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Taller trees, denser stands and greater biomass in semi-deciduous than in evergreen lowland central African forests

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A B S T R A C T

Accurate height-diameter allometry is crucial for the estimation of forest biomass and carbon stocks. Tree height measurements over a large range of diameters and species are urgently needed in the tropics, specifically in central Africa, for the development of locally derived height-diameter allometric equations and the conversion of forest inventory data into biomass estimates, and for the validation of remotely sensed canopy height that mostly rely on a few specific field sites. In this study, we aimed to identify the variation in height-diameter allometry of tropical trees between forest types and among species in central Africa, and we examined the consequences for biomass estimation. Height and diameter were measured for a total of 521 trees over a large range of diameters in two forest types in southern Cameroon, 10–240 cm in the evergreen forest and 11–182 cm in the semi-deciduous forest. A total of ten allometric models including asymptotic and non-asymptotic models were fitted to the height-diameter data. Measured tree diameters, grouped into 10 cm wide diameter classes up to 150, from commercial forest inventory data (0.5 ha plots, $n = 2101$ and $n = 5152$, respectively in the evergreen and in the semi-deciduous forests) were converted into biomass estimates using general allometric models with and without including our site-specific height-diameter allometry. Though debated in the literature, our results supported a saturation of tree height with tree diameter both at site and species level, with asymptotic models better depicting the height-diameter allometry. Height-diameter allometry significantly differed between forest types and these local height-diameter equations also differed from published equations. For a given diameter, trees tended to be taller in the semi-deciduous forest than in the evergreen forest, as already reported between moist and wet forests in pantropical studies. Similar trends were reported within species for the three species shared by both forest types, suggesting an environmental control of tree allometry. Because of the low performance of the bioclimatic stress variable to predict tree height and of the slight soil differences between the two forest types, the environmental determinants of height-diameter allometry remain to be explored. In addition to tree allometry variation, structural differences (basal area and density) were also identified between the two forest types using commercial forest inventory data at genus level, and both allometry and forest structure (taller trees and denser stands) contributed to the greater biomass per hectare of the semi-deciduous forest.

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1. Introduction

The Congo basin forms the second largest continuous block of tropical forests in the world with up to 200 Mg of carbon per hectare in standing trees (diameters greater than 10 cm, Lewis et al., 2009, 2013). Due to the lack of agreement in central Africa between the biomass maps produced (Baccini et al., 2008, 2011; Mitchard et al., 2011), a lot of uncertainty remains about the amount and spatial variation in biomass and carbon stocks. This is mainly due to the lack of appropriate allometric models to convert forest inventory data over large spatial scales. Forest inventory data in central Africa covers more than 12 million hectares (De Wasseige et al., 2012, p. 46) and national forest inventories have been

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conducted in several countries (http://www.fao.org/forestry/fma/73410/en/). If all these data could be gathered and jointly analyzed, a good picture of the biomass distribution may be obtained.

The choice of the allometric model is a critical step in the estimation of forest biomass (Chave et al., 2004; Molto et al., 2013). Until recently, there were only few available data on the biomass allometry of tropical African trees, and data were restricted to particular species and sites (Henry et al., 2011). The pantropical allometric models developed by Chave et al. (2005) were thus used to convert inventory data into estimates of biomass and carbon stocks, either including only diameter and wood specific gravity in the set of predictors (e.g. Gourlet-Fleury et al., 2011; Maniatis et al., 2011) or including diameter, wood specific gravity, as well as tree height (Kearsley et al., 2013; Lewis et al., 2013, 2009). Multi-species allometric equations have been recently established in south-eastern Cameroon (Fayolle et al., 2013) and in northern Gabon (Ngomanda et al., 2014) but with conflicting results. The local allometric equation we developed for south-eastern Cameroon (Fayolle et al., 2013) was found not to be different from the pantropical equation developed by Chave et al. (2005) for moist forests, while the local allometric equation of northern Gabon strongly differed from the pantropical equation developed for moist forests (40% overestimation of biomass) but was not different from the pantropical equation for wet forests (Ngomanda et al., 2014). While both sites have been assigned to a transition type between evergreen and semi-deciduous forests (White, 1983), the sampled trees, however, tended to be more deciduous in south-eastern Cameroon (79 trees and 15 species, out of 138 and 42, respectively) and to be more evergreen in northern Gabon (72 trees and 7 species, out of 101 and 10, respectively). According to Holdridge's classification system (1967), most of the central African forests are climatically attributed to moist forests. Strong variation in tree species composition from wet evergreen forests rich in Caesalpinioideae to semi-deciduous forests rich in Ulmaceae and Sterculiaceae (now included in Malvaceae) has, however, long been reported (Fayolle et al., 2014; White, 1983, and references therein). We suspect that this variation in species composition and overall deciduousness is correlated with variations in forest structure and tree allometry, and that the bioclimatic thresholds of the Holdridge's classification system (1967) are not suitable for distinguishing wet, moist and dry forests of Africa. In their recent synthesis work on the allometry of tropical trees, Chave et al. (2014) indeed abandoned these forest types and directly linked variation in tree allometry to a bioclimatic stress variable which compounds indices of temperature variability, rainfall variability and drought intensity.

According to Ketterings et al. (2001), between site differences in biomass allometry are due to two characteristics of the forest, the height-diameter allometry and the wood specific gravity of the trees. Since the wood specific gravity is generally included in the set of predictors of tree biomass, architectural differences between sites including height-diameter allometry, but also crown-diameter allometry (Goodman et al., 2013; Ploton et al., 2015), determine the variation in biomass allometry. It has been recently demonstrated that crown-diameter allometry is relatively stable while height-diameter allometry is highly variable, supporting the idea that tropical trees preferentially adjusted their height to growth conditions (Antin et al., 2013). The variation in height-diameter allometry has indeed been shown to be of extreme importance for the estimation of biomass and carbon stock (Chave et al., 2014; Feldpausch et al., 2012; Kearsley et al., 2013; Molto et al., 2014). In sites with specific height-diameter allometry, the use of conventional height-diameter allometric equations, i.e. those that have not been locally fitted, can induce a significant bias in the estimation of biomass and carbon stocks (as demonstrated in Indonesia by Rutishauser et al. (2013); and in Yangambi, DR Congo by Kearsley et al. (2013)). Total tree height is, however, extremely difficult to measure accurately in structurally complex and species-rich tropical forests (Larjavaara and Muller-Landau, 2013). As a result tree height measurements are rarely available in forest inventory data in central Africa and tree height is estimated from a height-diameter allometric equation established at a global (Lewis et al., 2009), regional (Feldpausch et al., 2012; Lewis et al., 2013) or local (Kearsley et al., 2013) scale. There is, however, no consensus on which height-diameter allometric equation should be used in central Africa. When tree height data are not available for the estimation of biomass, Chave et al. (2014) developed a pantropical biomass model incorporating wood specific gravity, tree diameter, and a bioclimatic stress variable. The validity of this recently developed pantropical model has not yet been tested on a validation dataset.

There is general agreement on the need for tree height data over a large range of diameters and species in the tropics for the development of locally derived height-diameter allometric equations (Chave et al., 2014; Kearsley et al., 2013; Molto et al., 2014; Rutishauser et al., 2013) and the conversion of forest inventory data into biomass estimates (Chave et al., 2004; Clark and Kellner, 2012; Molto et al., 2013). Tree height data are also needed for the validation of global and regional remotely sensed canopy height (e.g. Wang et al., 2016) that mostly rely on a few specific field sites, specifically for central African forests. In addition to these practical questions, both related to the estimation of forest biomass and carbon stocks, tree height data are also needed for addressing theoretical questions. There has been a historical debate on the shape of the height-diameter allometry for tropical trees. The origin of this debate can be found in the fact that Malaysian tree species supported an asymptotic shape and thus a determinate height growth (Thomas, 1996) while Ecuadorian tree species tended to support a power law model and thus an indeterminate growth (King, 1996). It was later demonstrated that similarly to Ecuadorian trees, Brazilian tree species also supported an indeterminate growth at species level, but based on a log-linear rather than a power law model (Nogueira et al., 2008). The recent need for height-diameter equations for the estimation of biomass and carbon stocks in tropical forests motivated scientists to establish plot-level height-diameter allometric equations, and thus renewed the debate. Some authors argued in favour of a truly asymptotic model (Kearsley et al., 2013; Lewis et al., 2009; Molto et al., 2014; Rutishauser et al., 2013), or a second order polynomial of the log–log data (Chave et al., 2014; Niklas, 1995) mimicking the saturation of tree height with tree diameter, while others argued in favour of the power law model (Djomo et al., 2010; Feldpausch et al., 2011; Hunter et al., 2013) such as predicted by the metabolic theory of ecology (West et al., 1997, 1999). The metabolic theory moreover predicts invariant morphological scaling between several tree dimensions, and specifically a 2/3 exponent between tree height and diameter (Muller-Landau et al., 2006).

In this study, we investigated the variation in height-diameter allometry between two forest types and among species in southern Cameroon, and we examined the consequences for biomass estimation using commercial inventory data. Given the quantitative information they contain (diameters are measured and trees are identified to species when possible) and the spatial extent they cover (De Wasseige et al., 2012), commercial inventory data as they are performed in central Africa (consecutive 0.5 ha plots, with a sampling rate of 1%) are reliable for biomass estimates (Gourlet-Fleury et al., 2011; Maniatis et al., 2011). In this study, we addressed the following research questions. (1) Are differences in height-diameter allometry due to the local conditions of the site or to the identity of species? We specifically tested the hypothesis that the evergreen and the semi-deciduous forests show contrasted height-diameter allometry. (2) Are published (regional

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