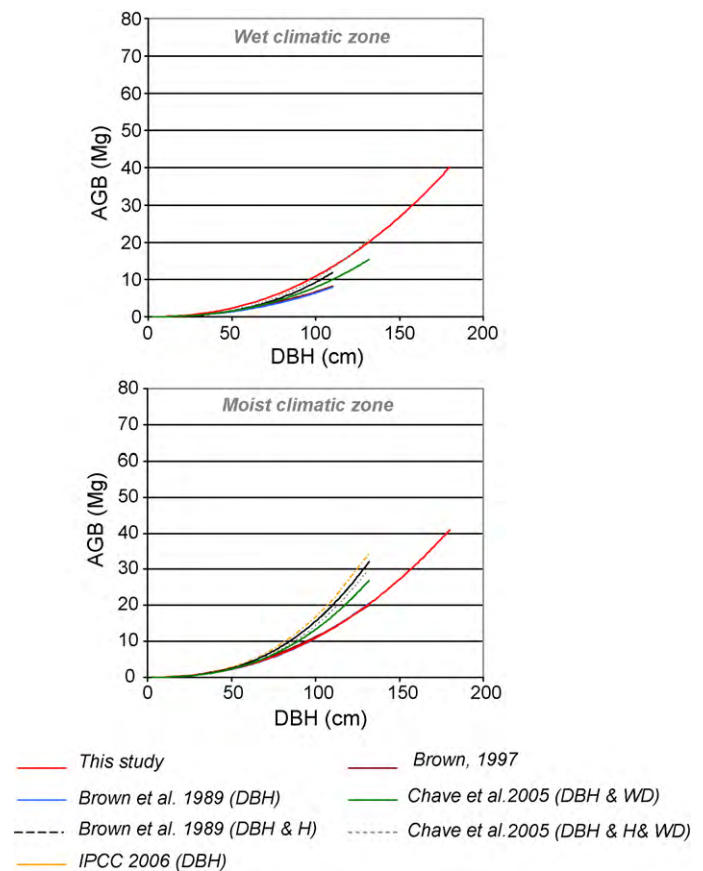

Fig. 5. Comparison with allometric equations found in the literature. The various generalized allometric equations found in the literature were used to compare the predicted biomass with the destructive biomass measurements from this study. Since it was unclear if the study site was in the wet or moist climate zone, the comparison was made using models developed for both zones.

equations found in Chave et al. (2005) were less bias and more precise than the other equations.

Fitting the data set into equations developed for the moist forest zone yielded better estimates (Fig. 5), the deviation of which ranged from −15 to 38% (Table 4). All the equations were significantly biased ($p < 0.05$), except Equations (4) and (10). The estimated error was lower with equations from the moist zone than those from the wet zone, which ranged from 16 to 42% of the mean. The inclusion of tree height improved the estimation by 2 and 5%, and decreased the bias by 1 and 2% for equation 4 and 10, respectively. The estimation improved by 17% and the bias decreased by 9% when specific wood density was considered. The use of tree species specific allometric equations did not significantly affect the estimation ($p < 0.05$). The highest modelling efficiency was exhibited by Equation (11) ($R^2 = 0.97$) (Table 4). On the other hand Equation (11) was significantly biased while equations (4) and (10) were not. The modelling efficiency for Equation 4 and 11 were 0.84 and 0.81, respectively. Moreover, the best model found in the literature (Equation (4)) exhibited an overestimation of 16%.

4. Discussion

4.1. Wood density

The overall average wood density of $0.59\,\mathrm{g\,cm^{-3}}$ reported in this study is very close to the reported values for trees in Africa. The average wood density of $0.62\,\mathrm{g\,cm^{-3}}$ reported by IPCC (2003) is 5% higher than that of this study, but the reported wood density for trees in Africa ranges between 0.58 and $0.67\,\mathrm{g\,cm^{-3}}$, with an average value of $0.60\,\mathrm{g\,cm^{-3}}$ (Table 5). The use of average wood density values instead of specific ones normally introduces

bias of the biomass estimation. Average wood density found in international databases are normally for trees with commercial importance that are normally denser, hence their application can result in overestimation. For instance only one reference was found for *Cecropia peltata* whereas 14 references were found for *Ceiba pentandra*, due to the level of their commercial importance. Average wood density values reported for trees in Africa are lower than those from South America, which have average value of $0.64\,\mathrm{g\,cm^{-3}}$ (Nogueira et al., 2008) and $0.69\,\mathrm{g\,cm^{-3}}$ for Puerto Rico (Brown et al., 1989). However, the variability of the wood density between databases is mainly influenced by the tree species considered.

The lower wood density for pioneer trees is similar to reported values (Denslow, 1980). Wood density is known to be a strong indicator of state of succession in tropical trees, with pioneer species being lighter than the trees that belong to the other guild types. The lighter species have great variation in wood density within the trunks of individual trees (Wiemann and Williamson, 1988) due to their initial fast growth, producing low-density wood, and later addition of a shell of harder wood for structural support (Rueda and Williamson, 1992). On the other hand, smaller difference between NPLD and SB was observed. This may originate from the fact that there is still some problems with the definition of NPLD and SB trees. The NPLD and SB trees seem to tread on different paths of growth strategies without really affecting their wood density. Baker et al. (2003) and Woodcock and Shier (2002) observed a difference between fast growing (pioneer) and late succession species without mentioning the NPLD group. However, the Guild classifica-
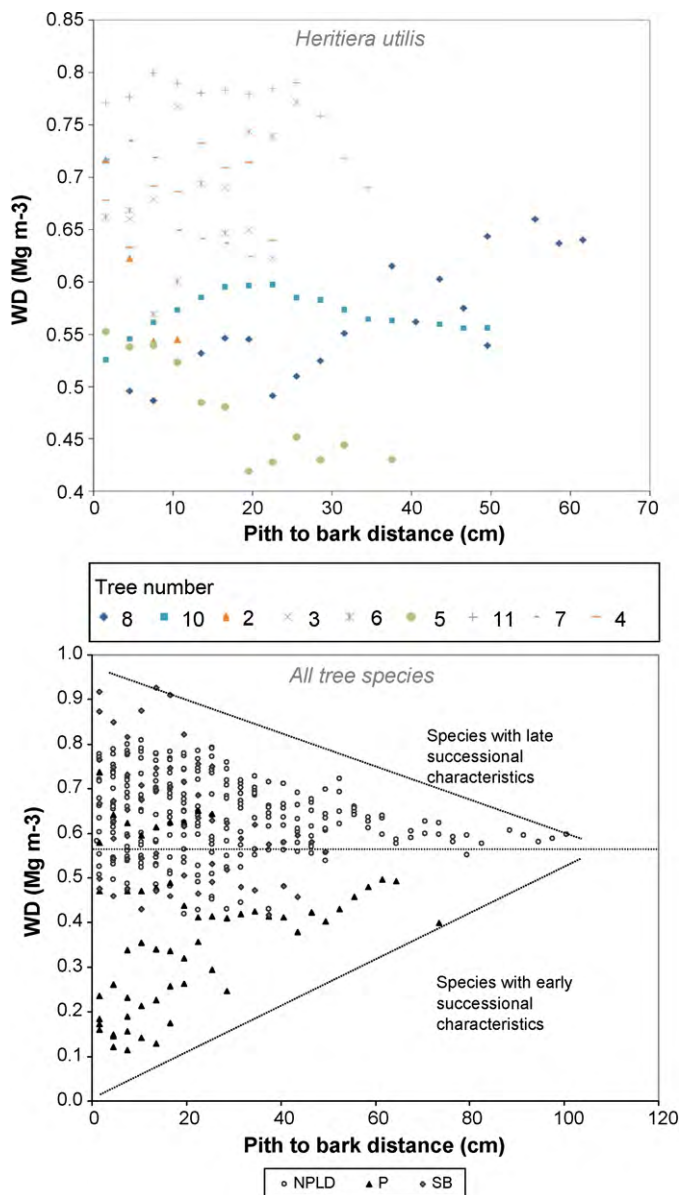
Fig. 6. Variation of wood densities. Top: variation of wood density (WD) for individual trees of the same species (*Heritiera utilis*). The number of the individual trees were noted T2, 3, 4, 5, 6, 7, 8, 10 and 11 were reported in Table 1; Below: variation of wood density for the different guild status (NPLD: non pioneer light demander, *P*: pioneer and SB: shade bearer).

tion is not a sufficient variable to understand the variation of wood density.

Size of the trees influenced the wood density. While no literature was found concerning this aspect, the bigger *P* tree species have lower sapwood to heartwood Ratio than the smaller trees. For hinoki cypress (*Chamaecyparis obtusa*) trees, Adu-Bredu and Hagihara (1996) also found out that the proportion of sapwood mass decreases with increasing stem mass per tree. On the other hand, wood density decreases slightly with tree size for SB and NPLD but not very pronounced. This could be related to increasing proportion of dead wood.

There was radial variation in wood density for all the guild types. The wood density decreased from pith to the periphery and seems to converge at a common average (Fig. 6b). The influence of the radial distance on the wood density was reported by Amorim (1991), and Fearnside (1997) also reported a 20% lower wood density for the bark. The rate of decrease of wood density from the

pith to the periphery was not significant among the guild types in this study. However, Woodcock and Shier (2002) reported that wood density reflected different growth strategy and there is a radial increase for pioneer trees and a decrease for late succession trees. The variation of wood density among individuals of the same species was also observed in this study (Fig. 6a). Moreover, increase in wood density for the pioneer's tree was not observed as Woodcock and Shier (2002) did.

The wood density model was based on only 13 tree species and cannot be used for other tree species. However, it provides good insights into the estimation of wood density, particularly in the tree sections where samples were not taken. Rather than taking an average wood density at a given height, the model showed that guild type, tree species, pith to bark distance and tree size influenced the wood density and should be taken into account when estimating the biomass of a tropical rainforest. There was also variation among trees of the same species (Table 6, Fig. 6a). The results of this study revealed a lot of uncertainties when estimating wood density. It means that many other factors not taken into account by this study could explain the residual variability. Forest and tree history, topography and soil fertility have been reported to influence wood density of trees of different species and these have to be considered in further studies. Slik et al. (2008) reported influence on wood density by different states of ecosystem disturbances. Whitmore (1998) and Suzuki (1999) reported different wood densities depending on life history strategies. Improvement of wood density estimation have to consider the position of the trees in the landscape, history of the ecosystem (windfall, fires, etc.) and, if possible, age of the trees (De Castro et al., 1993).

4.2. Modelling tree mass

Allocation of plant mass to the various organs namely, buttresses, trunk branches and foliage was compared with that of other ecological zones since similar work in the tropical humid forest is scarce. The average proportion of trunk mass of 69% reported in this study is very close to the value of 70% given by Peltier et al. (2007) for a tropical dry forest and higher than the value of 62% given by Henry et al. (2009) for tropical agroforestry systems in Western Kenya. The proportion of trunk mass value of 63% for trees with d_{bh} greater than 10 cm is higher than that of 54% reported by Araújo et al. (1999) for a tropical rainforest of Brazil. Volume of the buttress for trees with d_{bh} between 68 and 175 cm was given as 11.05 m^3 in tropical rainforest of Africa (Newbery et al., 2009), but in this study the values given ranged between 0.08 and 12.8 m^3. The wide range can be due to the fact that different tree species have different types of buttress and the form of the buttress is reported to be influenced by the position of the tree in the landscape and soil fertility (Newbery et al., 2009). In addition, the method used in this study might have underestimated the volume of the buttress, whilst Newbery et al. (2009) might have overestimated it because only trees with buttress were considered in their study. Although buttress can represent a significant part of the tree mass, it is generally not taken into account in forest inventory and allometric equations. The average proportion of foliage mass ($3.17 \pm 0.6\%$ (SD)) is lower than the value of 6.7 ± 1.1 and $11.2 \pm 1.3\%$ reported for forests in North Cameroon (Peltier et al., 2007) and Western Kenya (Henry et al., 2009). This could be mainly due to the fact that in their studies smaller and probably younger trees were considered.

Whereas the AIC was similar among the models, the *RMSE* was variable (Table 2) and sensitive to the few big trees. On the average, it ranges between 0.5 to 34.4% of the average plant mass (9 to 34% for *P*, 22 to 25% for NPLD, and 16% for SB). The model is therefore very dependent on few big trees hence; further work is required to consider big trees that represent an important part of the biomass

Table 6
Selected models for the analysis of the wood density.

Guild status	Tree species	Intercept	Distance	Dimension	GS	Dimension*GS	Tree species	Constant
Non-pioneer light demander	*Aubrevillea kertingii*	0.08	−1.18E−03	−2.45E−03	0.01	2.42E−03	−0.06	0.61
	Piptadeniastrum africanum						−0.10	0.61
	Tieghemella Hecklii						−0.01	0.61
	Heritiera utilis						−0.08	0.61
	Afzelia bella						0.00	0.61
	Total						−0.06	0.61
Pioneer	*Cecropia peltata*	0.08	−1.18E−03	−2.45E−03	−0.14	−8.29E−04	−0.43	0.75
	Ceiba pentandra						0.17	0.75
	Nauclea diderrichii						0.00	0.75
	Total						−0.04	0.75
Shade Bearer	*Strombosia glaucescens*	0.08	−1.18E−03	−2.45E−03	0.00	0.00E+00	−0.06	0.71
	Cola nitida						−0.24	0.71
	Nesogordonia papaverifera						−0.10	0.71
	Guarea cedrata						−0.21	0.71
	Dialium aubrevilliei						0.00	0.71
	Total						−0.12	0.71
Total		0.08	−1.18E−03	−2.45E−03	−0.02	1.42E−03	−0.06	0.65

The qualitative inputs were: the plant functional type (GF), the tree species (SP), and the location of the samples (Location). The quantitative inputs were: the radial distance from the earth (distance), the social status of the tree (H/CD and H/d_{bh}), the relative height (Hr) of the sample (height of the sample/tree height) and the dimension (dimension) of the tree (d_{bh}^2*Height).

in forest ecosystems. Trees with d_{bh} greater than 150 cm were not considered in the works of Chave et al. (2005) and Brown (1997), hence the inclusion of such big trees in this study increases the domain of applicability of the model.

The best predictive model was

$$Y = 0,03 \times d_{bh}^{(8.61E-02)} \times CD^{0.03} + WD^{0.04} \qquad (8)$$

Whilst the best practical models were

$$Y = 0.30 \times d_{bh}^{(2.31)} \qquad (9)$$

$$Y = 0.17 \times d_{bh}^{(1.97)} \times H^{(0.55.)} \qquad (10)$$

$$Y = 3.47 \times 10^{-3} \times d_{bh}^{(2.0)} \times H \times WD \qquad (11)$$

where Y is tree dry mass, CD is crown diameter, WD is wood density and H is tree height.

4.3. Status of generalized allometric equations

The site falls under the moist climatic zone according to the definition of IPCC (2003), which defines wet climatic zone as areas with rainfall above 2000 mm per annum. The equations of Brown (1989) were developed based on 69 and 168 trees with a maximum d_{bh} of 110 and 148 cm for wet and moist zones, respectively. On the other hand, the equations of Chave et al. (2005) were developed based on a much wider sampling size that involved 2410 trees. Comparison of existing allometric equations with that of this study (Fig. 5a and b) indicates that the allometric equations from moist climate zone give closer estimation than that from the wet climatic zone. The inclusion of tree height improves the estimation of tree mass particularly in the wet zone. However for the moist climatic zone, improvement in the estimation was mainly due to the inclusion of specific wood density rather than tree height. Equations that integrate more than one tree dimension improve the estimation. In using allometric equations by default, consideration should be given to variation of wood density and the relation between H and d_{bh} from the original data. When it is not possible to have specific wood density, then Equation 4 can give a better estimate. Inclusion of specific wood density improved the model efficiency with Equation 11 being more precise (deviation of 3%). Using species specific allometric equation such as Equation 14 is the best option.

4.4. Estimating biomass and carbon stocks

The inadequacy of allometric equations for African forests is evident in the Good Practice Guidance for Land Use and Land Use Change and Forestry or GPG-LULUCF (IPCC, 2003) in which only two allometric equations for tropical forests were presented (Appendix C). In tropical humid forests, irradiance is one of the most important limiting factor and species showed greater height growth (Baker et al., 2003). On the other hand, trees in tropical dry forest have less tree competition and are more limited by access to water, which limit tree growth. Trees on sites that are continuously flooded by saline or fresh water e.g. mangrove, allocate a great deal of plant mass to the roots to maintain a bottom-heavy tree form or a low ratio of shoot to root mass (Komiyama et al., 2008). Furthermore, in many African ecosystems in the tropical dry forest zone, trees are pruned to collect firewood and their growth, architecture and mass are modified (Smektala et al., 2002).

The accuracy or uncertainty of models is an important aspect that is mentioned in the Good Practices Guidelines and different instruments of the Kyoto Protocol. To reduce uncertainty, accurate C accounting methods are required. Some methods estimate biomass of stands, using proxies such as tree volume, wood density and biomass conversion and expansion factors or biomass expansion factors. In estimating the volume of a tree, height and d_{bh} are generally measured, and using a form factor, volume can be deduced (e.g. formula given in Ponce-Hernandez, 2004). The form factor have been reported to be 0.6 (Cannell, 1984), 0.55 (Ponce-Hernandez, 2004) and 0.33 for conic trees in (CTFT, 1989). In this study the form factor ranged between 0.11 and 1.66, with an average value of 0.24. The whole tree and not only the trunk was considered and this might have contributed to the low form factor value. Using a form factor of 0.6 (Cannell, 1984) and average wood density of 0.62 (IPCC, 2006) resulted in a significant overestimation of tree mass by 28%. Although this method provided more precise estimations than Brown (1989, 1997), the form factors and the wood density data have to be improved for tree species and tree size. The IPCC (2003) reported biomass expansion factors (BEF) of about 3.4 for tropical forest stands whereas this study reported BEF values ranging from 1.13 to 2.20 for tree volume of 3.83 to 31.71 m³. Moreover, the BEF proposed by the IPCC largely overestimated the mass of the branches in this study. The IPCC (2003) reports biomass conversion and expansion factors (BCEF) ranging from 0.95 to 9.0 for forest volume of between 10 and 200 m³ ha⁻¹,

whereas this study reports BCEF for individual trees ranging from 0.24 to 0.86 for tree volume 0.001 to 65 m^3 (Table 1). The use of default biomass expansion factors may lead to an overestimation of stand biomass.

Although, the allometric equations developed in this study for the African tropical humid forest were based on only 42 trees, various ranges of diameter and tree species were integrated into the equation. Future improvements should integrate greater number of larger trees and all the guild types should be well represented. Based on the results of this study, it is also recommend that further biomass studies in tropical forests of Africa should take wood samples at regular intervals from the pith to the bark for the trunk and branches.

In the estimation of C stocks of forests, not only the aboveground but the below ground component should as well be considered. The belowground component is found to represent about two thirds of the terrestrial C stocks (Jobbagy and Jackson, 2000), and the rooting system is a significant part of it. However this study did not consider the belowground component, further work should consider it. Only few studies have considered the relationship between the belowground and the aboveground component (e.g. Cairns et al., 1997) or the root to shoot ratios as proposed by Mokany et al. (2006). Measuring the rooting system is costly and time consuming and requires important investments. However, making benefit of the windfall would allow facilitating access to the rooting system.

5. Conclusion

This study presented, for a tropical forest in Africa, variation of wood density as a function of tree species, plant guild types, pith to bark distance and tree size. A model was developed to predict the wood density for 16 tree species. The model explained 62% of the variability of the wood density. Factors affecting wood density such as topography and soil fertility should be investigated. It appeared that wood density was not a necessary variable in the estimation of tree mass of pioneer's species, but a significant variable for Non Pioneer tree species. In addition, crown diameter predicted tree mass better than height. All the previously published tree biomass models for wet forest in tropical regions predicted significant different biomass than those measured in this study. This could be mainly due to the fact that those allometric equations were not specific to African ecosystems and were limited by their domain of validity. The best tree allometric equation that was found in the literature was the equation of Brown et al. (1989) which considered d_{bh} and tree height. However, when specific wood densities are available the equation of Chave et al. (2005) yielded the best estimate. Choosing a default allometric equation is difficult and improvement of the estimates have to include a precise identification of the climate zone, the wood density and tree height.

Acknowledgements

Appendix A.

The various wood density models used in the analysis
Where *int* is the intercept, GS is the guild status, SP is the tree species, Hr is the relative height, dim is the tree dimension (m^3), dist is the pith to bark distance (cm) and location is stump, trunk or branch.

Appendix B.

Wood density data found in the literature

Appendix C.

Relationship between tree height and DBH for three tropical African forest types (dry, montane and wet) Data on tree height and girth were collected from different studies in order to make comparison. Solid lines show separate fits to small (< 20-cm diameter) and large ($\geq$20-cm diameter) individuals for tropical forests worldwide (except Africa) found in (Muller-Landau et al., 2006). Data from Sirlawé in Cameroon were collected in agricultural land (Aka Etom et al., 2006). Data from Mafa Kilda in Cameroon were collected in agricultural land, forest and mountain forests (Manlay et al., 2002). Data from Vihiga in Kenya were collected in agroforests and agricultural land (Henry et al., 2009). Data from Boi Tano (this study site) were collected mainly for big trees (unpublished).

Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.07.040.

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