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The limited contribution of large trees to annual biomass production in an old-growth tropical forest

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Abstract
Although the importance of large trees regarding biodiversity and carbon stock in old-growth forests is undeniable, their annual contribution to biomass production and carbon uptake remains poorly studied at the stand level. To clarify the role of large trees in biomass production, we used data of tree growth, mortality and recruitment monitored during 20 years in 10×4-ha plots in a species rich tropical forest (Central African Republic). Using a random block design, three different silvicultural treatments, control, logged, and logged + thinned, were applied in the 10 plots. Annual biomass gains and losses were analyzed in relation to the relative biomass abundance of large trees and by tree size classes using a spatial bootstrap procedure. Although large trees had high individual growth rates constituted a substantial amount of biomass, stand-level biomass production decreased with the abundance of large trees in all treatments and plots. The contribution of large trees to annual stand-level biomass production appeared limited in comparison to that of small trees. This pattern did not only originate from differences in abundance of small versus large trees or differences in initial biomass stocks among tree size classes, but also from a reduced relative growth rate of large trees and a relatively constant mortality rate among tree size classes. In a context in which large trees are increasingly gaining attention as being a valuable and a key structural characteristic of natural forests, the present study brought key insights to better gauge the relatively limited role of large trees in annual stand-level biomass production. In terms of carbon uptake, these results suggest, as already demonstrated, a low net carbon uptake of old-growth forests in comparison to that of logged forests. Tropical forests that reach a successional stage with relatively high density of large trees progressively cease to be carbon sinks as large trees contribute sparsely or even negatively to the carbon uptake at the stand level.

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Contents

1. Introduction

Large old trees have extremely high ecological and socio-economic values, but are among the most endangered organisms in forests worldwide (Lindenmayer and Laurance, 2017). They provide unique habitats to a vast variety of organisms and have significant impacts on nutrient cycling, hydrological regime and numerous ecosystem processes. Large and old trees contain a large proportion of above-ground forest carbon stock (Bastin et al., 2015; Fauset et al., 2015); although, in natural forests, they are far less abundant than small trees. In tropical forests, trees with a diameter greater than 60 cm have been shown to contribute to up to one third of forest above-ground biomass (Feldpausch et al., 2012) and their abundance is generally a good proxy of the inter-regional (Slik et al., 2010) or even inter-continental variation in forest biomass (Slik et al., 2013). While large trees are known to retain a significant part of forest biomass, their contribution to annual biomass dynamics at the forest level remains unclear as it depends on multiple processes operating at different scales. Their contribution to biomass dynamics encompasses processes affecting the evolution of forest biomass stock (biomass net change), that depends particularly on the growth of large trees (biomass gains), their mortality (biomass losses), their abundance as well as their interactions with smaller neighboring trees.

Regarding the growth of large trees, contrasting results can be found in the literature (Sheil et al., 2017). Decreasing biomass accumulation in the oldest and largest trees has classically been assumed (Vanclay, 1994; Avery and Burkhart, 2015) but increasing biomass accumulation with tree size has recently been claimed (Sillett et al., 2010; Stephenson et al., 2014; Sillett et al., 2015).

A decreasing biomass accumulation in the largest trees has particularly been observed in intensively managed plantations and modelled with sigmoidal relationships between tree size and age, that corresponds to unimodal relationships between tree growth and tree size (Vanclay, 1994; Smith and Long, 2001; Avery and Burkhart, 2015). In natural mixed forests, such as tropical forests, unimodal relationships of tree growth have also been reported (Hérault et al., 2011).

Nevertheless, in mixed forests, many additional interactions must be considered as they can affect the relationships between tree size and biomass accumulation. Only a few species are capable of reaching large size growing at species-specific growth rates (Baker et al., 2003). Moreover, large trees often have a particular life history (e.g. establishing in gaps) (Brienen and Zuidema, 2006) and capture a disproportionate amount of incident light because of their emergent position within the canopy, implying a subsequent strong asymmetric competition for resource with the other neighboring trees (Enquist et al., 2009). In contrast to the classically observed decline in tree growth in large trees, different patterns are possible in complex natural forests. Besides, the metabolic theory of ecology predicts, under the assumptions of demographic and resource steady state, that the growth rate of individuals continuously increases with body size. This theory hence predicts that, at the forest level, large trees should contribute to forest biomass accumulation as much as small trees (Enquist et al., 1999). Corroborating this theory with empirical findings, Stephenson et al. (2014) showed that the biomass growth rate of individual trees continuously increases with size, and that this pattern holds true across species, continents and forest biomes regardless of the competitive environment. This result must however be interpreted with caution as it was obtained by analyzing biomass growth at the scale of an aggregated population for each species (Stephenson et al., 2014; Sheil et al., 2017). Different patterns may thus be observed at the tree level, for example by analyzing tree rings (Sheil et al., 2017). Similarly, different patterns are also expected at the forest level, where trees of different size, age and species coexist.

Furthermore, tree mortality and particularly the mortality of large trees, is also an important demographic driver of biomass dynamics (Phillips et al., 2009; Rozendaal et al., 2017). Large trees store a large amount of biomass and variation in their mortality rates strongly impacts biomass dynamics (Sheil et al., 2000; Rutishauser et al., 2010). The mortality of large trees has indeed been shown to be the main driver of biomass dynamics in French Guiana (Rutishauser et al., 2010). But tree mortality events are rare and scattered. They are rarely monitored and remain poorly predicted (Fisher et al., 2008; Allen et al., 2010) mainly because they depend on the interplay of numerous endogenous and exogenous factors (Coomes et al., 2003; Sheil et al., 2017). Relationships between tree size and tree mortality rates have been proposed but not consensually validated. In old-growth forests, within the assumption of demographic equilibrium, the metabolic theory of ecology suggests that the mortality rate decreases with body size (Enquist et al., 1999). Smaller and shorter trees grow in the shade of large trees, resulting in reduced tree growth and greater mortality rates. Deviation from this theory has however been reported, especially for large trees that suffer from higher mortality rates than expected by the model because of the overwhelming importance of unpredictable exogenous factors (Coomes et al., 2003; Muller-Landau et al., 2006; Enquist et al., 2009).

Theoretical developments of forest dynamics mainly concern forests at demographic equilibrium but should also be adapted to forests at disequilibrium recovering from past disturbance because such forests are a larger carbon sink than old-growth forests (Pan et al., 2011). In contrast to old-growth forests at equilibrium, where the density of large trees is supposedly constant, the abundance of large trees can greatly vary in forests at disequilibrium and it may then become a major driver of biomass dynamics in these forests (Sheil et al., 2000). The abundance of large trees gradually increases through forest succession (Rozendaal et al., 2017) or can decrease after size-dependent perturbations. Logged tropical forests are an interesting study model in that respect. Similar to natural perturbations, logging creates canopy openings, disrupts the equilibrium, reduces forest biomass and induces size-dependent changes in tree growth and mortality (Van Breugel et al., 2006; Coomes and Allen, 2007). Typically, logging increases biomass accumulation rates, especially promoting the growth and survival of intermediate-size trees (Peña-Claros et al., 2008; Gourlet-Fleury et al., 2013b) and affects forest composition (Gourlet-Fleury et al., 2013a).

Although previous studies have suggested that the role of large trees in forest biomass dynamics and carbon cycling could be predominant (Bastin et al., 2015; Fauset et al., 2015), scaling up the individual processes (e.g. tree growth and mortality) at the forest level to assess their quantitative contribution to biomass dynamics remains to be further explored (Meakem et al., 2017; Sheil et al., 2017). In other words, the expectation regarding the contribution of large trees to biomass dynamics may vary with the level under consideration, i.e. from individual or species levels to forest level. In this study, we thus aim to clarify the relative role of large trees in biomass dynamics at the forest level and to analyze how perturbation may modulate this role. By analyzing tree growth, mortality and recruitment over 20 years in 40-ha of an old-growth tropical forest, including unlogged stands as well as stands recovering from silvicultural interventions (Gourlet-Fleury et al., 2013b), we attempt to answer three research questions.

1. What is the contribution of large trees to forest biomass gains (i.e. due to tree growth) in comparison to the contribution of smaller trees?
2. What is the contribution of large trees to forest biomass losses (i.e. due to tree mortality) in comparison to the contribution of smaller trees?
3. Does the forest biomass net change (i.e. gains minus losses) vary with the abundance of large trees?

2. Methods

2.1 Study site and forest experiment

The study site (3° 54′N, 17° 55′E) is located nearby the city of M'Baïki, Lobaye province, Central African Republic. Average annual rainfall is 1739 mm (1981–2008) with a 3-month dry season. Annual average monthly temperature is 24.9°C (19.6–30.2 °C, 1981–1989). The site is located on a large plateau (500 to 600 m a.s.l.). Soils are deep ferralitic soils, classified as acrisols in the WRB system (Freycon et al., 2015). The vegetation belongs to the moist semi-deciduous forest of the Guineo–Congolian Region (White, 1983) and specifically to the moist Central African type (Fayolle et al., 2014). The canopy is dominated by species in the Ulmaceae (now included in Cannabaceae), Myristicaceae and Meliaceae families (Gourlet-Fleury et al., 2013b) and specifically by the genus Celtis (Fayolle et al., 2014).

A total of 10 permanent plots of 4-ha (200 m × 200 m) were established in 1982 in three protected forest sites with no recent logging history. All trees with a diameter $\geq$ 10 cm were individually marked, geo-referenced and identified. The girth was measured with a tape to the nearest half centimeter and a permanent mark was placed on tree trunk to ensure that circumference was monitored every year at the same height. For trees with buttresses and other sorts of stem irregularities at breast height (1.3 m), the point of measurement was raised 50 cm above the buttresses in the cylindrical part of the stem and up to a permanent height of 4.50 m later on (Gourlet-Fleury et al., 2013b). The plots have been remeasured yearly since 1982 and until 2012 (except in 1997, 1999 and 2001 for political and socio-economic reasons). In 1984-86, the 10 plots were assigned to three different silvicultural treatments according to a random block design: control (3 plots), logging (3 plots), logging and thinning (4 plots). Logging consisted in harvesting all trees with a diameter $\geq$ 80 cm and belonging to one of 16 commercial species. Thinning consisted in killing all trees with a diameter $\geq$ 50 cm of non-commercial trees (Ouédraogo et al., 2011). From 1984-86 until 2012, no other logging or thinning activities have been performed. Since 1992, every monitored tree has been determined mostly to the species level. Further information about the experimental design, forest structure (density, basal area and biomass) and composition (dominant species and diversity) can be found in Ouédraogo et al. (2011) and Gourlet-Fleury et al. (2013b). In this study, we used inventory data collected between 1992 and 2012. A total of 29,729 trees of 225 taxa including 200 species, 151 genera and 54 families, were monitored over the study period. Up to 60% of the trees were monitored during the entire 20-year period as some existing trees died (19%) and new recruits (21%) reached the inventory diameter threshold of 10 cm. Six percent of the measured trees had their point of measurement (POM) raised due to wounds or buttresses during the study period. For these trees, the diameter increment of the year of the POM change was assumed to be zero (0.7% of all increment observations) and subsequent diameters were corrected using measured taper ratios (Gourlet-Fleury et al., 2013b).

2.2 Estimating biomass stocks, gains and losses

Biomass refers hereafter to the above-ground biomass (AGB) of trees as we did not take into account the below-ground biomass as well as the biomass of coarse woody debris and wood decomposition. The above-ground biomass (AGB in kg) of a tree i belonging to species s was estimated using the pantropical allometric equation developed by Chave et al. (2005) for moist forests (eq. 1) including tree diameter (D, in cm) and species wood specific gravity (ρ_s, in g cm^{-3}) since height measurements or local height-diameter allometry were not available.

$$AGBi = \rho_s \times e^{-1.499+2.148\times ln(D)+0.207\times ln(D)^2-0.0281\times ln(D)^3} \tag{1}$$

ρ_s was extracted from a global database (Chave et al., 2009; Zanne et al., 2009). Equation 1 was chosen among others because it has been validated with local destructive measurements for trees with a diameter up to 192 cm in the same forest type (Fayolle et al., 2013), Celtis forest (Fayolle et al., 2014). We ensured the independence of our results and conclusions with the chosen method of biomass computation by repeating our analyses using other biomass allometric equations (Loubota Panzou et al., 2016) or even basal area (Appendix 5.1).

At the stand level, biomass gain is the sum of all biomass increments of all trees calculated annually and the biomass of the trees recruited during the census interval (1992-2012).

Biomass loss is the sum of the biomass of all trees that died during the census interval and corresponding to the last measurement before tree death. The biomass net change is the difference between stand AGB in 1992 and 2012 and equals the difference between biomass gains and losses.

To disentangle the contribution of large trees to biomass dynamics, biomass gains and losses were computed in 20 cm wide diameter classes: 10-30 cm, 30-50 cm, 50-70 cm, 70-90 cm, 90-110 cm, 110-130 cm, 130-150 cm and with a last group including all trees with a diameter $\geq$ 150 cm. As biomass stock, tree size and abundance of large trees in forest are inevitably linked (Bastin et al., 2015; Fauset et al., 2015), relative gains and losses were also computed dividing gains and losses by the corresponding initial biomass stock. The latter ratios enabled accounting for the potential confounding effect of initial biomass and had the advantage of being interpreted in terms of the efficiency in producing biomass per unit of biomass stock. To assess the relationships between biomass gains and losses and the abundance of large trees, we computed the percentage of biomass held in large trees (relative biomass abundance). According to the definition of Slik et al. (2013), we considered large trees as trees with diameter greater than 70 cm whereas small trees and medium trees referred to trees of respectively 10-30 cm and 30-70 cm. Other expressions of the abundance of large trees (amount of biomass held by large trees, percentage of the number of large trees, quadratic mean diameter) were also tested (not shown) and led to the same conclusions.

2.3 Statistical analyses

Each 4-ha plot was divided in 16 subplots of 50m×50m (0.25 ha) using a square grid. Biomass estimates were then computed at the 4-ha plot level and at the 0.25-ha subplot level. To test for significant differences between biomass estimates among diameter classes or silvicultural treatments at the 4-ha plot level, confidence intervals and P value of statistic tests were computed using a spatial bootstrap procedure computed over the 0.25-ha subplots (Chave et al., 2008; Chernick and LaBudde, 2014). The absence of spatial autocorrelation between observations among subplots was verified using Moran's I test for each variable (e.g. biomass stock, biomass production), diameter class and plot (600 tests). In total, 3.4% of the tests showed a significant correlation which is acceptable given the effect of such multiple inferences on type I error (Benjamini and Hochberg, 1995). Estimated confidence intervals and P values of Student T tests of the differences between pairs of diameter classes were computed using the quantiles 2.5% and 97.5% of the bootstrap distribution of the statistics replicates (Appendix 5.2).

The relationships between biomass gains and losses and the relative biomass abundance of large trees were examined with Pearson correlation tests and graphically illustrated with linear regressions.

All analyses were implemented in the R statistical environment version 3.3.2 (Team, 2016) using the boot package version 1.3-18 (Canty and Ripley, 2016), the ape package version 4.0 (Paradis et al., 2004) and BIOMASS package version 1.0 (Rejou-Mechain et al., 2016).

3. Results

3.1 Initial forest structure

In 1992, stem density ranged from 506 to 677 trees ha^{-1} among the 4-ha plots. The quadratic mean diameter (QSD) of trees was about 25 cm and mean basal area was about 29 m^2 ha^{-1} (Appendix 5.2, Table S1). The quadratic mean diameter and basal area (BA) were the greatest in control plots (QSD = 27.7 cm and BA = 34.1 m^2 ha^{-1}) and the lowest in logged + thinned plots (QSD = 23.1 cm and 25.4 m^2 ha^{-1}).

In every 4-ha plot, the distribution of tree diameter followed a classical reverse J-shaped distribution (Appendix 5.2, Fig. S1). The mean density of large trees (diameter $\geq$ 70cm) was the highest in control plots (18.3 trees ha^{-1}, 2.5% of total stem number) and the lowest in the logged + thinned plots (5.0 trees ha^{-1}, 0.8% of total stem number).

Large trees in 1992 belonged to 63 different species. The five most frequent species showing large trees were *Entandophragma cylindricum* (Sprague) Sprague (12.4% of biomass in large trees in 1992), *Triplochiton scleroxylon* K. Schum. (9.4%), *Terminalia superba* Engl. & Diels (7.3%), *Manilkara mabokeënsis* Aubrév. (7.2%) and *Petersianthus macrocarpus* (P. Beauv.) Liben (5.0%). The largest observed tree was an *Entandrophragma utile* (Dawe & Sprague) Sprague of 221 cm in diameter (in control plot 16).

In 1992, plot biomass was on average about 321 Mg ha^{-1} and varied significantly among the 4 ha-plots and silvicultural treatments (ranging from 228 to 436 Mg ha^{-1}, Fig. 1) (Gourlet-Fleury et al., 2013b). The greatest biomass was found in the control plots (377-436 Mg ha^{-1}) and the lowest in the logged + thinned plots (227-261 Mg ha^{-1}) (Fig. 1). We observed similar pattern when looking at basal area instead of biomass.

Total biomass stock was strongly and positively correlated with the percentage of biomass stocked in large trees (diameter $\geq$ 70cm) at the 4-ha plot level ($r = 0.959$, $P < 0.001$, $n = 10$) as well as at the 0.25-ha subplot level ($r = 0.816$, $P < 0.001, n = 160$) (Fig. 1). In control plots, large trees constitued about 45.0% of plot biomass whereas, in the logged + thinned plots, large trees constitued only about 16.5% of plot biomass (Appendix 5.2, Fig. S2).

3.2 Biomass gains, losses and net change

Mean biomass gain due to tree growth in 4-ha control plots was about 7.7 Mg ha^{-1} year^{-1} (1.9% of initial biomass stock) while that in logged + thinned plots was about 10.4 Mg ha^{-1} year^{-1} (4.1%). Mean biomass loss due to tree mortality was about -5.7 Mg ha^{-1} year^{-1} (-1.4%) in control plots and -3.1 Mg ha^{-1} year^{-1} (-1.2%) in logged + thinned plots. Tree recruitment was limited in all plots ranging between 0.27 and 0.53 Mg ha^{-1} year^{-1} (<0.2%, Table 1). The average biomass net change was always significantly positive in treated plots

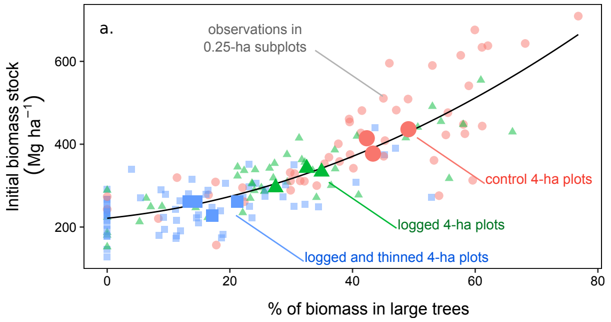

Figure 1. Variation in initial (recorded in 1992) biomass stocks with the percentage of biomass stocked in large trees (diameter $\geq$ 70 cm) observed in 4-ha plots and 0.25-ha subplots. Black line shows a second degree polynomial regression.

(logged, and logged + thinned), suggesting a significant carbon sink. In control plots, it was not significantly different from zero in two of the three control plots (Table 1).

The importance of the demographic drivers (growth and mortality) for biomass variation appeared scale-dependent. At the 0.25-ha subplot level, variation of biomass net change resulted mostly from tree mortality ($r = 0.887$, $n = 160$) and tree growth ($r = 0.609$, $n = 160$). Among 0.25-ha subplots, the variability of biomass losses (standard deviation = 3.1 Mg ha^{-1} year^{-1}) was indeed greater than the variability of biomass gains due to tree growth (s.d. = 1.8 Mg ha^{-1} year^{-1}). In contrast, at the 4-ha plot level, variation of biomass net change resulted equally from tree mortality ($r = 0.975$, $n = 10$) and tree growth ($r = 0.975$). Recruitment played logically a negligible role in biomass dynamics at both scales.

3.2.1 Biomass dynamics and abundance of large trees

At the 0.25-ha subplot level and for each treatment, biomass net change decreased with the relative biomass abundance of large trees (Fig. 2a). The same pattern was observed both looking at absolute and relative biomass net change (Fig. 2a and Fig. 2b).

Absolute biomass gains did not vary significantly with the relative biomass abundance of large trees in the 0.25-ha subplots ($|r| < 0.03$, Fig. 2a). In contrast, relative biomass gains decreased with the relative biomass abundance of large trees ($r = -0.51$ in logged + thinned plots and $r = -0.81$ in control plots, Fig. 2b). The production of biomass per unit of biomass stock decreased with the abundance of large trees, but the generally greater biomass stock of stands with abundant large trees ($r = 0.820$) compensated for this reduction.

In contrast to absolute biomass gains, absolute biomass losses were significantly correlated with the relative biomass abundance of large trees (r ranged between -0.24 and -0.48, $P < 0.05$, Fig. 2a); whereas relative biomass loss was not significantly correlated with the relative biomass abundance of large trees (r ranged between 0.02 and -0.041, $P > 0.78$, Fig. 2b) in the 0.25-ha subplots. The ratio between biomass losses and initial biomass stock thus remained approximately constant and biomass losses thus increased with the abundance of large trees.

3.2.2 Contribution of tree size classes to biomass gain, loss and net change

Across all 4-ha plots and treatments, the stand-level contribution to average annual biomass gains decreased with tree size (Fig. 3a). The stand-level contribution of small trees ranged between 37% and 59% while that of large trees ranged between 4% and 18%. In all 4-ha plots, the biomass gains for large trees (diameter $\geq$ 70 cm) per area unit was significantly ($P < 0.05$) lower than for medium (diameter = 30-70 cm) or small trees (diameter = 10-30 cm). For example, in logged plot 11, there were initially about 489 small trees ha^{-1}, 78 medium trees ha^{-1} and 8 large trees ha^{-1} that contributed respectively 4.4 Mg ha^{-1} year^{-1} ($\pm$ 0.63 of standard deviation among 0.25-ha subplots), 3.67 Mg ha^{-1} year^{-1} ($\pm$ 0.96) and only 0.65 Mg ha^{-1} year^{-1} ($\pm$ 0.61).

The stand-level contribution of large trees to average annual biomass losses varied across treatment (Fig. 3a), but was generally weak in comparison to that of smaller trees. The death of large trees represented in average 32.2% ($\pm$ 13.9% of standard deviation among 4-ha plots), 19.0% ($\pm$ 4.4%) or 7.08% ($\pm$ 6.9%) of plot biomass losses in the control, logged, and logged + thinned 4-ha plots, respectively (Fig. 3a). The contribution to biomass losses significantly decreased with tree size in logged plots, and in logged + thinned plots. Losses of biomass thus originated mostly from the death of small trees rather than the death of large trees in these plots. This pattern was however not significant in control plots.

In all 4-ha plots, the stand-level contribution to average annual biomass net change significantly decreased with tree size and the biomass net change of large trees (diameter $\geq$ 70 cm) was clearly lower than that of small trees (Fig. 3b, Appendix 5.2, Fig. S3). Differences between biomass net change in large and medium trees were significant in all but logged plot 11 (Appendix 5.2, Fig. S3).

These patterns of stand-level biomass contribution with tree size were observed both on absolute and relative biomass gain, losses or net change indicating that the differences did not originate solely from differences in initial biomass stock among the tree size classes. For example, across all treatments, the mean rate of relative biomass gain ranged between 4.4-6.3% for small trees and between 0.9-1.5% for large trees.

4. Discussion

Analyzing the biomass dynamics monitored during 20 years in 40 ha of a tropical forest, we found that average annual net change in biomass decreased with the relative biomass abundance of large trees at the stand level (third research question), and this pattern held true across different levels of silvicultural intervention. In undisturbed forests, the initial biomass stock in large trees can be substantial but the stand-level contribution of large trees to biomass gains remains

Table 1. Mean estimates and bootstrap confidence intervals of overall biomass gains due to tree growth, biomass losses due to tree mortality and biomass net change over 20 years, 1992-2012 (Mg ha^{-1} $year^{-1}$). Biomass net changes significantly greater than zero are indicated in bold format.

Id	Treatment	Site	Growth		Mortality		Recruitment		Net change	
13	Control	Boukoko 1	8.42	(7.9;8.96)	-4.89	(-6.5;-3.51)	0.27	(0.24;0.31)	**3.8**	(2.31;5.11)
16	Control	Boukoko 2	7.83	(7.27;8.44)	-5.94	(-8.47;-3.96)	0.46	(0.42;0.52)	2.36	(-0.24;4.4)
24	Control	La Lolé	6.97	(6.44;7.48)	-6.19	(-7.9;-4.77)	0.34	(0.3;0.38)	1.13	(-0.6;2.59)
11	Logged	Boukoko 1	8.74	(8.22;9.31)	-6.03	(-7.36;-4.81)	0.35	(0.31;0.4)	**3.06**	(1.64;4.35)
14	Logged	Boukoko 2	9.16	(8.45;9.88)	-4.59	(-6.27;-3.23)	0.35	(0.29;0.4)	**4.91**	(3.14;6.56)
21	Logged	La Lolé	8.89	(8.34;9.43)	-5	(-6.95;-3.62)	0.32	(0.28;0.37)	**4.22**	(2.47;5.69)
12	Logged + T.	Boukoko 1	10.12	(9.35;10.79)	-3.59	(-4.34;-2.85)	0.53	(0.46;0.6)	**7.06**	(5.9;8.1)
15	Logged + T.	Boukoko 2	10.84	(10.3;11.46)	-1.96	(-2.22;-1.72)	0.32	(0.28;0.37)	**9.2**	(8.63;9.79)
22	Logged + T.	La Lolé	10.64	(9.77;11.49)	-3.66	(-4.75;-2.78)	0.43	(0.38;0.47)	**7.41**	(6.38;8.35)
23	Logged + T.	La Lolé	9.88	(9.11;10.54)	-3.15	(-3.85;-2.44)	0.3	(0.27;0.34)	**7.03**	(5.97;7.96)

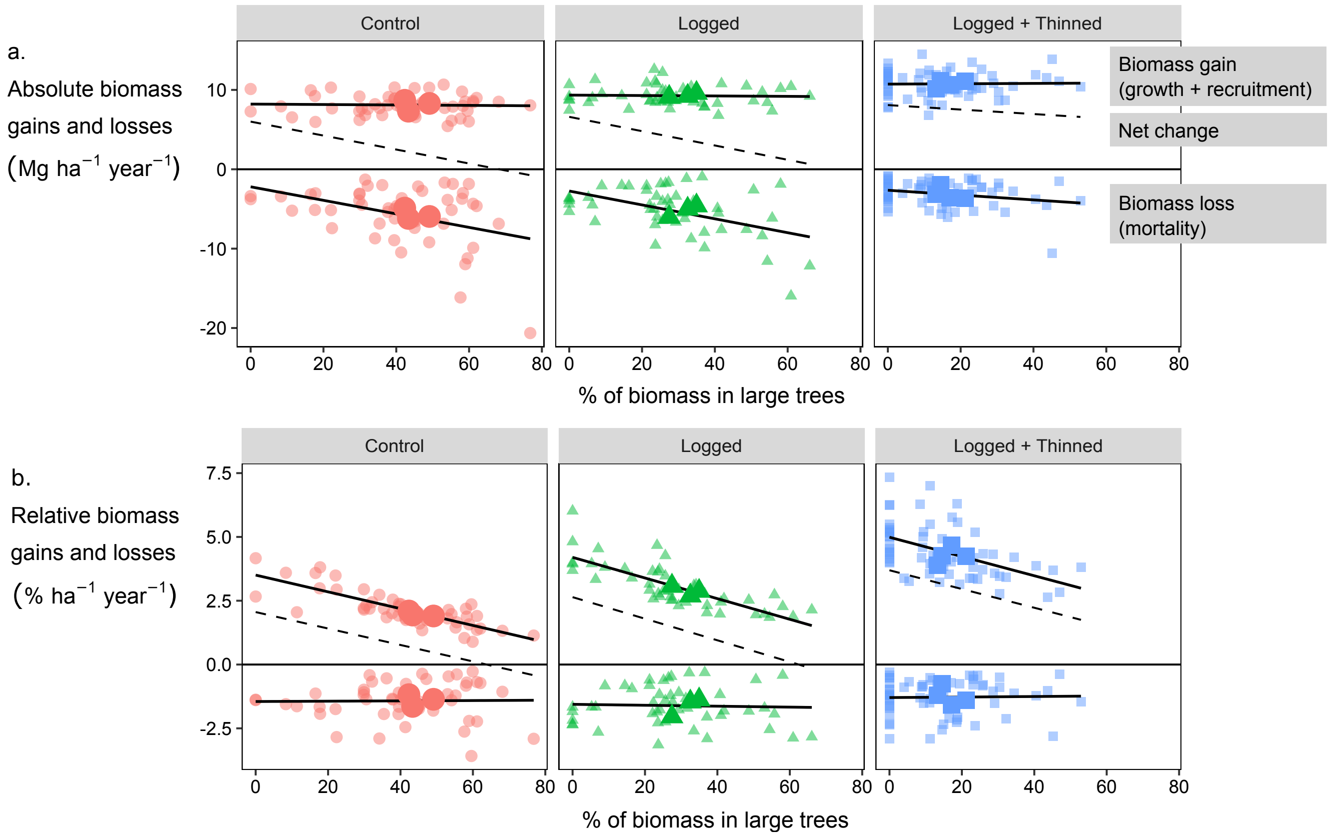

Figure 2. Absolute (a) and relative (b) biomass gains and losses with the relative biomass abundance of large trees over the studied period (1992-2012). Solid lines within the positive and negative values show a linear regression of the variation in biomass gains (tree growth and recruitment) and losses (tree mortality). Dashed line shows a linear regression of the variation in biomass net change. Large and small symbols corresponds to the 10×4ha plots and 160×0.25-ha subplots, respectively, with a symbols and colors varying according to silvicultural treatments (see Fig. 1).

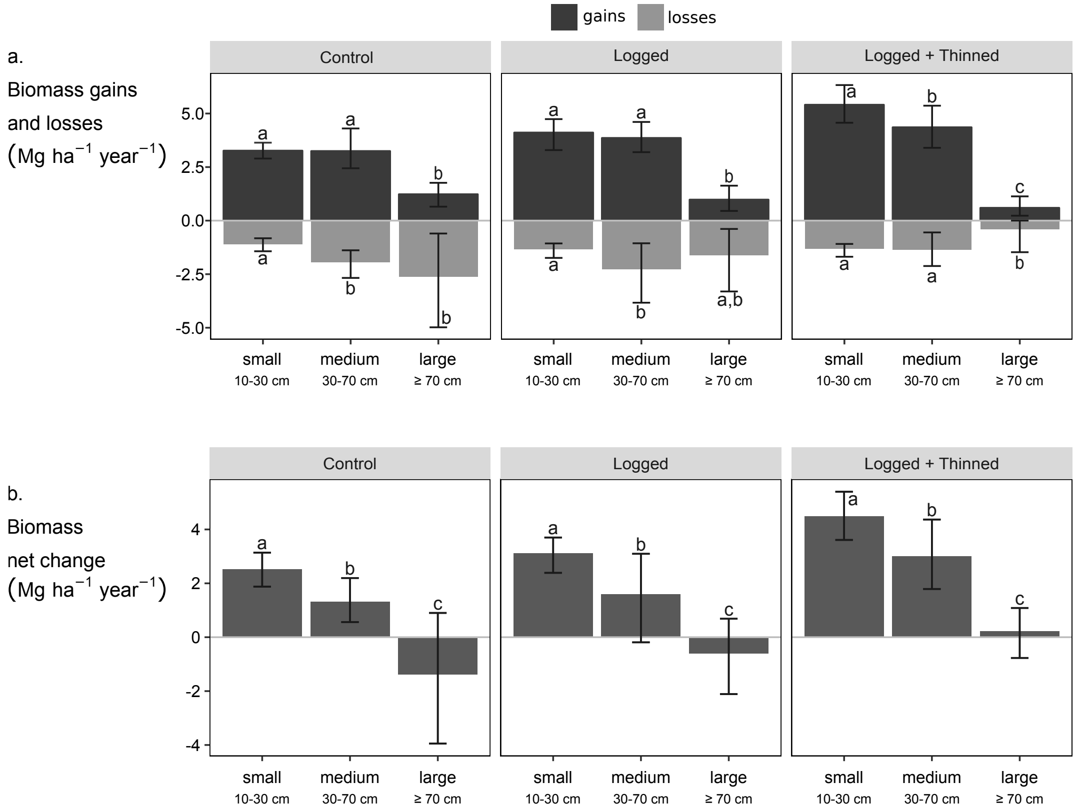

Figure 3. Mean estimates and bootstrap confidence intervals of biomass gains and losses (a) or biomass net change (b) for each treatment and by tree size classes. The stand-level contribution to biomass gains significantly decreased in all treatments with tree size. For the large trees, biomass losses generally exceeded biomass gains, whereas, for smallter trees, average annual biomass losses were generally lower than gains.

limited due to reduced relative growth rate and important biomass losses. In plots recovering from logging and logging + thinning interventions, the initial stock of large trees has been reduced and the contribution of large trees to biomass gains is hence weak in comparison to that of small or medium trees.

Hereafter, we discuss these results and attempt to unravel the important demographic drivers of biomass dynamics (Rozendaal et al., 2017). We discuss successively the role of biomass initially stocked in large trees, diversity in size and species of large trees, interactions among growth rate, tree size and density and the interactions among mortality rate, tree size, and density.

4.1 Biomass stock of large trees

As expected, large trees (diameter $\geq$ 70 cm) held substantial amount of biomass and this amount depends on past silvicultural intervention and is well correlated with forest biomass stock (Slik et al., 2013). In the M'Baïki forest, the share of biomass held in large trees was about 45% (15.0 large trees ha^{-1}) in the control plots and about 16% (3.3 large trees ha^{-1}) in the logged + thinned plots. Very similar large stocks of biomass in large trees have already been reported for intact lowland moist African forests (Slik et al., 2013, Table 1) and also in other forest ecosystems. The share of large trees was, for example, estimated to be around 25% in South-American forests, 39% in Asian forests (Slik et al., 2013, Table 1), 49% in Eastern Amazonian forests, 13-30% in Brazilian forests (with large trees defined by diameter $\geq$ 60 cm) (Sist et al., 2014), and 51-57% in Mediterranean and Temperate old-growth forests (with large trees defined by diameter $\geq$ 50 cm) (Sagheb-Talebi and Schütz, 2002; Piovesan et al., 2005). In addition, our results corroborated that the relative biomass abundance of large trees is strongly correlated with forest biomass. Such a result has been observed among 1 ha-plots across the tropics (Slik et al., 2010, 2013) and we further found that this correlation is also observed at a very local scale using 0.25-ha subplots ($r = 0.984$).

The definition of large trees is inevitably ecosystem-specific (Lindenmayer and Laurance, 2017) and large trees thus include trees of very different sizes, ages, shapes and species. However, in all forest ecosystems large trees inevitably stock a substantial amount of biomass as tree diameter and biomass follows, at least approximately, a positive power relationship (Brown et al., 1989; Picard et al., 2015). In our study, large trees spanned individuals with a diameter ranging from 70 cm to 221 cm, and they contributed highly to forest biomass, but finally played a limited role in annual stand-level biomass production. It is additionally important to note that this pool of biomass in large trees is rarely monitored with accuracy due to trunk deformations (e.g. buttresses), holes, and crown damage (Sheil et al., 2017), and also because allometric relationships are necessarily calibrated with a limited number of such large trees (Chave et al., 2005). Additionally, large trees may live for centuries whereas monitoring periods are necessarily more limited. Long-term monitoring of forest dynamics, as in this study, with 20 years of biomass dynamics in 40 ha of tropical forests, are rare gems, but it still may not be long enough to capture very rare events such as particular mortality events.

4.2 Interactions among growth rate, tree size and stem density

The contribution to forest biomass gains of the few large trees was lower than that of the numerous smaller trees (first research question). This was observed for all silvicultural treatments and all 4-ha plots as well as in most 0.25-ha subplots (97.5%), highlighting the generality of the phenomenon. Although large trees constitued up to 49% of biomass, their contribution to forest biomass gains remained generally limited (mean = 10.2% $\pm$ 5.0% of standard deviation) in comparison to the contribution of medium (diameter = 30-70 cm: 42.0% $\pm$2.7%) and small trees (diameter = 10-30 cm: 47.9% $\pm$ 6.2%). Such a decrease in stand-level biomass gains with tree size is corroborated by previous studies. In particular, Sist et al. (2014) estimated that small trees (diameter = 20-40 cm) yielded 2.3 Mg ha^{-1} year^{-1} while large trees (diameter$\geq$ 60 cm) yielded 0.5 Mg ha^{-1} year^{-1} in Brazilian forests (Sist et al., 2014, Table 1). Yuan et al. (2016) observed that carbon accumulation was almost entirely the result of the increase in stems of 30-70 cm diameter in the temperate Changbai forest (China) and Caspersen et al. (2011) showed that dense hardwood stands dominated by small trees produced more wood than stands dominated by fewer large trees in Ontario (Canada). Meakem et al. (2017) also showed a decrease in the contribution to plot biomass gains with increasing tree size for trees larger than 10-50 cm diameter across three tropical forests in Panama. As they measured very small trees, with diameter ranging between 0 and 10 cm, they further noted that the relationships between stand-level biomass contribution and tree size might be hump-back, with a maximum around 10-50 cm diameter rather than a monotonic decrease as suggested by our results. These observations tend therefore to confirm that across unlogged and logged forests, the contribution to biomass production at the stand level generally decreases with tree size (Hérault et al., 2011).

This result is not in contradiction with studies performed at the tree level that showed a continuous increase of tree growth with tree size (Sillett et al., 2010; Stephenson et al., 2014). Analyzing our data with the method proposed by Stephenson et al. (2014), we indeed found a continuous increase for 24 out of 52 selected species (Appendix 5.3). Our study highlights that the patterns observed at the tree or species levels cannot be up-scaled to the stand level without caution. Some large individuals may indeed show large and sustained biomass increment but such large increment does not mean that large individuals have an overwhelming contribution in biomass production at the stand level. As reviewed by Sheil et al. (2017), individual and aggregated trends in biomass production can be different and our study demonstrates that this is likely to be true for the relationship between tree size and forest biomass production.

4.3 Interaction among mortality rate, tree size, stem density and sampling effort

No clear trend was observed regarding the loss of biomass with tree size (second research question), in contrast with previous observations (Rutishauser et al., 2010). The loss of biomass in large trees tended to be lower than that in smaller tree size classes but this trend was only statistically significant in logged plots. The loss of biomass in large trees depends logically on the initial stock of biomass in each tree size class and also on the intensity and frequency of past perturbations whereas the loss of biomass in small trees is mainly driven by competition (Coomes et al., 2003). It is noticeable that the variability in biomass losses due to the death of large trees was considerable at the level of the 0.25-ha subplots (coefficient of variation of 69%) because of their low mortality rate and substantial amount of biomass held in large trees. The variability of biomass loss in large trees was clearly lower among the 4-ha plots (coefficient of variation was 31%). While the mortality of large trees has been noted as the primary driver of biomass net change (Rutishauser et al., 2010; Sist et al., 2014; Yuan et al., 2016), our results suggest that this observation critically depends on the scale of investigation (Fig. 2). As it is a rare phenomenon, monitoring biomass losses is difficult and requires large plots monitored over a long period of time (Fisher et al., 2008).

4.4 Perspectives

In a context in which large trees are increasingly gaining attention as being a valuable and key structural characteristic of natural forests (Lindenmayer and Laurance, 2017), the present study brought key insights to better gauge the role of large trees in the annual biomass dynamics at the forest scale, nuancing the apparently contrasted results of investigations performed at the tree versus stand levels. In terms of biomass production or carbon capture, forests with abundant large trees could be compared to a high capital investment, with a high risk level and low profitability rates. Such intact forests that classically reach late successional stages progressively cease to be carbon sinks. Nevertheless, although large trees may play a limited role in terms of annual carbon capture, their importance is undeniable in terms of total carbon stock and timber production as well as ecological and cultural roles.

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5. Appendices

5.1 Analyzing basal area dynamics

Appendix available online

5.2 Supplementary table and figures and description of the bootstrap procedure

Appendix available online

5.3 Modelling individual tree growth

Appendix available online