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Forest stand structure, tree species architecture and carbon storage in the Maymbe forest

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Diplôme : Master en bioingénieur : gestion des forêts et des espaces naturels, à finalité spécialisée
Année académique : 2017-2018
URI/URL : http://hdl.handle.net/2268.2/5131

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Acknowledgement:

A master’s thesis is the conclusion of an important step of life, it ends the years of developing knowledge and experience and marks the beginning of a new era, misleadingly named by the terms of “Active Life”. My master’s thesis led me, once more, in the heart of Africa and during this extraordinary journey, my path crossed many extraordinary people. This text, may it be sufficient, is written to honor them and to thank them for everything they taught me and allowed me to discover.

First, my thoughts go to my Professors whom allowed me to become useful in my area of interests. I would like to specially thank Pr Adeline Fayolle who has made my lasts years of study an incredible adventure so fulfilling that I will forever keep this happiness level as my further reference level. She allowed me to discover one of the most impressive places on earth in Gabon, and she accompanied me all along the way for this final work. I would never be as completely trained as I am now without her and this work would not be as interesting as I find it to be! Thank you! Of course, all these appreciations also apply to Pr Jean-Louis Doucet without whom I would never have step a foot in DRC. And who taught me much more than how to sustainably exploit a forest or the tropical forest botany. Thank you both for the amazing formation and the support you offer to your students, I hope we will have many opportunities to collaborate in the future, I still have so much to learn from you, and it would always be a great pleasure for me.

Then, I would like to thank the staff of the Royal Museum for Central Africa, without whom I would never have get access to Luki’s station and who supported my research with everything I needed. Thanks especially go to Dr Hans Beeckman, Dr Tom De Mil, Dr Nils Bourland and Dr Wannes Hubau they assisted me in the setup of my research and made it possible, please, know that I am very grateful for everything you have put in place to make this adventure possible.

A very very special thanks goes to I.N.E.R.A.’s agent, soon to become a doctor, Ir Bhely Ilondea Angoboy. He made my life and experience in Luki amazing, he was always there when I needed him, he provided me with a good organization, interesting thoughts about my research and he showed me how to appreciate Kinshasa. I wish him the best of luck for his phd and I am looking forward to see him again. In the process I would like to thank all I.NE.R.A. agents that I met in Luki and in Kinshasa, especially Fils Mbungu Phaka, the botanist who accompanied me every day on the field. His knowledge is beyond comprehension and I really enjoyed talking with him about the life and future of the human race. Pr Tolerant Lubalega who was acting as Chief of station, who provided me good comfort, explications and allowed me to meet many of his students. (Good luck to them as well, the UKV in Boma will forever live on!) Special thanks go to Hossan who showed a lot of bravery by accompanying us in the field.

Then, outside of work, I would like to say THANK YOU to Charleston and Naasson without whom my life in Luki would have been miserable! They took care of me and taught me everything that is impossible to learn in a classroom! I miss our shared meals around a good snake, our afternoon spent at collecting always bigger and tastier avocados, our Linguala-English exchange classes, our discussion about the future of DRC and you guys in general. They are brave and awesome young men, I wish them all the best! This extends to Ir Maurice, Papa Diacre and Américain who showed me all the greatest Congolese preparations, and accepted me as one of their own. I wish them the best of luck. Of course, in Belgium I thank my family for giving me the opportunity of following my own path, my friends whom are always curious, never tired of my stories and always supportive. And I would like to conclude this thank you note by saying thanks to all the members of the Gustave Brass Band, they illuminated my summer by offering me something else to do than cogitate on my master’s thesis. It will always be a pleasure to unleash the crowds in their company, I hope this adventure will keep on going for a long time…

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Abstract

Tropical forests play a key role in terms of carbon storage and biodiversity hosting. Here we compare Luki's forest located in the margins of the tropical African forest in terms of forest structural, compositional and architectural attributes to core Congo basin forests from inventory data collected on eight one-ha plots. We then, report the carbon storage status of such margin forests and we correlate local-scale variations in AGB stocks and AGB stock changes to different forest attributes to determine whether forest attributes impact local scale variations in AGB stocks and stock changes or not. Then, we explore the complex canopy's constituting species in terms of architecture by comparing 30 representative species of the Mayumbe forest. We first, test the hypothesis of convergence in allometry among coexisting tree species. And then, we try to distinguish different ecological strategies from allometry derived architectural traits linked to other functional traits. Finally, we test the hypothesis of architectural and functional traits involvement in hyperdominance computed on stem number or AGB.

We detected similarities between margin and core African forests and, in agreement with Lewis (2009), we found that the Mayumbe forest constitutes a sink in carbon storage. We detected strong correlation between forest attributes variations and AGB stock variations at local scale (Especially for Lorey's height, basal area and density of large trees). Regarding allometry, we detected strong interspecific variations among the studied species which were related to the adult stature of the species. We found that small statured species tend to maximize light capture from their earlier stages in ontogeny by developing a large and wide crown. While large statured species maximize their vertical growth by producing a small and shallow crown until they reach the canopy and outcompete the competitors. At that point they start producing a very large and wide crown. At a reference diameter, large statured trees are taller than small statured trees. Only few correlations were found between tree architectural traits and the light requirements at sapling stage. Architectural traits were found to impact hyperdominance in terms of AGB but not in term of stem density.

In summary, our study suggests that margin forests are able to support similar ecosystem productivity as core forest in central Africa, that a few forest attributes can explain local-scale variation in AGB stocks and that the ontogenetic variation in tree height and crown dimensions among coexisting tropical tree species is related to key functional traits and depict the overall ecological strategy. The productivity rate of a forest is thus a function of its constituting species, their state of development and their architectural characteristics.

Résumé

Les forêts tropicales jouent un rôle clé en termes de stockage de carbone et d’accueil de la biodiversité. Ici, nous comparons la forêt de Luki située en marge de la forêt tropicale Africaine aux forêts du coeur du bassin du Conge en fonction des différents attributs forestiers de structure, composition et d’architecture à partir de données d’inventaire récoltées sur huit hectares. Nous rapportons ensuite le statut de la forêt de Luki en terme de stockage de carbone et nous corrélons les variations à échelle locale de stock de biomasse et d’évolution de ceux-ci aux variations des différents attributs de la forêts, afin de déterminer si les attributs forestiers impactent ou non les variations de stocks de biomasse. Ensuite, nous explorons les espèces constitutrices de la canopée complexe des forêts tropicales en fonction de leur architecture en comparant 30 espèces représentatives de la forêt du Mayombe. Premièrement, nous allons tester l’hypothèse de convergence des allométries parmi les espèces qui cohabitent dans la canopée de Luki. Ensuite, nous tenterons de distinguer différentes stratégies écologiques à partir de traits architecturaux dérivés d’équations allométriques spécifiques. Finalement nous testerons les hypothèses selon lesquelles des traits architecturaux et fonctionnels pourraient influencer l’hyperdominance de certaines espèces par rapport au nombre de pieds ou par rapport à leur biomasse.

Nous avons détecté des dissimilarités entre les forêts en marges et au cœur des forêts africaines, et, en accord avec Lewis (2009) nous avons découvert que les forêts du Mayombe représentent un puis de carbone. Nous avons identifié de fortes corrélations en les attributs forestiers et les variations locales en stock de biomasse (spécialement pour la hauteur de Lorey, la surface terrière et la densité de gros arbres). En ce qui concerne l’allométrie, de fortes variations entre les espèces étudiées ont été découvertes et elles étaient surtout liées à la taille adulte des espèces. Nous avons découvert que les espèces de petites statures maximisent la capture de lumière en développant un houppier large et profond durant leurs premiers stades ontogéniques. Alors que les espèces de grandes statures maximisent, dans un premier temps leur croissance verticale en produisant un houppier petit et peu profond jusqu’à ce qu’ils atteignent la canopée où elles vont alors développer un très large et très profond houppier pour maximiser les chances de se reproduire. A un même diamètre, les espèces de grandes statures sont significativement plus grandes que celles de petite stature. Peu de corrélations ont été trouvées entre les traits architecturaux et les besoins en lumière des juvéniles. Et nous avons montré que les traits architecturaux avaient bien un lien avec l’hyperdominance de biomasse, mais pas par rapport au nombre de pied.

En résumé, notre étude suggère que les forêts marginales sont capables de supporter une productivité similaire aux forêts du cœur d’Afrique centrale, que la variation à échelle locale des attributs forestiers explique bien la variation des stocks de biomasse, et que les variations ontogéniques de la hauteur de l’arbre et de la taille du houppier parmi les espèces coexistente permettait bien de distinguer différentes stratégies écologiques. Le taux de productivité d’une forêt est donc fonction de ses espèces constitutrices, de leur état de développement et de leurs caractéristiques architecturales.

1. Introduction

Tropical forests play a key role in terms of carbon storage and biodiversity hosting. They store approximately 25% of the terrestrial above- and belowground biomass (Bonan, 2008) and account for 96% of the world wide's estimated number of tree species (Fine et al., 2008), even though they cover less than 10% of the Earth's land surface. Their high species richness is believed to improve the ecosystem's productivity through (1) an optimized use of complementary niche (Tilman et al., 2001), (2) the selection effect which provides, by chance, very productive species to the community (Loreau et al., 2001) and (3) the insurance effect, which states that each year depending on the environmental conditions, different species will have varied implications in the overall productivity (Yachi et al., 1999; Isbell et al., 2011). But no correlations where found between tree diversity index and carbon storage among tropical forests. Instead, the biological diversity appears to improve the resilience of desirable ecosystem states by providing a large range of reactions to environmental changes (Elmqvist et al., 2003). Knowing this, in the context of global warming, it is important that initiatives like the UN Reducing Emissions from Deforestation and Degradation (REDD+), which are supposed to help the conservation of carbon storage capacity of tropical forests, also focus on biodiversity protection (Poorter et al., 2015). The REDD+ mechanism depends greatly on above ground biomass (referred to as AGB) estimations. In 2005, Chave et al showed that accurate AGB estimations could be obtained by using a single equation including trunk stem diameter, wood specific gravity and total tree height. They mentioned that these estimations were only slightly improved when including site, successional status or forest type to the model (Fayolle et al., 2013).

Globally, there seems to be an increase of carbon storage in the tropical forests (Lewis et al., 2009) explained by either the increment of resources availability, especially CO_2 in the atmosphere, or because the forest is recovering from past disturbances (Wright, 2005; Clark, 2007; Lewis et al., 2004; Phillips et al., 2008), the question is still debated. Locally, in Africa, important variations in carbon stocks have been reported at plot-level (Gourlet-Fleury et al., 2011; Doetterl et al., 2015; Fayolle et al., 2016; Imani et al., 2017), they are correlated to plot-level variations in forests structural attributes (basal area ,BA, stem density ,N, wood density, WD and in density of large trees, N_{70}) (Lewis et al., 2013; Slik et al., 2013).

Scientists focus on the AGB of trees and its variations to study how forests are stocking carbon overtime because it represents best the carbon pool evolution in tropical trees (Eggleston et al., 2006). The AGB consists of all the biomass contained in every tree per unit area. The heterogeneity of the African tropical forest in terms of structure, composition and architecture explains the highly variable nature of the biomass estimations (Rutishauser et al., 2010). Unfortunately the impact of these forest structural and taxonomic attributes on AGB variations at plot-level remains poorly studied (Loubota Panzou et al., 2016).

The investigation of how forest structure and composition affect carbon stocks needs to be combined with the study of the forest's dynamic processes, which contain 3 components. First, a tree needs to establish, to become a recruit. This occurs when a tree reaches the lower diameter limit of 10 cm in diameter. Then, the tree will grow, accumulating AGB (survivor). The cycle ends with the mortality, step during which the tree dies because of either competition or external disturbance. The remaining's of trees left to decomposition could have an important impact on the carbon budget of the forest and yet, in this study, they are not included because of the hardness of their consideration (Bonan, 2008; Ligot et al., 2018; Rutishauser, 2010).

Most study sites used to estimate AGB and connect AGB stocks variations to structural forest attributes are located within the core of the tropical forests, leaving the forests located int its margins less studied. The Luki forest (Fig 1) constitutes the last and southernmost patch of the Mayumbe forest which extends alongside the Atlantic Ocean from middle Gabon to Luki covering 2000 km² (Monimeau, 1990). The Mayumbe forest's vegetation belongs to the tropical semi-evergreen rain forest of the Guineo-Congolian forest complex (Lebrun et al., 1954). It contains a high floristic diversity, large timber trees (Monteiro, 1962) and is thought to be one of the sub-mountainous glacial forest refuge (SOSEF, 1996; Maley, 1996). It is a continuum of forested hills (maximal elevation of 930 m) characterized by deciduous and evergreen species in the upper stratum and mostly evergreen species in the understory (Donis, 1948; Couralet et al., 2010). The main indicators of these types of forests belong to the *Fabaceae (Caesalpinioideae)*, *Cannabaceae*, *Malvaceae (Sterculioideae)* and *Meliaceae* family ; best represented by the *Prioria*, *Celtis*, *Cola* and *Entandrophragma* genera (Lebrun, 1954; Maley et al., 1998).

The natural complexity of the tropical rain forest canopy generates multiple ecological strategies adopted by different coexisting tree species (Kohyama et al., 2003; Turner, 2001; Kohyama, 1992; King, 1996). Indeed, species must adapt to the different living environments which arise from the combination of multiple conditions. These conditions, from the understory to the canopy, follow both a vertical and a horizontal gradient creating a continuum of microclimates. Light availability and wind speed increase from the ground to the top of the canopy, irradiance can even change from 2% to 100% following that same direction, while [CO_2] and relative humidity decrease. The horizontal light gradient comes from the openings of the canopy created by small-scale disturbances like tree falls or harvesting (Yoda, 1974; Chiariello, 1984; Rutishauser, 2010; P. B. Reich et al., 2003). The division of the vertical gradient by tree species is probably best explained by either different adaptations to understory and canopy conditions (King, 1996), by the trade-off between early reproduction and annual fecundity (Thomas, 1996; Davies et al., 1998), or by the tradeoff between a fast vertical growth to quickly reach the canopy and an early reproduction in the understory (Kohyama et al., 2009) which is supported by (Iida, Takashi S. Kohyama, et al., 2011).

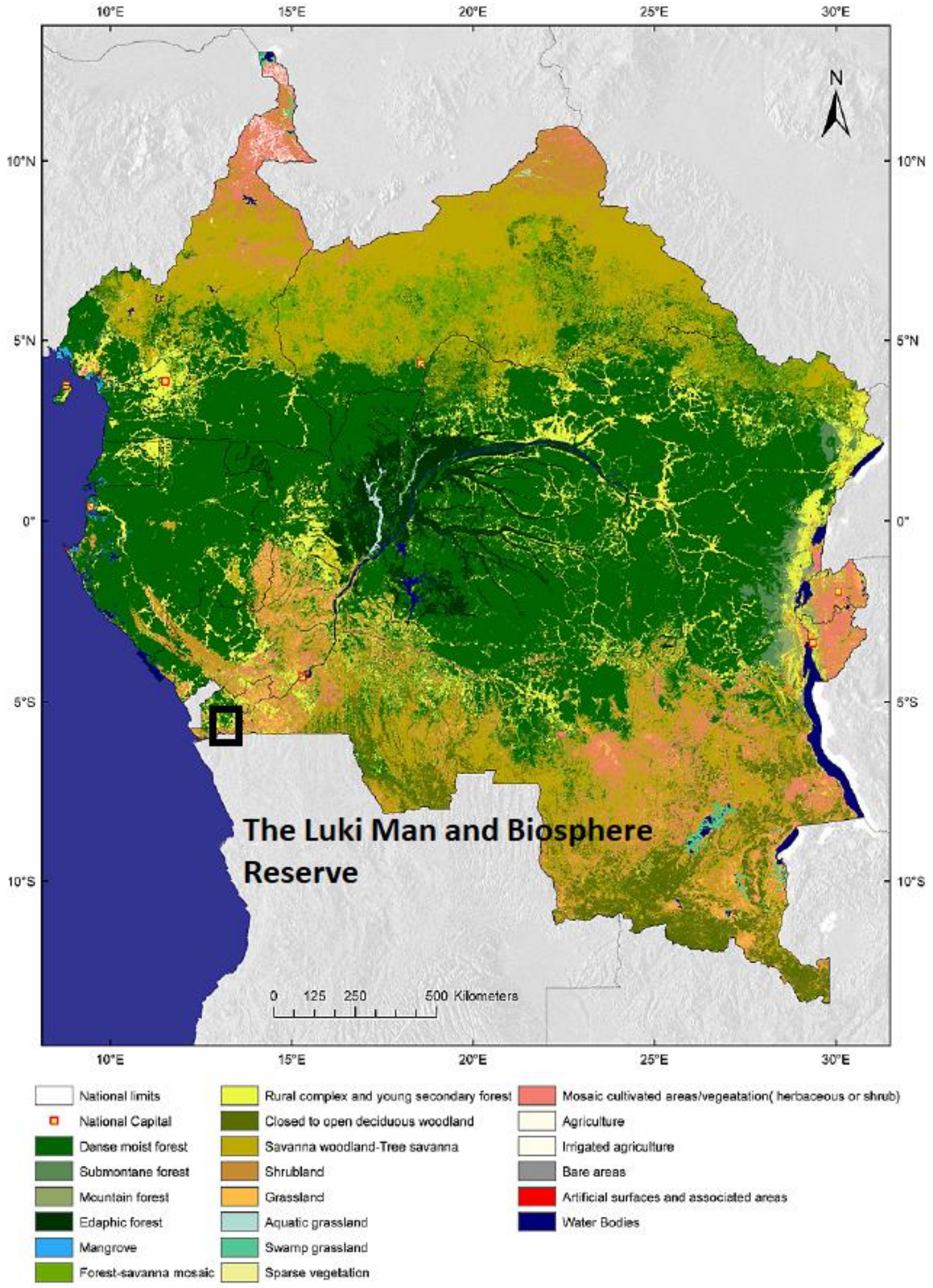


Figure 1. Luki Man and Bioshere Reserve located in the Congo Basin vegetation map from (Verhegghen et al., 2012).

In comparative ecology, they distinguish, describe and define different ecological strategies using functional traits. They are defined as any morphological, physiological or phenological characteristic that can be measured at the individual level. Here, they will be used to investigate the constituting species of the tree community located at the southern limit of the Congo basin forests. Ecological strategies arise from the association of trait values (Reich et al., 2003). Trait covariations do not distinguish the different species with sharp discontinuities, in fact the different ecological strategies are part of a continuum as reported by Swaine et al., (1988) and Chave (2005). These functional traits affect the individual's fitness, its performance, by affecting the individual's growth, reproduction and survival (Ackerly, 2003; Violle et al., 2007). Historically, the key traits used to differentiate tropical tree species are (1) wood density (Chave et al., 2009), (2) light requirements (Sheil et al., 2006) and (3) adult stature (Poorter et al., 2003). More recent studies have shown a special interest in architectural traits, which are a group of functional traits that refer to the shape and size of the tree and of its components (Poorter, 2003).

Through the comparison of architectural traits, extracted from species-specific allometric models, which compare the shape of a tree (Height, crown radius, crown depth) to its dimensions (Diameter or height), different light capturing strategies might emerge. So far, adult stature (Hmax) and juvenile light requirement (CEIjuv) are thought to explain the major variations in functional and architectural traits found among the tropical tree species and they are considered as the best characteristics to explain the different light capturing species-specific strategies (Poorter, Bongers, Bongers & Bongers1, 2006; Thomas, 1996; Loehle, 2000; Turner, 2001; Iida, 2011).

Studies that attempted to differentiate ecological strategies among coexisting species gave, to this point, equivocal results. Theoretically, large statured trees should, at their small sizes, maximize vertical growth by producing a slender stem that carries a narrow and shallow crown. Once they reach the canopy, they should produce a wide and deep crown to start maximizing carbon gain and reproduction instead of vertical increment (Iida, 2011; Poorter, 2006; Poorter, 2003; Kohyama, 2003; King, 1990; Thomas, 1996). Small statured trees, which are intended to stay in the understory for their all lifespan, should produce a wider, deeper and stronger crown at their early ontogenetic stages to maximize light capture, carbon gain and reproductive output as soon as they sprout (Iida, 2011; Poorter, 2006; Poorter, 2003; Clark et al., 1991; Thomas, 1996; Sterck et al., 2001; Wright et al., 2005). At the same reference height, they produce bigger stems compared to large statured trees and create solid branches to resist shocks from fallen branches higher in the canopy.

Light demanding species which are defined as species with a high mortality rate in juveniles under shadow conditions (Poorter, 2006), need to grow fast to exceed the competition in the struggle for light and to minimize self-shading. Again, their stems will be slender and higher at a certain diameter than stems from shadow-tolerant species, their crown will be smaller, similar and wider depending on their sizes compared to more shadow-tolerant species but always shallower (Kohyama, 1987; Poorter, 2006; Iida, 2011; King, 1996).

Here we will first report data on structure, composition and tree species architecture, of Luki's forest, located at the southernmost margin of the Congo basin tropical forests. Then the following objectives are targeted:

1) Forest structural attributes : Using eight one-ha inventory plots, we will describe the structural forest attributes (N, N_{70}, BA, WD, H_{Lorey} and QSD) of Luki's forest, and compare our values to the reported values across the Congo basin's core forests from the AFRITRON plot network (Lewis, 2013).
2) AGB stocks and dynamics: Local-scale variation, i.e. between plots, in AGB stocks and dynamics will be examined, to determine the importance of Luki's stocks, and to what extent Luki's forest is a source or a carbon sink. Then, relationships between forest structural attributes at plot level and both AGB stocks and dynamics will be tested. The contribution of large trees to plot level AGB (Slik, 2013) and AGB dynamics (Ligot, 2018) will finally be examined.
3) Species-specific allometry: Tropical forests are species rich and structurally complex. Here, we analyzed the allometric variation among 30 selected and characteristic species found in the canopy and understory of Luki's forest. Using additional data of tree dimensions, including tree diameter, total height, height of the first branch and crown radius, sampled over the diameter range for each species, we will analyze between-species variations in tree allometry. We specifically test the null hypothesis of community convergence in tree allometry reported by Iida et al (2011) in Malaysia, even though between-species variation is often reported among coexisting species (Poorter, Bongers, Bongers, Ecology, et al., 2006; Fayolle, 2016).
4) Species traits and strategies: Finally, the species-specificity in tree allometry id used to quantify species specific architectural traits at juvenile stage (10 cm in Dbh) and at adult stage (maximum Dbh). Theses architectural traits will be related to other key functional traits of tropical tree species, specifically light requirement (regeneration guild according to Hawthorne, 1995), CEIjuv (Poorter, 2006 and Sheil, 2006), and wood density (Chave, 2009) to study if multiple correlations between traits allow us to distinguish different ecological strategies among the 30 tropical tree species. Species traits and strategies will then be related to species density and AGB, to identify the traits involve in hyperdominance, computed on stem number (Ter Steege et al., 2013) or AGB (Fauset et al. 2015, Bastin et al. 2016).

2. Material and Methods

2.1 The Luki Man and Biosphere Reserve

The fieldwork was conducted in the Man And Biosphere Reserve of Luki, located in Kongo Central, DRC, between 05°30’ to 05°45’S and 13°07’ to 13°15’E (Couralet, 2010), which serves as an I.N.E.R.A. (Institut National pour l’Etude et la Recherche Agronomique) forestry research station. It covers 33000 ha and its region belongs to the sub-equatorial humid category also described as an Aw_5 type in the Köppen climate classification. A mean of 1180 mm yr^{-1} of precipitations and an average temperature of 24.6°C characterize its climate, according to data from Luki’s meteorological station over the 1947-2017 period. Throughout the year, two dry seasons occur ; the first, with a 3-4 months period of mean precipitation lower than 50 mm, lasts from mid-Mai to mid-September and the second, with a higher rainfall rate, appears in January (Lubini, 1997). A mist brought by the Benguela marine current, lowering the irradiance, combined with the self-regulating effect of the vegetation and the shape of the landscape allow the establishment of the dense humid forest even though such low annual precipitations usually prevent this type of forests to settle (Pendje et al., 1992; Sénéchal et al., 1989). The soils are quite poor in regards to their chemical content, they are generally ferallitic but heterogenous (Monimeau, 1990). Its vegetation belongs to the moist central Africa floristic cluster according to (Fayolle et al., 2014). According to Donis (1948), in the old climacic Mayumbe forest, *Staudtia stipitata* and *Coelocaryon spp* all *Myristicaceae* are the most remarkable tree species. Plant phenology and growth have been previously studied showing a strong seasonality in plant functioning. Many tree species start shedding their leaves during the long dry period (July-August) and the number of trees shedding their leaves keeps increasing until the transition period between the dry and the rainy season when it reaches a maximum (September -October). Trees generally start their flowering when the rainy seasons returns (maximum in October and March) (Couralet et al., 2013). This forest-wide bimodal flowering pattern is thought to explain the differing onset of tree growth for the understory species (De Mil et al., 2017).

Fig 2. Shows the evolution of the percentage of greenness calculated by the amount of green divided by the sum of the amount of green, red and blue present in pictures of the tree community taken twice a day, over a year. The first picture was taken October 2, 2013, the last picture was taken September 26, 2014. The shedding period begins around day of the year 230 and reaches its maximum at the end of the graph. As trees shed their leaves the percentage of greenness decreases.

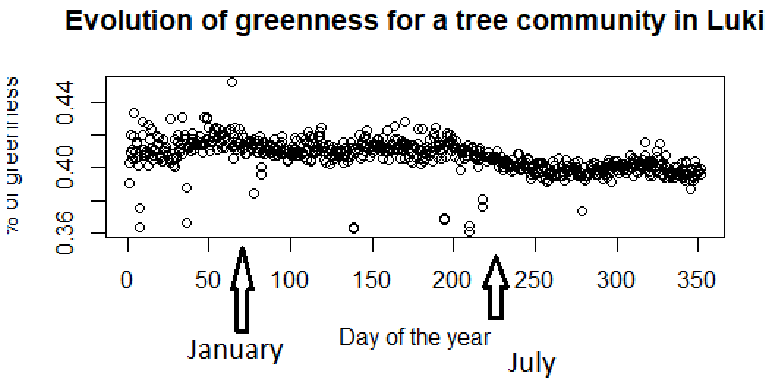


Figure 2. Percentage of greenness found in community wise pictures taken twice a day throughout the year.

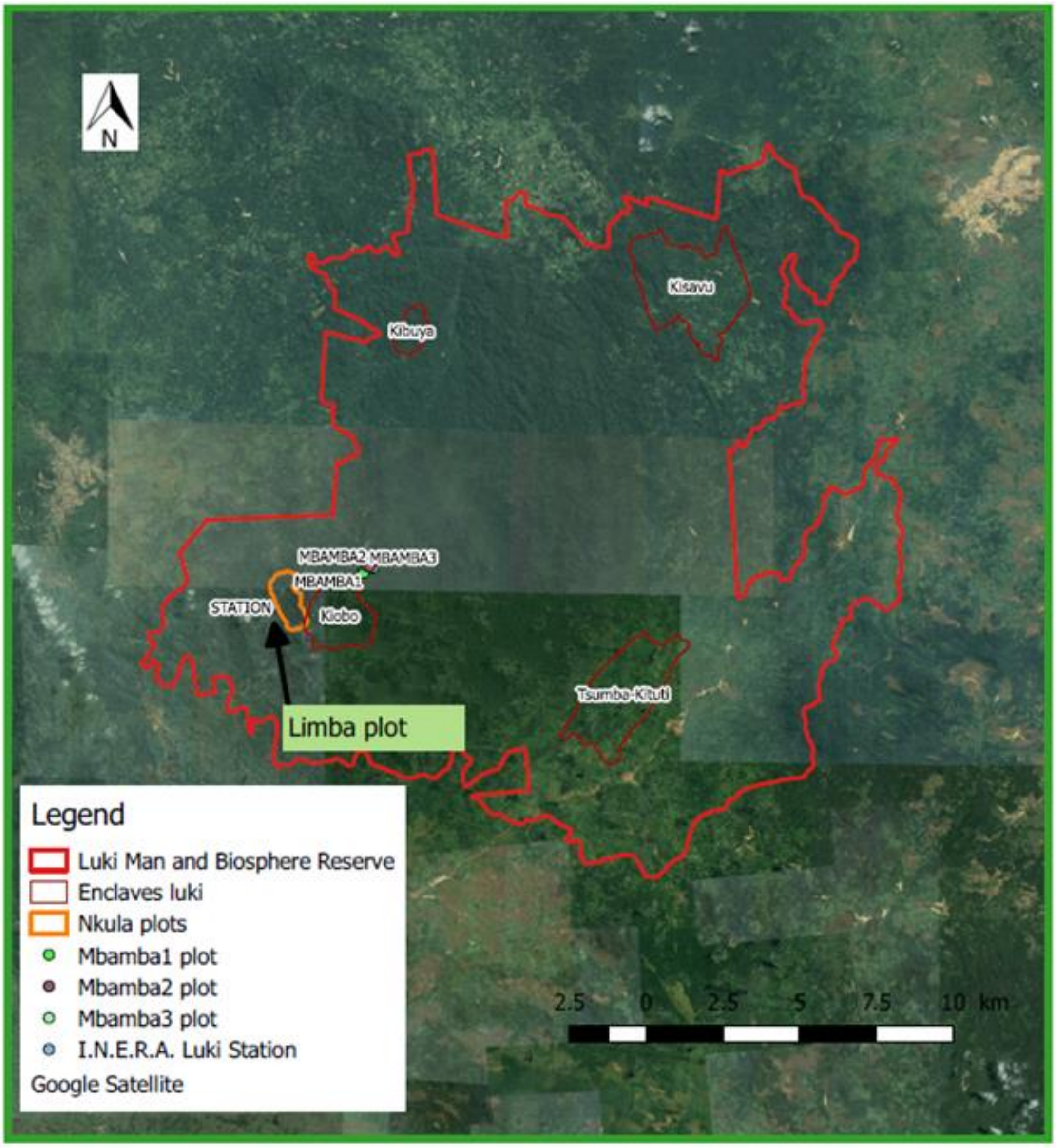


Figure 3. Map of the Luki Man and Biosphere Reserve. Author: Arthur Chantrain. Data from I.N.E.R.A. and personally collected. Coordinates system: IGCB 1955/ TM Congo zone 12. Background credit to Google Satellite.

2.2 Forest inventory data and tree measurements

In total, eight one-hectare plots were surveyed for informing on forest structure and composition. These permanent plots had been installed in 2009 and were inventoried for the third time according to the RAINFOR field manual for plots establishment and remeasurement (2009-2016-2018). Every woody stem bigger than 10 cm in Dbh was identified, tagged, mapped and its Dbh was measured using a diameter tape (inventory data). For the three "Mbamba" plots, the tree height was also measured. Previously collected data had to be standardized to facilitate further analysis, and the "Mbamba 2" plot data from 2009 and 2016 were inoperable because the trees did not match the reported diameters, a part of the data frame had been mixed up and, with no way to make sure that the correction was valid, this plot had to be removed from the forest dynamic analysis. Species average wood density (WD) was extracted from the international data base (Chave, 2009) using the BIOMASS R package. Which allows the user to retrieve and correct the taxonomy, and estimate wood density and its uncertainty (Réjou-Mechain et al., 2018). When no information was available for the species, genus or site, average wood densities were calculated.

Among these plots, additional tree measurements and crown observations were performed on 30 selected species to study tree allometry (allometry data). A total of 310 individuals from 30 different tree species, sought to be representative of the Mayumbe forest, were randomly selected among different diameter class. Species selection was limited by the number of individuals on a broad range of diameter, 20 being the minimum. Then, we tried to maximize the family, temper and place in the canopy diversity within the selection. Eventually, the sampled species accounted for 48,51% of the basal area of all inventory data. For each individual, the stem Dbh, the tree height (H), the height of the lowest foliage (H1stbr), and four crown radii according to the four cardinal directions were measured if it showed a healthy, undamaged crown. Crown depth is calculated by subtracting the height of the lowest foliage (H1stbr) to the tree height (H). The crown's position in the canopy was estimated using the Dawkins index (CEI) on a five-point scale (from one = lower understory to five = emergent) because this index provides the most accurate predictions of diameter increment (Moravie et al., 1999) (See appendix X). The Cohen's Kappa value obtained for the CEI observations reached 0.95 between the two observers, this index determines the agreement between two observers for qualitative data recording (one meaning that the two observers always agreed on the estimation, zero meaning that they always disagreed). It was calculated following Santos (2010). Crown fragmentation and liana infestation were estimated using a four-point scale from 0% to >50% of the crown fragmented or infested in order to capture the most contrasting cases (Rutishauser et al., 2011). The height and length measurements were performed with a VERTEX IV dendrometer. To ensure precise height measurements, each height was measured from two distinct points at a distance the closest to the length that needed to be measured, then the mean value was used for the analyses.

2.3 Forest attributes at plot level

Six structural forest attributes were computed at plot level (inventory data) for the 2018 inventory of the eight one-ha plots: stem density (N, ha^{-1}), density of trees bigger than 70 cm in diameter (N_{70}, ha^{-1}), basal area (BA, $m^2\ ha^{-1}$), the basal area weighed wood density (WMD_{BA}, g cm^{-3}), Lorey's height (H_{Lorey}, m) and the quadratic mean diameter (QSD, cm). The firsts important structural plot attributes are stem density (N) and density of big trees (N_{70}), calculated as the number of stem bigger than the 10 cm diameter limit or bigger than the 70 cm diameter limit reported per plot (Slik, 2013). Then, the most important one (Lewis, 2013; Imani, 2017), computed from the Dbh, is the plot basal area (BA in $m^2\ ha^{-1}$), calculated using this formula: $BA_{plot} = \sum(\pi * dbh_i^2)/40000$ ($m^2\ ha^{-1}$). It represents the sum of all the projected area computed from the diameter of all trees within a one ha plot. The BA-weighted wood mass density (WMD_{BA}) is the mean of the wood density of each stem weighted by its BA (Lewis, 2013). Lorey's height (Basal area weighted total height) was calculated using this formula: H_L (m) = $\sum (H_i * BA_i * BA_{Tot}^{-1})$, representing the mean height of uneven-aged forest stands (Pourrahmati et al., 2018). And finally, the quadratic mean diameter QSD (cm) which is the square root of the arithmetic mean of squared values, results from the following formula:

QSD (cm) = $((\sum DBH_i\ / N))$ ^ ½ = 200 * $(BA / (\pi * N))$ ^ $^{1/2}$ (Curtis et al., 2000).

In addition to structural attributes, AGB stocks were computed in 2009 and 2018, as follows. First, the AGB at the tree level was computed using the most recent pantropical model (Chave et al., 2014).

AGB = 0.0673 * (Wood Density * (DBH^2) * (Height)) ^0.976 in Mg of dry mass.

Where DBH corresponds to the diameter of the tree measured at 1,3 m above ground or above buttresses.

Then, within a plot, all AGB's at tree level were summed to derive AGB at plot level (Mg of dry mass ha^{-1}). It was then possible to analyze the stock changes between 2009 and 2018, giving us the AGB dynamics (dAGB). dAGB results from the following equation:

dAGB (Mg of dry mass $ha^{-1}\ yr^{-1}$) = $\Delta AGB * \Delta T^{-1}$ with T being the time in number of years.

The lack of tree height measurements in the previous inventories and in the other plots than "Mbamba" inducted the use of modelling to estimate tree height. From the height and diameter data collected on the three one-ha plots called "Mbamba 1,2,3" three models were tested, first the power law model which is accompanied by a bias in the estimations, then the Michaelis-Menten and Weibull models which are both nonlinear asymptotic models (Fayolle, 2016). The Weibull model was the best fitted model on the basis of the lowest Akaike's criterion, in addition to the lowest residual standard error for the 4131 studied trees. It was thus selected to estimate tree height for the trees which were missing height measurements.

2.4 Allometric modelling and architectural traits

When trees are considered on a population scale, it is clear that dimensions of an individual are statistically related one with another (GOULD, 1966). This relation arises from the ontogenetic trajectories of individuals which stay the same for all, accepting a low life-history related variability. This means that for trees belonging to the same species and growing under similar conditions, regardless of their size, the proportions between different characteristics (height, diameter, crown height, crown radius…) will follow rules and thus will be predictable (King, 1996; Archibald et al., 2003; Bohlman et al., 2006; Dietze et al., 2008). In this study, all allometric models are built using the power law model $Y= a\ X^b$. Ordinary least-square regressions were used on the log-log transformation which renders the relation linear. Poorter explains that "The coefficient b indicates the ratio of the relative growth rate of part Y linked to the relative growth rate of part X" (Poorter, 2006)

Here is the equation based on diameter (Dbh) of tree (i) from the species (s):

$\text{Log}\ (Y_{is}) = a_s + b_s * \log\ (dbh_{is}) + \mathcal{E}_{is}$ which becomes : $Y_{estimated} = \exp\ (a_s) * (dbh\ _{is}{}^{b})* \exp\ (\sigma^2/2)$ once transformed back with a correction for the bias.

Coefficient a and b represents respectively the intercept and the slope of the model, they are referred to as "scaling coefficients", Y is either tree height (H), crown radius or crown depth and $\mathcal{E}_{is}$ is the error term. An estimation bias is inherent to the use of this model, it can be corrected by multiplying the term with the total variance divided by two. The normality and homoscedasticity of residuals were tested graphically.

Species-specific modelling was used to derive a set of architectural traits including height, crown radius and crown depth at a 10 cm reference diameter (H_{10}, cr_{10}, and cd_{10}), and at maximal size (hmax, crmax and cdmax) using the 98th percentile for computing maximum diameter (Dmax).

A similar approach was used to compute CEIjuv, but using a multinomial logistic regression relating tree size to semi-quantitative CEI, as proposed by Sheil et al (2006). Regeneration guild according to Hawthorne (1995) was classified as Pioneer (3 species), Non Pionner Light-Demanding (11 species) and Shade Bearers (16 species) (Doucet, pers comm.)

Three allometric models were built, the first compares the height of the tree to its diameter (scaling coefficient = bH, bHfut). The two other models compare crown radius and crown depth to the height of the tree giving respectively bcrh and bcdh as slope coefficients. The explicative variables were chosen following Poorter (2006) and Iida (2011).

2.5 Data analysis

Spearman's rank order correlations were computed between AGB and the different structural attributes to understand how the structural attributes influence the plot-level AGB. If a forest attribute showed the same value for two or more plots, Spearman’s rank order correlation was replaced by Pearson’s correlation coefficient which accepts unranked or equals values.

To detail the biomass estimation and carbon stock change analysis, the inventory dataset was split into 3 diameter classes to encounter for biomass variations among different diameter ranges and to see if they had the same importance in the tree community. First, the “small” class, which contains trees ranging from 10 cm to 29.9cm, the second class is called “medium”, it comprises trees between 30cm and 69.9cm in Dbh, and the last class is named “large” and contains all trees bigger than 70 cm in Dbh. Biomass gains and losses were distinguished one from another, the gain is the sum of the biomass from stem recruitment and the biomass acquired by the survivors over the studied period. Losses correspond to the mortality of trees during the census interval. The biomass net change is the total of the gains minus the losses (Ligot, 2018).

We tested the convergence in species allometry, using an ANCOVA with ln (crown radius) or ln(crown depth) as dependent variable, species as a factor and ln(height) as a covariate according to (Poorter, 2006)

To determine whether traits were correlated one to another, Pearson’s correlation were performed on the raw trait data to test for bivariate trait relationships. WD and CEIjuv were added to the list of existing architectural traits ((H_{10}, cr_{10}, cd_{10}, hmax, crmax, cdmax and Dmax).

Multivariate trait covariations were analyzed with a Principal Component Analysis (PCA). Only the architectural traits were used to define the PCA’s two axis, then the scaling coefficients from the multiple models (bH, bHfut, bcrh and bcdh), the specific number of stems (N) and the specific AGB were added as supplementary variables to the graph.

All statistical analyses were performed using the open source R environment (Rstudio version ‘1.1.383’, from the R core team 2016). The ggplot2, ade4, factoextra, foreign, nnet, reshape2, car, stat, corrplot, PerformanceAnalytics, Hmisc and doBy packages were especially needed.

3. Results

3.1 Luki's forest description

In total, 4131 individuals from 191 species belonging to 38 families were found in the sampling area of eight ha (inventory data), where the *Fabaceae (Caesalpinioideae and Mimosoideae)* and *Sapindaceae* family represent 35% of the total basal area. The three most represented species in term of basal area are *Ganophyllum giganteum* (*Sapindaceae*), *Hylodendron gabunense* and *Prioria balsamifera* (both *Caesalpinioideae*), they account for 15% of the total basal area. All following figures are reported in table 1. (Table 1)

We observed strong local-scale variation in forest structure attributes among the eight one-ha plots. In 2018, the average stem density for the eight one-ha plots is 442 stems ha^{-1}, it varies between 369 trees and 535 trees. The density of tree bigger than 70 cm in Dbh varies between eight and 20. Four plots have a N_{70} equivalent to eight but they represent between 1,69 % of all stems and 5,21 % of all stems. The mean basal area reaches 28.2 m² ha^{-1} (23,6 m² ha^{-1} – 34.3 m² ha^{-1}). The mean basal area weighted wood density equals 0.6325 g cm^{-3} for the eight plots and ranges from 0.544 to 0.674 g cm^{-3}. The quadratic mean diameter (QSD) varies between 25,87 cm in "Limba" and 32,83 for "Mbamba 2" the average QSD reaches 28,55 cm. (Table 1)

In terms of composition forest attribute, the mean wood density also shows variation among plots with a global mean of 0.6625g cm^{-3} ranging from 0.569 g cm^{-3} for Limba to 0.726 g cm^{-3} for Nkula crête.

Regarding the architectural forest attributes, we found that Lorey's height varies from 25,26 m in "Limba" to 30,48 m in "Mbamba 2".

The "Mbamba 2" plot shows the greatest values for almost all forest attributes except for stem density, while "Limba" supports almost all the smallest values.

During the last inventory (2018), in terms of number of stems, the most represented families in the eight ha are the *Fabaceae* (*Caesalpinioideae)* (17,64%), the *Annonaceae* (15,78%) and the *Rubiaceae* (10,48%). The 5 most represented species are, in order of importance, *Xylopia wilwerthii*, *Hylodendron gabunense*, *Corynanthe paniculata*, *Aidia ochroleuca* and *Manilkara spp*.

Table 1. Plot structural, compositional and architectural forest attributes.

	Mbamba 1	Mbamba 2	Mbamba 3	Limba	Nkula crete	Nkula plateau	Nkula masevo	Nkula source
N 18	369	384	427	449	459	535	439	474
Inventory date ('18)	22-03-18	03-04-18	29-03-18	28-09-17	16-09-17	01-09-17	07-09-17	18-09-17
N 09	369	NA	421	357	477	523	393	464
Inventory date ('09)	01-09-09	09-09-09	19-09-09	26-09-09	03-10-09	10-10-09	17-10-09	24-10-09
Number of years	8,56	8,57	8,53	8,01	7,96	7,89	7,90	7,91
BA 18 tot (m^2 ha^{-1})	24,2	32,5	27,4	23,6	34,3	29,2	25,2	29,1
BA 09 tot (m^2 ha $^{-1}$)	22,9	NA	25,1	18,0	33,7	26,7	24,6	27,2
Mean WD (g cm^{-3})	0,649	0,682	0,670	0,569	0,726	0,652	0,709	0,643
WMD(ba) (g cm^{-3})	0,644	0,673	0,674	0,544	0,666	0,592	0,648	0,619
Hlorey (m)	26,53	30,48	28,18	25,26	28,47	27,47	28,14	26,73
QSD (cm)	28,9	32,83	28,58	25,87	30,85	26,36	27,03	27,96
AGB 09 (Mg dry mass ha^{-1})	261,1	NA	304,8	172,1	414,1	270,5	281,4	292,2
AGB 16 (Mg dry mass ha^{-1})	268,6	NA	315,2	212,7	423,6	296,4	290,3	303,5
AGB 18 (Mg dry mass ha^{-1})	272,9	431,3	343,2	215,5	419,7	315,8	292,6	317,9
dAGB (Mg dry mass ha-1 year^{-1})	1,3785	NA	4,5018	5,4182	0,7035	5,7414	1,4177	3,2491
AGB 09 > 70cm (Mg of DM ha^{-1})	60,56	NA	69,42	6,43	111,48	102,16	81,57	58,71
N 09 > 70 cm	9	NA	10	2	14	17	10	9
AGB 18>70cm (Mg of d.m. ha^{-1})	66,6	186,26	99,3	44,79	95,28	120,74	78,61	60,97
N18 >70cm	8	20	10	8	14	15	8	8
% AGB >70cm	24,40	43,19	28,93	20,78	22,70	38,23	26,87	19,18
%N>70cm	2,17	5,21	2,34	1,78	3,05	2,80	1,82	1,69
Most repr sp (N)	Coelocaryon botryoides (61), Maranthes Glabra (21), Tapura Lujae (19), Staudtia kamerunensis (19)	Greenwayodendron suaveolens (46), Xylopia wilwerthii (42), Petersianthus macrocarpus (21) Dialium corbisieri (21)	Xylopia wilwerthii (61), Hylodendron gabunense (53), Greenwayodendron suaveolens (43)	Trichilia prieureana (100), Trilepisium madagascariense (47), Celtis zenkeri (25)	Corynanthe paniculata (86), Garcinia punctata (55), Manilkara sp (43)	Celtis mildbraedii (65), Manilkara sp (54), Eriocoelum microspermum (51)	Xylopia wilwerthii (68), Manilkara sp (43), Corynanthe paniculata (40)	Xylopia wilwerthii (66), Aidia ochroleuca (62), Funtumia latifolia (42)
Most repr sp (BA 18)	Coelocaryon botryoides, Ganophyllum giganteum, Uapaca guineensis	Piptadeniastrum africanum, Gilletiodendron kisantuense, Plagiostyles africana	Gilletiodendron kisantuense, Hylodendron gabunense, Piptadeniastrum africanum	Trichilia prieureana, Terminalia superba, Trilepisium madagascariense	Prioria balsamifera, Corynanthe paniculata, Hylodendron gabunense	Antiaris toxicaria, Celtis mildbraedii, Nesogordonia kabingaensis	Dacryodes buettnerii, Ganophyllum giganteum, Corynanthe paniculata	Ganophyllum giganteum, Funtumia latifolia, Aidia ochroleuca

3.2 AGB stocks and AGB dynamics

In 2018, local-scale variations in AGB stocks and AGB dynamics are still observed, the total AGB goes up to 2177,6 Mg of dry mass for the seven plots (total AGB in 2018 = 2608,9 Mg of dry mass for the eight ha, but the "Mbamba 2" plot had to be removed from the analysis because previously acquired data had been lost). In average, the eight one-ha plots support 326,1 Mg of dry mass ha $^{-1}$. Their AGB stocks vary from 215.5 Mg of dry mass ha $^{-1}$ for "Limba" to 431.3 Mg of dry mass ha $^{-1}$ for "Mbamba 2"

Stock changes between 2009 and 2018 are positive, which indicates that the Luki's forest is increasing its carbon stock and is a carbon sink. The mean value for dAGB is 3.201 Mg of dry mass ha^{-1} yr^{-1}. A strong local scale variation is detected among the different plots. The AGB increment varies from 0.704 Mg of dry mass ha^{-1} yr^{-1} in "Nkula crête" to 5,741 Mg of dry mass ha^{-1} yr^{-1} in "Nkula plateau".

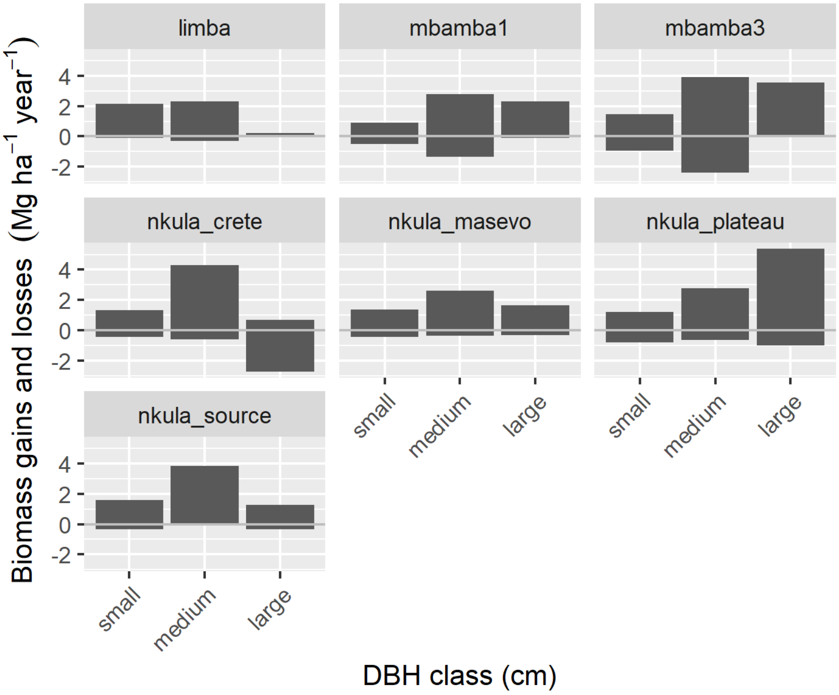
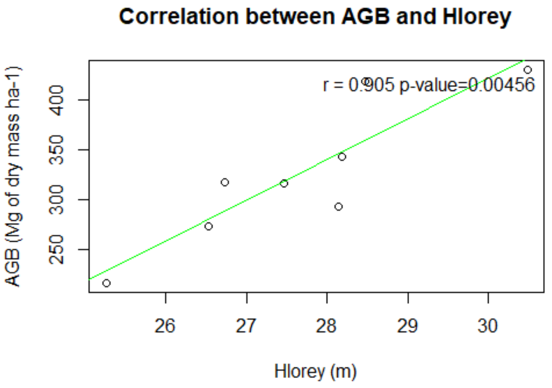


Figure 4. Plot- specific biomass gains and losses for the different diameter classes. Gains represent the total of the newly recruited trees plus the growth of survivors, losses correspond to mortality. The different classes contain varied Dbh ranges: small [10-30]cm, medium [30-70] cm and large >70 cm.

When the relationship between forest attributes and AGB stocks and dynamics are examined, we find that AGB stocks variations among plots is driven by both architectural and structural attributes (fig. 5). In fact, almost all attributes are positively correlated to AGB, in order of importance there is: (1) Lorey's height, (2) the basal area, (3) the number of trees bigger than 70 cm in diameter, and (4) the quadratic mean diameter. Only stem density appears to be unrelated to AGB stocks in the different plots. In terms of composition attributes, no significant correlation was found between AGB and wood density.



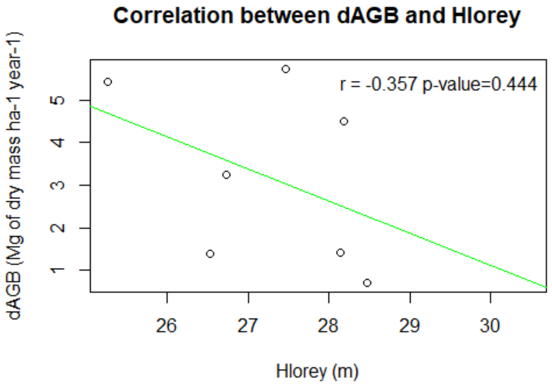
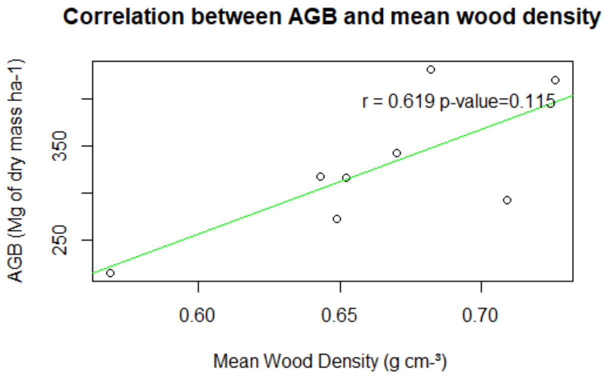


Figure 5a. Correlation between AGB and Hlorey

Figure 5b. Correlation between dAGB and Hlorey



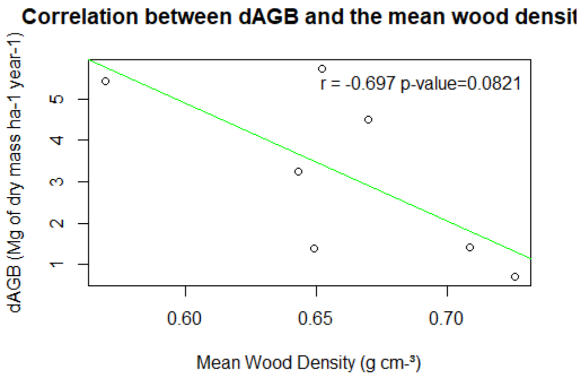
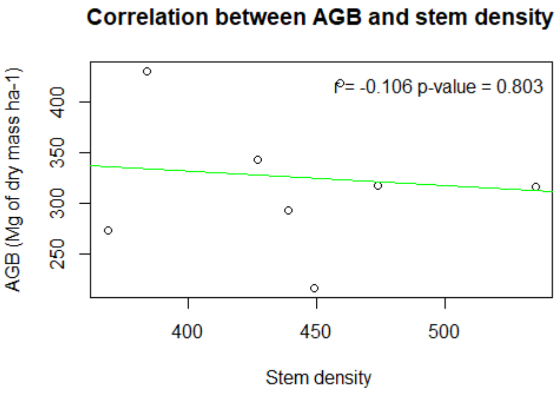


Figure 5c. Correlation between AGB and mean WD

Figure5d. Correlation between dAGB and mean WD



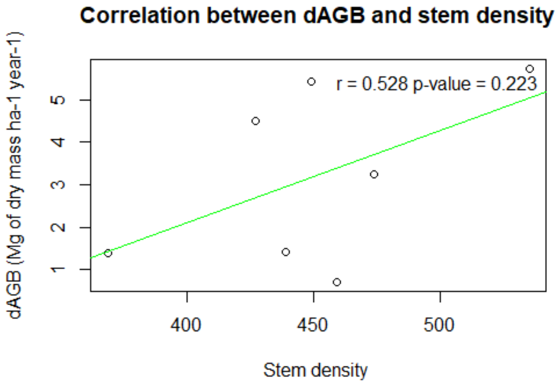


Figure 5e. Correlation between AGB and N

Figure 5f. Correlation between dAGB and N

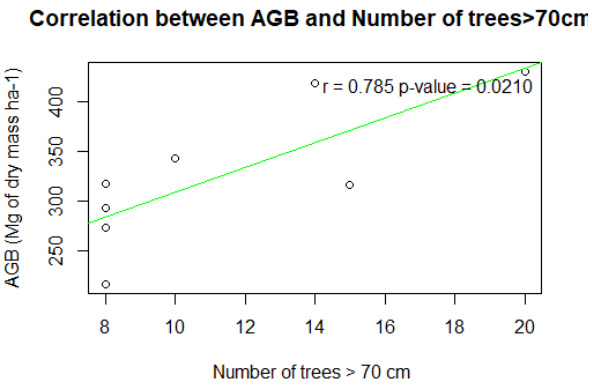


Figure 5g. Correlation between AGB and N70

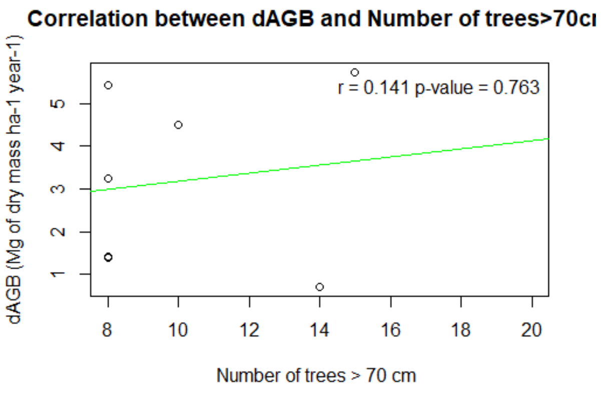


Figure 5h. Correlation between dAGB and N70

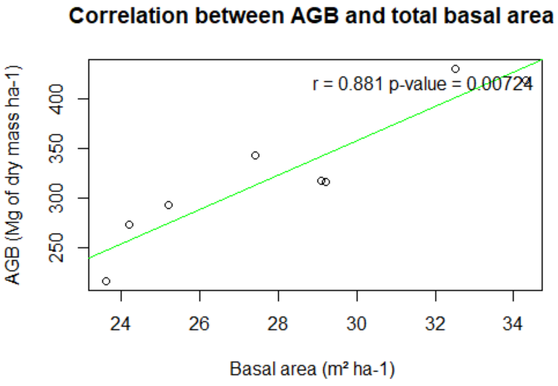


Figure 5i. Correlation between AGB and BA

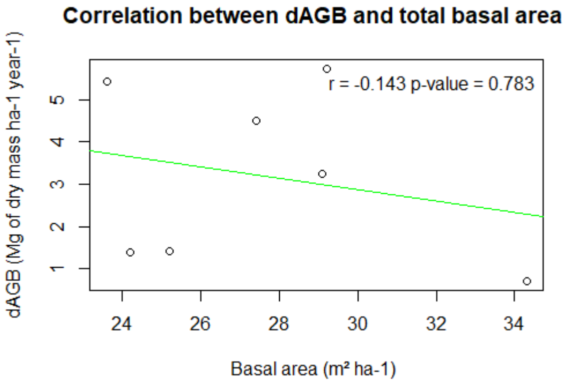


Figure 5j. Correlation between dAGB and BA

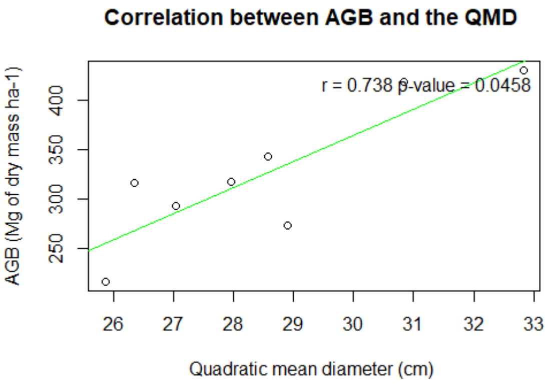


Figure 5k. Correlation between AGB and QMD

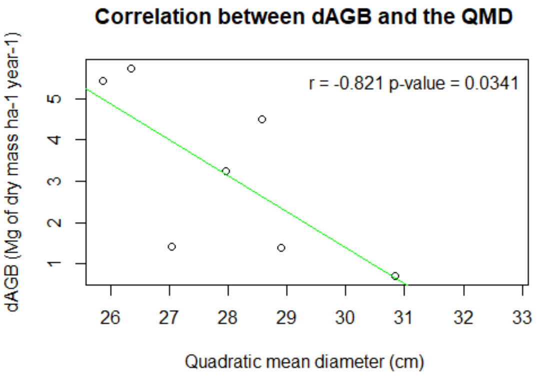


Figure 5l. Correlation between dAGB and QMD

Figure 5 (a,b,c,d,e,f,g,h,i,j,k,l): Relationship between forest attributes and plot-level AGB (Mg of dry mass ha^{-1}) (a,c,e,g,i,k) and between forest attributes and dAGB (Mg of dry mass ha^{-1} yr^{-1}) (b,d,f,h,j,l). Forest attributes include forest structure (stem density, N, density of trees bigger than 70 cm in diameter, N70, basal area in m² ha^{-1} BA, and quadratic mean diameter in cm, QMD), composition (Wood density *in g cm^{-3}, WD) and architecture (Lorey's height in m, Hlorey)*. *The regression coefficient r and the p-value associated with the regression are reported as well.*

Regarding the relationship between forest attributes and AGB dynamics, a significant negative correlation was found between the quadratic mean diameter (Fig.5l) and dAGB but no other forest attributes were correlated to AGB dynamics. Probably because of our limited sampling (n=8, 1-ha plots).

When the effect of the different size classes on AGB stocks are examined, it is clear that big trees (>70 cm in Dbh) have a very strong effect on AGB stock at plot-level. In fact, they stock up to 43,2% of the total plot area when they only represent 5% of the stem number.

When we examine the contribution of small, medium and large trees to carbon dynamics, we findd that the contribution of big tress to dAGB is very controversial (Fig. 4). Again, a local-scale variation is observed but, in most plots, the big trees growth is more important than their mortality. In "Nkula crête", the only plots where the mortality of the large class is higher than their growth we find that the large class impacts negatively the overall AGB gain resulting in the lowest dAGB value of all plots. The steadiest class is the medium one, it shows an important mortality only in two plot and its gains are always high. Mortality seems to touch every plot at a different rate in different size classes.

3.3 Architectural traits

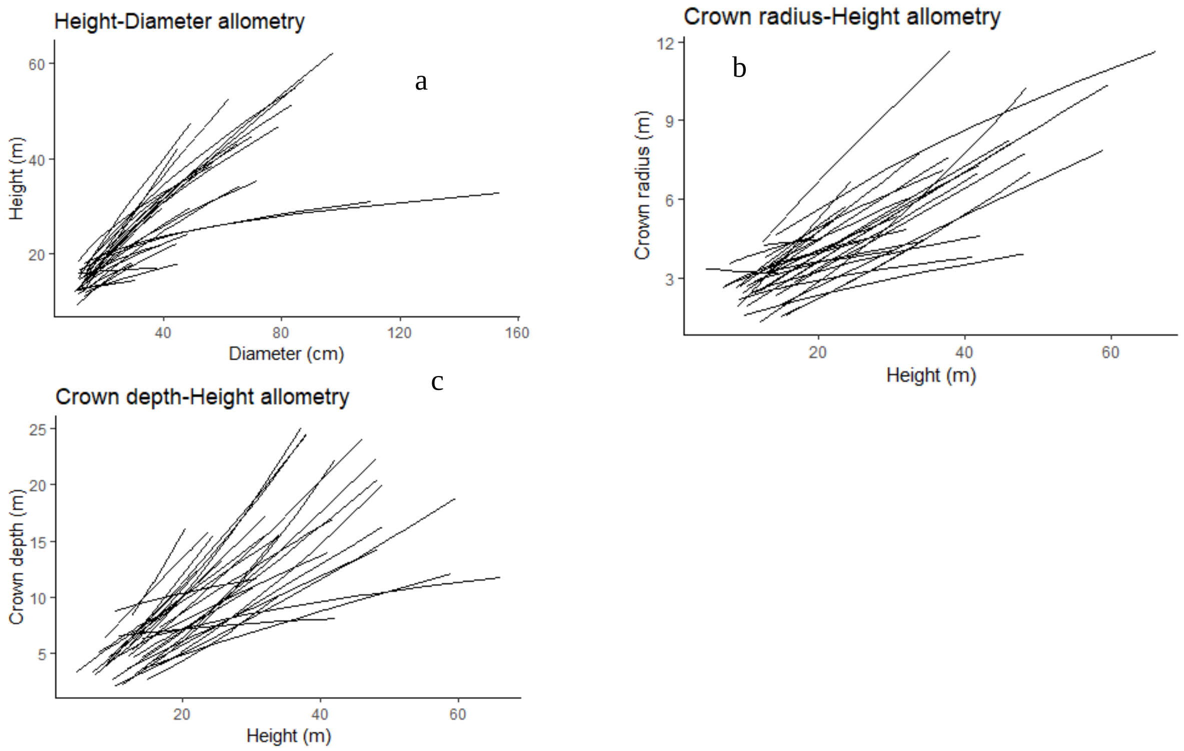


Figure 6. (a,b,c) Species-specific allometric relationships for 30 coexisting tree species. Power law models were fitted to depict: (a) height and diameter allometry, (b) crown radius and height allometry, and (c) crown depth and height allometry. Each species is represented by a different curve.

We then examined species architecture for a set of 30 abundant species in Luki's forest both from the understory and the canopy; following Poorter (2006), species-specific allometries were fitted using the power law model. We observed that all allometric models reached the same overall goodness of fit, the average species-specific r² values obtained are 0.55, 0.44 and 0.56 for the height-diameter, crown radius-height and crown depth – height models respectively. The maximum height varies between 14,65 m (Tapura lujae) and 66,15 m (Terminalia superba) and the height at a 10 cm Dbh ranges from 9,8 m (Garcinia epunctata) to 18,7 m (Pterocarpus tinctorius) among the 30 species. The different models showed a significant difference between the species (ANCOVA with species as factor on all 3 models with p-values < 0.001), indeed, the significant species effect means that both the intercept and slope coefficient significantly vary based on the species.

In terms of crown shape, significant differences were found between the slope coefficients of the species-specific models. At small size (10 cm in Dbh), the smallest calculated crown radius was found for *Celtis mildbraedii* (1,90 m), and the widest for *Monodora angolensis* (6,40 m). Regarding the calculated crown depth (total height – height of the first branch), the vertical length of the crown goes from 2,10 m for *Zanthoxylum gilletii* to 9,60 m for *Strombosia glaucescens*. At maximal size, crown radius ranges from 4,83 m for *Pseudospondias longifolia* to 9,60 m for *Strombosia glaucescens*. And crown depth varies between 11,15 m for *Tapura lujae* to 31,60 m for *Plagiostyles africanum.*

In fig. 6a, different trends are clear, as some curves level off from a certain height, they attained their asymptote, while others keep increasing.

These models were used to derive species-specific architectural traits at both minimal and maximal size (10 cm Dbh and Dmax).

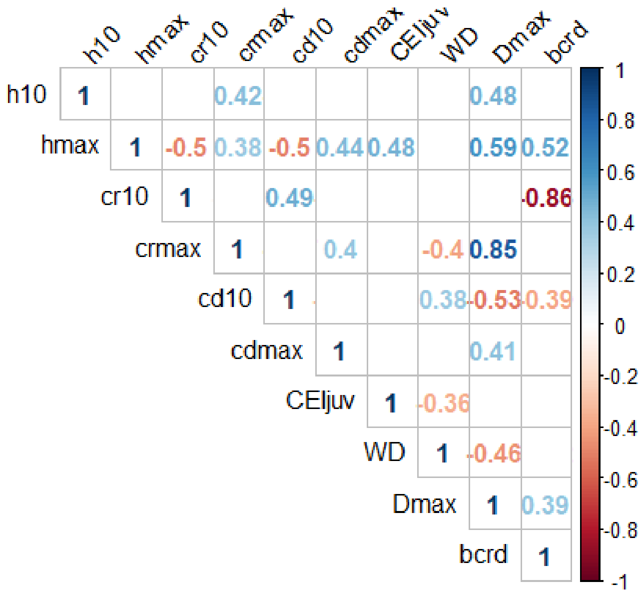
3.4 Species traits and strategies

Figure 7 shows the significant pearsons's r values for the correlation between all the allometry derived traits that were studied. The firsts interesting observations are that Hmax is positively correlated to both the maximal crown radius ($r=0.38$, $p<0.001$) and the maximal crown depth ($r=0.44$, $p = 0.0114$) but negatively correlated to crown radius and crown depth at 10 cm of diameter (both $r = -0.5$, p crown radius<0.001 and p crown depth <0.003). Then Hmax is positively and strongly correlated to the slope coefficient of the crown radius – diameter model ($r=0.52$, $p <0.0001$) which means that when a species has a higher adult stature, the crown radius has a bigger relative increment in crown radius than in diameter. Hmax is also positively correlated to the juvenile light requirement with a $r = 0.48$ and a p value of 0.0151.

Wood density is negatively correlated to the maximum diameter (r = -0.46, p value < 0.0001) and with the maximal crown radius (r = -0.4, pval < 0.0001) but it is positively correlated to crown depth at a diameter of 10cm (r = 0.38, pvalue <0.01).

Crown radius at maximal size is positively correlated with the height at 10 cm Dbh (r = 0.42, p-value < 0.03), with crown depth at maximal size (r = 0.40, p-value < 0.05), and strongly positively correlated to Dmax (r = 0.85, p-value <0.001). But it is negatively correlated to wood density (r = -0.4, p-value < 0.002).

Dmax is positively correlated to both h10 and hmax (r = 0.48 and 0.59, p-value < 0.02 and 0.003 respectively).



	h10	hmax	cr10	crmax	cd10	cdmax	CEIjuv	WD	Dmax	bcrd
h10	1			0.42					0.48	
hmax		1	-0.5	0.38	-0.5	0.44	0.48		0.59	0.52
cr10			1		0.49					-0.86
crmax				1		0.4		-0.4	0.85	
cd10					1			0.38	-0.53	-0.39
cdmax						1			0.41	
CEIjuv							1	-0.36		
WD								1	-0.46	
Dmax									1	0.39
bcrd										1

Figure 7. Bivariate relationships between architectural, functional traits and one scaling coefficient of the crown radius-diameter model of 30 coexisting tree species. Architectural traits were extracted from species specific allometric models at both small (Cr10, Cd10, h10) and maximum sizes (Crmax (m), Cdmax (m), Hmax (m), Dmax (cm)). Functional traits were extracted from literature. Pearson's correlation coefficients are written only if the correlation was significant (p < 0.05) among architectural traits and between architectural traits, functional traits (WD (g cm^{-3}, CEIjuv) and the scaling coefficient (bcrd)

An ordination was used to study the multivariate association between functional and architectural traits (fig. 8a). Axis were defined using only architectural and functional traits, then the allometry models scaling coefficients, the species-specific stem density and AGB were plotted on the graph as supplementary variables in order to see if the strategies were actually represented in the forest and had an impact on density and AGB. The first axis explains 40.8% of the total variability of the dataset and is stretched mainly by all architectural traits at maximum size. CEI juv, which lies just under "cdmax" is also found to explain the variation in axis one confirming the negative correlation with wood density. These trends confirm the results coming from fig. 7. The second axis explains 15.8% of the total variation, and is mainly stretched by crown radius at minimal size. On its opposite side, the scaling coefficient of the height-diameter allometric model are exposed (bH and bHfut), meaning that when a tree has a higher crown radius at its minimal size, it will show a low slope in its height-diameter curve, thus that increment in diameter at high diameters are related to small increase in tree height which is confirmed by the negative Pearson's correlation coefficient found in fig. 7. Most scaling coefficient and species-specific AGB follow the trends of the architectural traits at maximal sizes, but they are opposed to wood density. Stem density seems quite unrelated to architectural traits at maximal sizes and wood density.

Fig. 8b shows how the species spread over these two axis based on their architectural characteristics. Large statured canopy tree species with eventually large crowns and great heights are found on the bottom right side of the panel, they are opposed to understory species with greater crown depth and crown radius at a 10 cm Dbh size and a higher wood density (negative end of axis 1)

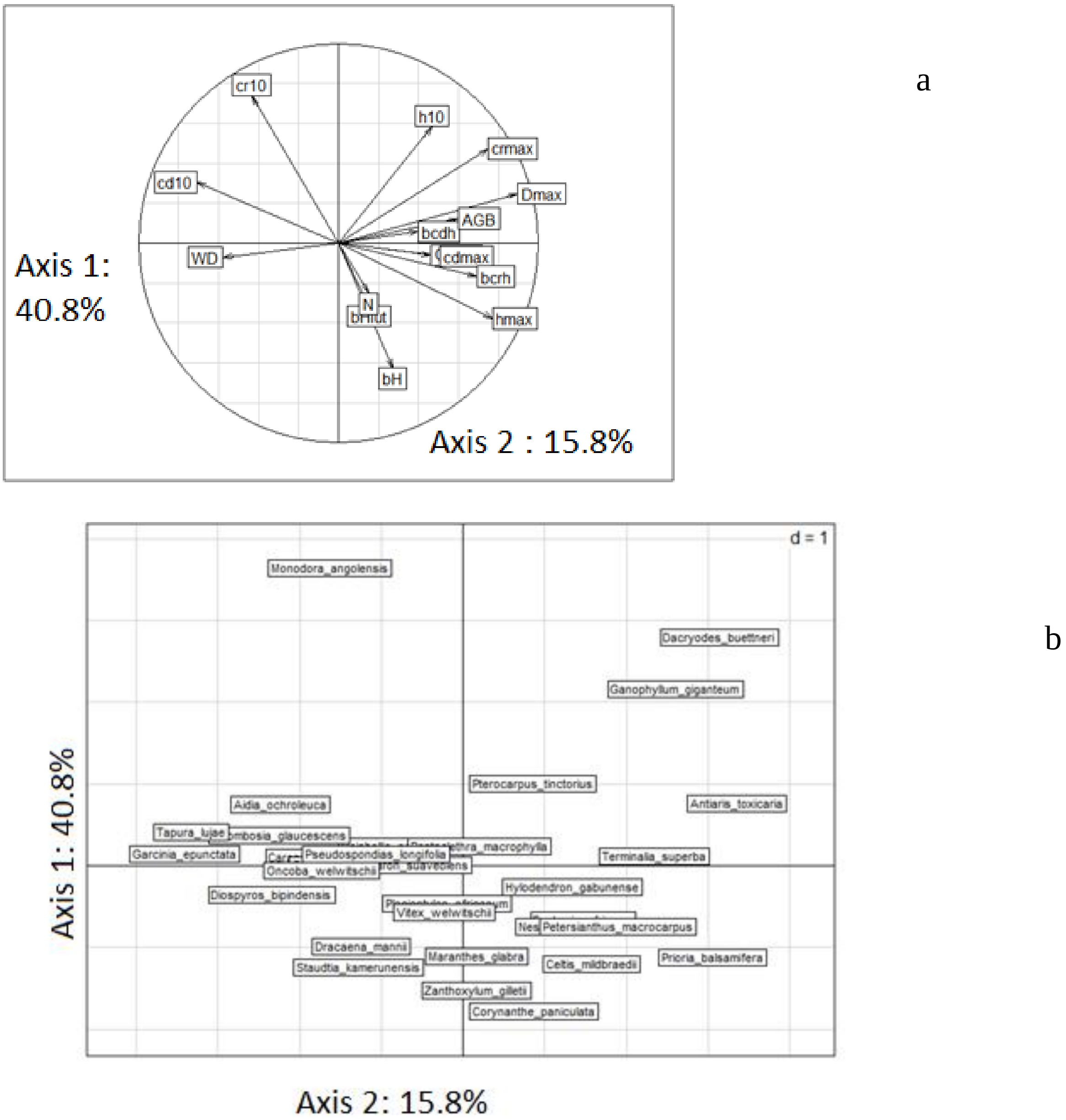


Figure 8 a-b. Ordination of architectural traits at small size (h10, cr10, cd10 in m) and maximum size (hmax, crmax, cdmax in m and Dmx in cm), of functional traits (CEIjuv, WD in g cm^{-3}). Species abundance (N in number of trees ha^{-1}), AGB (in Mg of dry mass ha^{-1}) and all scaling coefficient from allometry models (bH, bHfut both from H-D allometry, bcrh from crown radius- height, bcdh from crown depth-height allometry) were added as supplementary variables in the analysis. Axis 1 explains 41.8% of the total variability. Axis 2 accounts for 15.8% of the total variability.

4. Discussion

4.1 Central African tropical Margin forest compared to core forest of the Congo basin

When Luki's forest attributes are compared to data from other tropical forest at a continental scale, the Luki dataset confirms the African pattern exposed by Lewis (2013). It is distinguished by a low stem density (442 stems ha^{-1}) compared to both Amazonian and Bornean forests which reach 600 stems ha^{-1}, but a high AGB (up to 431 Mg of dry mass in Luki) which equals the Bornean mean AGB and is considerably higher than for the Amazonian forests (Lewis, 2013)

In contrast to Lewis's central Africa mean values, Luki exhibits some significant and insignificant variations. First, in terms of basal area, Luki is under Lewis's reference value (28,2 m² ha^{-1} opposed to 30,3 m² ha^{-1}). The same trend appears with a much smaller difference for the wood mean density weighed by the basal area (0.63 g cm^{-3} for Luki against 0.65 g cm^{-3} for central Africa). In Luki however, the wood mean density is a little higher (0.66 g cm^{-3} against 0.65 g cm^{-3}) and the mean stem density is much higher (442 stems ha^{-1} against 425 stems ha^{-1}). But Luki's forest seems to stock far less AGB than the average Congo basin core forest, with values of 326,1 Mg of dry mass ha^{-1} for the margin forest of Luki against 395,7 Mg of dry mass ha^{-1} in the core forests of central Africa.

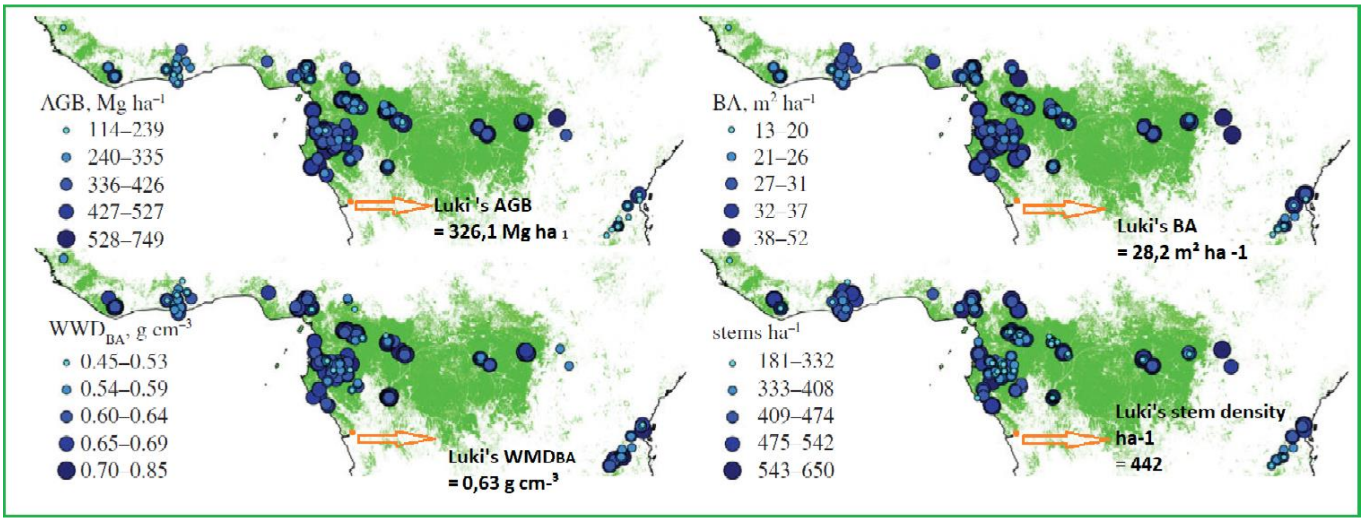


Figure 9. Above ground biomass (AGB), basal area (BA), basal area weighted wood mass density (WMD_{BA}), and stem density for 260 plots in closed-canopy tropical forest. Green represents 'closed forest' categories from the 300 m resolution European Space Agency Globcover (v. 2.3) map for the year 2009. Luki's values are added to Lewis's map (Lewis, 2013).

Variations in forest structural attributes and AGB in Luki, compared to the tropical African averages, may arise from the southernmost location of Luki. Luki's forest is one of the further African tropical forest from the equator and receives very low annual precipitations. The precipitations follow a more seasonal pattern and according to Slik et al. (2010) the rainfall seasonality is negatively correlated to the basal area, the AGB stocks and the stem density. Luki's stem density is higher than the average stem density in the core tropical African forest, and it is probably due to its higher elevation. (Slik, 2010).

These variations in forest structural attributes and AGB between Luki, and the tropical African averages, could also be explained by the treatment the plot had received. Indeed, during the year 1949, the plots had endured a treatment called “uniformisation par le haut” which can be translated by “standardization from the top” and implies that the biggest, healthiest and best shaped trees were kept alive while all others were killed using chemicals. Then, trees would only grow from the seed bank present in the different plots. This treatment aimed to increase the economic value of luki’s forest and almost 60 years later, we can see that the plots have a medium AGB but keep increasing it. If this treatment is the reason of these large-scale variations, then Luki can be expected to develop until it attains the reference values of Lewis (2013).

4.2 Luki’s carbon storage capacity

All plots in Luki showed a sink trend in terms of carbon storage. Indeed, their AGB stock changes are always positive, but they are not all equally increasing their carbon stocks. In accord with Loubota Panzou et al. (2018), the local-scale (plot-level) variability of carbon stocks arises from the plot-level differences observed in terms of structural and architectural attributes. When we studied the relationships between forest attributes and AGB stocks, we found out that, the architectural forest attribute, Lorey’s height, was found to be the best predictor of AGB in Luki, which follows Loubota Panzou (2018)’s findings. Lorey’s height is widely used as the mean tree height of forest stands in remote-sensing studies to derive AGB maps (Saatchi et al., 2011).

According to Lewis (2013), Doetterl (2015) and Fayolle (2016), the denser the forest is the greater its AGB stock is. In fact, basal area was found to be the best structural attribute to describe AGB variations among Luki’s multiple plots, it is confirmed that basal area expresses best the level of above ground space utilization (Jucker et al., 2015). From 2009 to this day, all plots in Luki showed an increase in basal area, they might keep increasing until they reach Lewis (2013)’s average African tropical forest basal area. The elevation of carbon storage would then, be expected to follow the same trend as long as no major mortality event occurs (Rutishauser, 2010). Stem density is not correlated to AGB stocks which corroborates the findings of Lewis (2013).

In contrast to Gourlet-Fleury (2011) and Loubota Panzou (2018), this study did not show significant correlation between AGB and wood density which is categorized as a composition forest attribute. We assume that if more than eight plots had been studied, a significant correlation would emerge because when we observe fig. 5c, a certain trend can be guessed.

The low sampling effort (eight plots) did not allow us to find many correlations between structural, architectural or compositional forest attributes and AGB dynamics. In fact, only the quadratic mean diameter was negatively correlated to the AGB increments which meets Ligot (2018)’s findings about the limited contribution to AGB dynamics of big trees. In Luki, the contribution of big trees to AGB dynamics is quite variable among the different plots, but the negative correlation with the quadratic mean diameter shows the limiting effect to AGB dynamics of trees bigger than 70 cm in diameter. To improve fig. 4, bootstrap confidence intervals could have been reported over the mean estimated biomass gains and losses using many 25 acres plots found in the one ha plots.

In accord with Slik (2013) and Bastin et al. (2015), the density of trees bigger than 70 cm in diameter was proved to be an important AGB stock describer. In fact, they play an important role as we discovered in some plots that they only account for less than 5% of the total stem density but account for more than 40% of the total AGB at plot level, this is, once more, confirmed by the positive correlation with the quadratic mean diameter.

From these results, we understand that a forest increases its AGB stock by supporting large trees, but once these large trees are present in the canopy, they slowly limit their contribution to AGB dynamics, slowing down the community wise dynamic. Once a plot supports large trees that have reached their maximal height growth, the secondary growth (in diameter) will keep increasing the AGB plot stock but with a much lower rate than when big trees were still increasing their heights. At that point the forest has reaches a certain equilibrium, where all the light and space resources are used to slowly increase the carbon stocks until a disturbance occurs and restarts the dynamic process.

In accord with Lewis (2009), Luki's margin forests constitute a carbon sink as they increase their carbon stocks each year, but no great mortality has been observed which could overturn the trend as Rutishauser (2010) describes it.

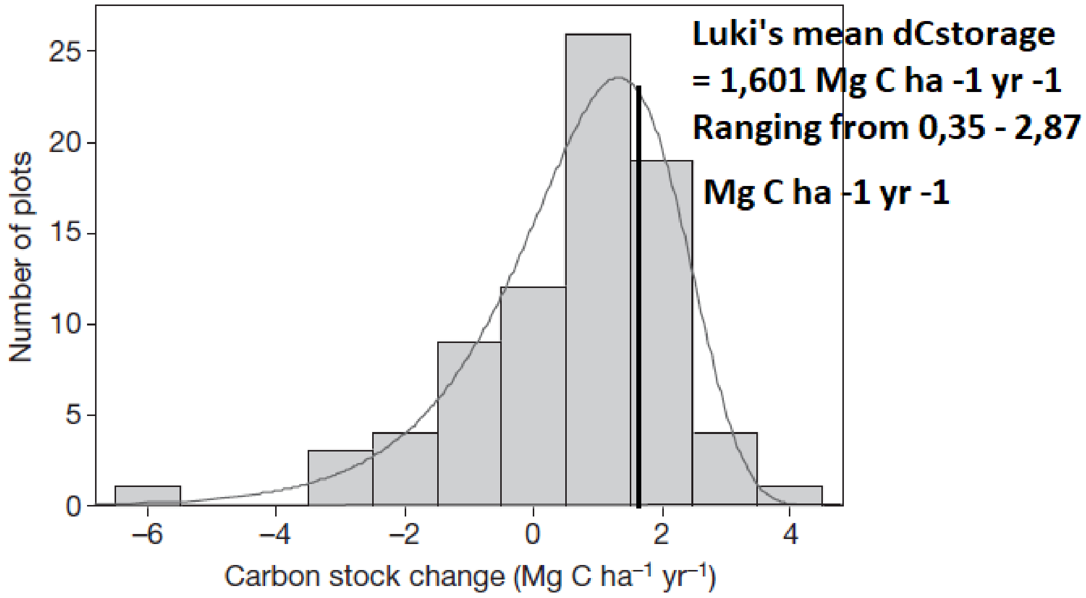


Figure 10. Histogram of annualized change in carbon stocks from 79 long-term monitoring plots across 10 countries in Africa. Results presented are weighted by sampling effort (plot size and census-interval length), and fitted three-parameters Weibull distribution. Luki's value was added to Lewis (2009)'s graph.

In the end, a general consensus was reached between this study and all the followings ((Lewis, 2013; Lewis, 2009; Loubota Panzou, 2018; Ligot, 2018; Fayolle, 2016) saying that structural and architectural forest attributes are good predictors of the local scale variations in AGB and that African tropical forests constitute carbon sinks, as they increase every year the AGB they support.

4.3 Species-specific allometry

In this study, strong variations of tree architecture among coexisting tree species were confirmed. The same trend was reported in the tropical forests of Liberia according to Poorter, (2003), Cameroon (Fayolle, 2016), Bolivia (Poorter, 2006), Malaysia (King, 1996; Sterck, 2001) and most recently with the tropical forests of Republic of Congo (Loubota Pansou et al., n.d.). The curves in fig. 6, represent the path of a species through its ontogeny. The different ways the species tend to establish from the understory to the canopy. The use of common allometric coefficient is inherent to the estimation of ecosystem properties in tropical rainforests and relies on the convergence of allometry (Chave, 2005), if the community does not show any convergence among its constituting species including the type of forest in the model would only slightly improve the estimation's accuracy (Fayolle, 2013).

The height-diameter curves (Fig. 6a) allow us to see and distinguish tree species from the understory and tree species that will reach the canopy, as some curves level off at low height and others keep increasing. Thomas (1996) explains that the understory species stop their vertical growth to engage their reproduction. They reproduce much earlier in their ontogenetic trajectories, but are thus expelled of the race to the canopy as reproduction has a cost and requires a slowdown in height growth rate. The higher curves do not seem to reach an asymptote but it is probably explained by the small size of the sampling for the canopy species, because, according to Poorter (2006) canopy species should start to expand their crown once they have reached the canopy (>20 m), then they need to invest strongly in their diameter growth and in their internal resistance to be able to resist to the increasing static loads submitted to greater wind stress (Sterck et al., 2005). For the understory species, no asymptotic trend are expected in accord with Iida (2011).

The relations between height and crown size (crown radius – height and crown depth-height) allow us to see that multiple species have different strategies in regard of their crown development. The limited lateral crown expansion protects the tree from unsustainable mechanical stress in more winded environment (Sterck et al., 1998). While the reasons of different crown depth development are still unclear (Sterck et al., 2007).

4.4 Ecological strategies identified from architectural traits variation

In contrast with Poorter (2006), a stronger correlation was found between architectural traits and Hmax (the adult stature) of the trees while no correlations were found between architectural traits and CEIjuv which characterizes the light requirements at early stages. This is probably explained by the fact hypothesized by Poorter (2006) that, the vertical light gradient is large and predictable while the horizontal light gradient is relatively small and unpredictable

In this study we observed that Hmax is negatively correlated to both crown radius and crown depth at small sizes, but positively correlated to crown radius and crown depth at maximal sizes. This means that large statured species tend to have a smaller and shallower crown in their early ontogenetic stages, but that, once they reach the canopy, they begin to develop larger and deeper crowns. The same conclusions were drawn for Liberian , Bornean and Malaysian forests (Kohyama, 2003; Poorter, 2003; Iida, 2011). This can be explained by the need of large statured trees to attain large sizes before they commit to their reproduction (Poorter, 2003). They produce slender stems and their wood tends to be less dense to favorize their vertical growth, defeat the competition and reach the canopy as fast as possible to start reproducing.

Small statured species have a lower light requirement during their early stages (positive correlation between Hmax and CEIjuv), because they develop larger and deeper crowns as early as possible in their ontogeny to maximize light capture in accord with (King, 1996; Poorter, 2003; Sterck, 2001). In accord with Iida, Takashi S Kohyama, et al. (2011) small statured species tend to have a denser wood, probably to be able to withstand debris and achieve reproduction at small sizes (Clark, 1991; Thomas, 1996; Davies et al., 1999; Sterck, 2001; Wright, 2005).

Unfortunately, these results do not allow us to confirm one hypothesis regarding the vertical light gradient partitioning among species, in fact, there seems to be a clear distinction between understory species and canopy species strategies as advanced by King (1996), but it could still be explained by a tradeoff between the will to reach the canopy as fast as possible and the will to reproduce as quickly as possible which was hypothesized by Kohyama et al. (2009) and supported by (Iida, 2011). The hypothesis of a tradeoff between early and annual reproduction supported by Thomas, (1996) and Davies et al. (1998) seems less adequate to explain the variations found among species but it cannot be totally excluded.

CEI juv is positively correlated to Hmax, which suggests that large statured species are mostly light demanding whilst understory species tolerate more shadow. The same trends were found in both Asian and American tropical forests (respectively Iida, (2011) and Poorter (2006). At first, scientists hypothesized that shade tolerant species should develop a crown as shallow as possible to avoid self-shading (Horn, 1971), but the opposite trend was found in Bolivia (Poorter, 2006) and in this study. The multi-layer crown of shade tolerant species is thought to develop because they retain their branches as long as they increase the carbon gain of the tree. Plus, they might have a lower photosynthetic light compensation point which means that they need less light than light demanding species to match their cellular respiration rate (Poorter, 2006), allowing them to keep more branches for a longer period. Light demanding species need to have a higher vertical growth rate to be able to stay above competitors, they do not maximize the light capture at their early ontogenetic stages as they need to maximize height expansion to compete with other species. To do so, they allocate the major part of their biomass to the stem rather than to the branches, and they have a low wood density (Poorter et al., 1999).

Dmax is positively correlated to all architectural traits at maximal sizes, with H10, and especially with crown radius max, which supports Sterck (2005) by proving that large statured trees, once they reach the canopy and before they start developing a very wide crown, need to invest firmly in their mechanical strength. Large statured trees which will develop larger diameters, are correlated to a greater height at 10 cm in diameter, according to the findings in Malaysia, Liberia and Bolivia (Iida, 2011; Poorter, 2003; Poorter, 2006).

The scaling coefficient corresponding to the slope of the crown radius – diameter allometry (bcrd) is strongly negatively correlated to Cr 10 wich means that the smaller the crown radius at a 10 cm diameter is, the bigger the relative increment in crown radius compared to the increase in diameter will be.

Wood density, in contrast to Iida (2011) and Kohyama et al (2003), is negatively correlated to crown radius at maximal size, fortunately a large wood density does not mean a higher mechanical strength according to Anten et al., (2010). It is also negatively correlated to Dmax and positively correlated to crown depth at small sizes. This may support the fact announced by Poorter et al. (1999) that understory species tend to have a higher wood density.

Carapa procera, *Strombosia glaucescens* and *Maranthes glabra* were common to both our study and the study in Liberia (Poorter, 2003) and showed different trends between the two sites. *Carapa procera* showed the exact same trend between in Liberia and Luki (Hmax = 24 m in both Liberia and Luki), *Strombosia glaucescens* seemed to be smaller in Luki than in Liberia and *Maranthes glabra* is taller in Luki. This might be explained by a smaller canopy but a more developed understory in Liberia compared to Luki.

The species contribution to AGB is dictated by all the maximal architectural traits (fig.8), this supports the fact that big trees have a high contribution to AGB and it is in accord with Fauset et al. (2015). Species with a large potential of reaching great sizes contribute disproportionally to biomass stocks in a forest, indeed they have the chance to reach the canopy and to develop huge crowns supporting a greater leaf area than small statured species. With their better access to light, and the maximization of their photosynthetic apparatus, they increase their potential for high rates of carbon fixation and biomass production. In the contrary, small sized trees species were not found to contribute disproportionally to the stem density. Wood density does not seem to influence stem density according to the findings of Ter Steege (2013) and Fauset (2015).

Regarding the different ecological strategies, the light requirement (regeneration guild according to Hawthorne, 1995) was related to the architectural traits and the continuum theoretical pattern was confirmed, according to Swaine (1988) and Chave (2005). The left end of axis 1 gathers small statured species with larger and deeper crowns at small sizes, which have a denser wood. While on the opposite side, large statured species with wide and deep crowns at maximal sizes are found. The pioneer species were expected to differ from the two other light requirement groups but only three species were identified as pioneers and it could explain why they overlap on both shade bearers and non-pioneer light demanding species.

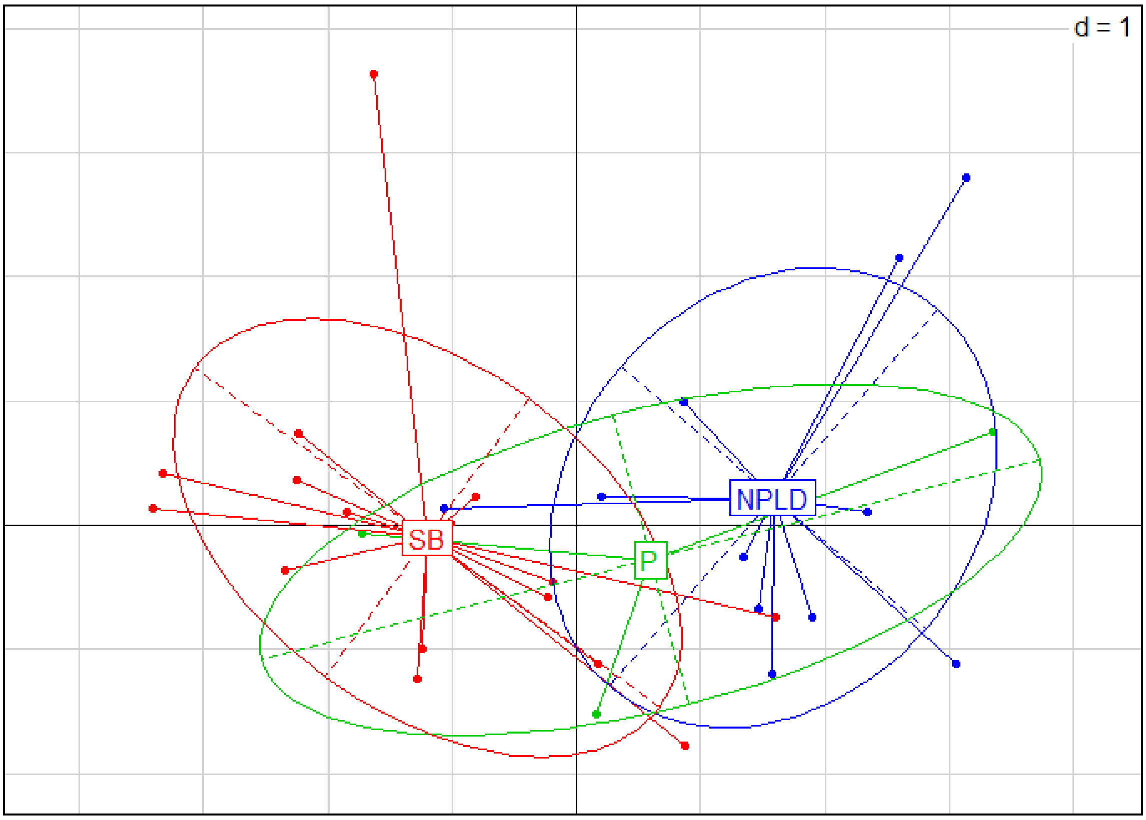


Figure 11. Ordination of architectural traits at small size (h10, cr10, cd10 in m) and maximum size (hmax, crmax, cdmax in m and Dmx in cm), of functional traits (CEIjuv, WD in g cm^{-3}). Showing the species repartition depending on their light requirements.

When we assemble our results from the two main parts of this study (AGB stocks/dynamics and ecological strategies), we understand that the the AGB stock size at the equilibrium state where AGB stock is maximized and AGB dynamic is slow because of the complete use of light and space resources by large trees mentioned earlier in the discussion depends on the community's constituting species, and especially on their architectural characteristics. In Luki, the southernmost location does not prevent large trees to establish, and the canopy to be as high as in other core African tropical forests. Thus, we believe that Luki's forest will remain as carbon sinks until they reach the equilibrium state after which mortality events will occur and the forest dynamic will be restarted.

5. Conclusion

This article provides new information regarding the forests located in the margins of the Congo basin. They show different trends that could be explained by a recent disturbance in terms of local-scale structure and architecture forest attributes compared to the core tropical African forests but remain in the same overall pattern. Luki’s forest constitutes a carbon sink, as its AGB keeps increasing. We found strong correlation between forest structure (Basal area, density of big trees, quadratic mean diameter) and architecture attributes (Lorey’s height) and AGB stocks but no correlation with the composition attributes (Wood density). The complex canopy was found to shelter different ecological strategies best explained by the adult stature of the tree as species showed divergent allometries. Understory species are thought to have a denser wood and to develop wide and deep crowns all along their ontogenetic trajectories. While canopy species begin their growth by maximizing vertical extension and thus minimizing the crown development costs (smaller and shallower crown) until they reach the canopy where they will start maximizing light capture by developing a larger and deeper crown to ensure reproduction success. These strategies were found to impact the hyperdominance regarding AGB stock but not the stem density.

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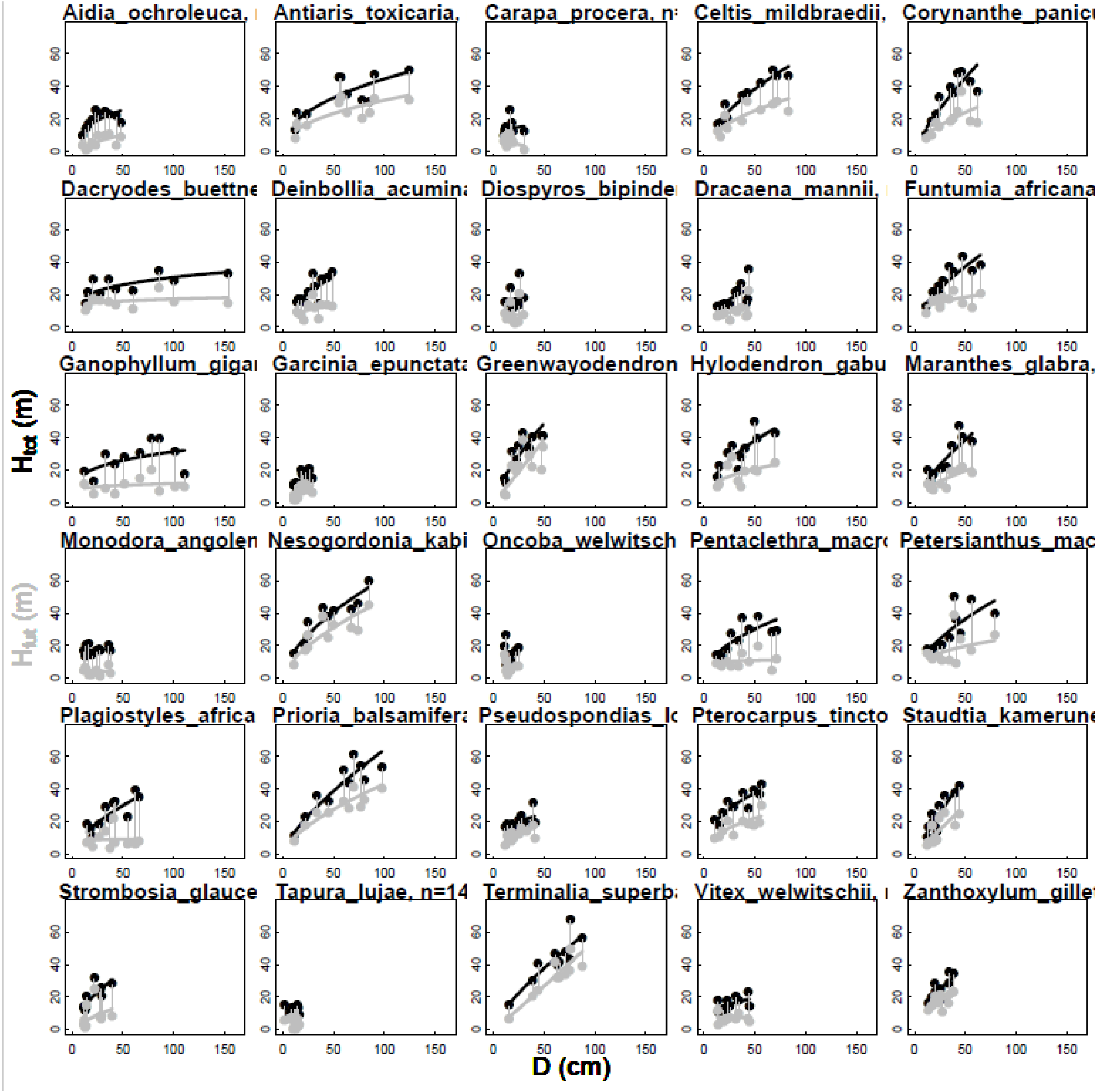
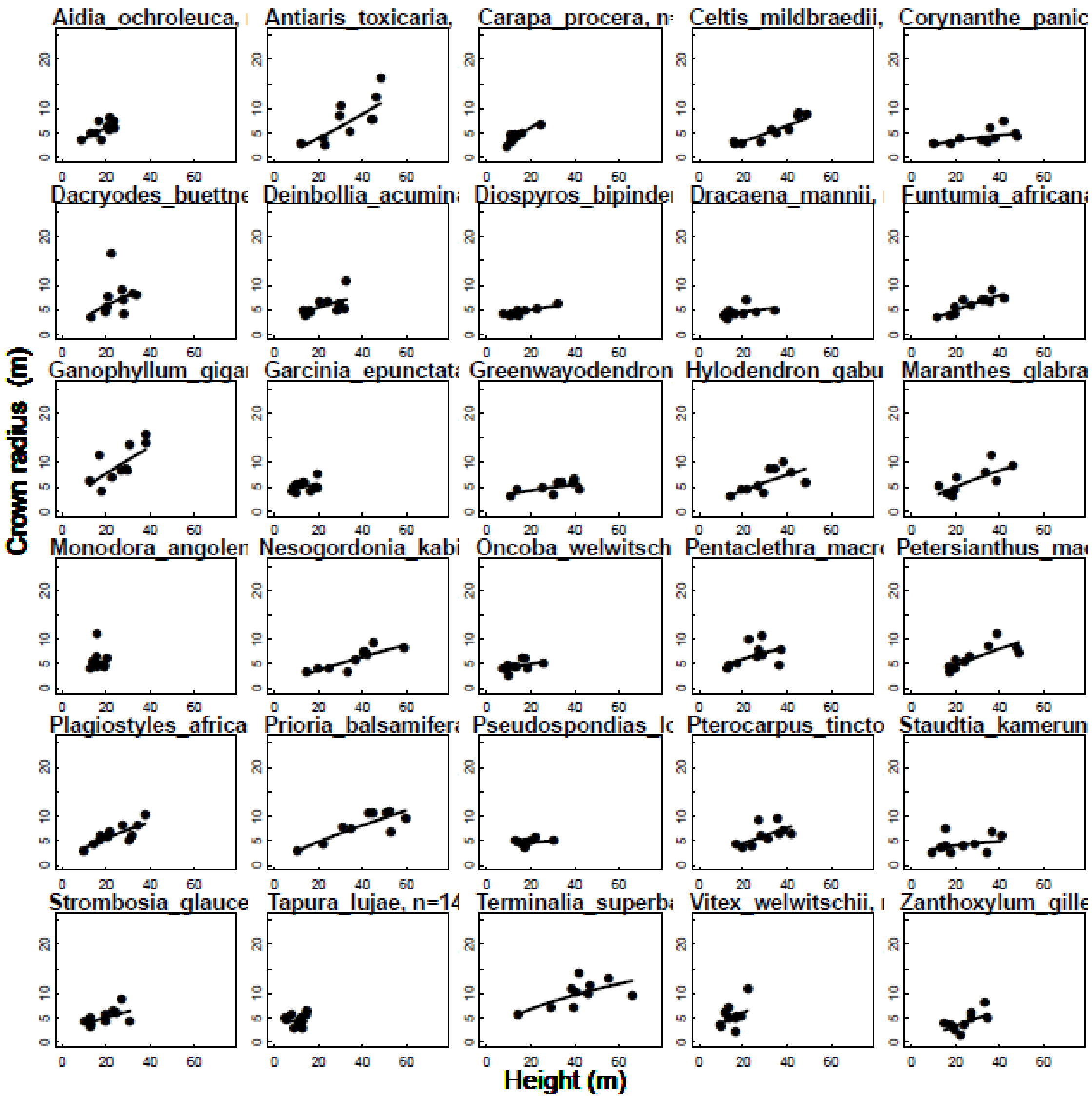
Appendix

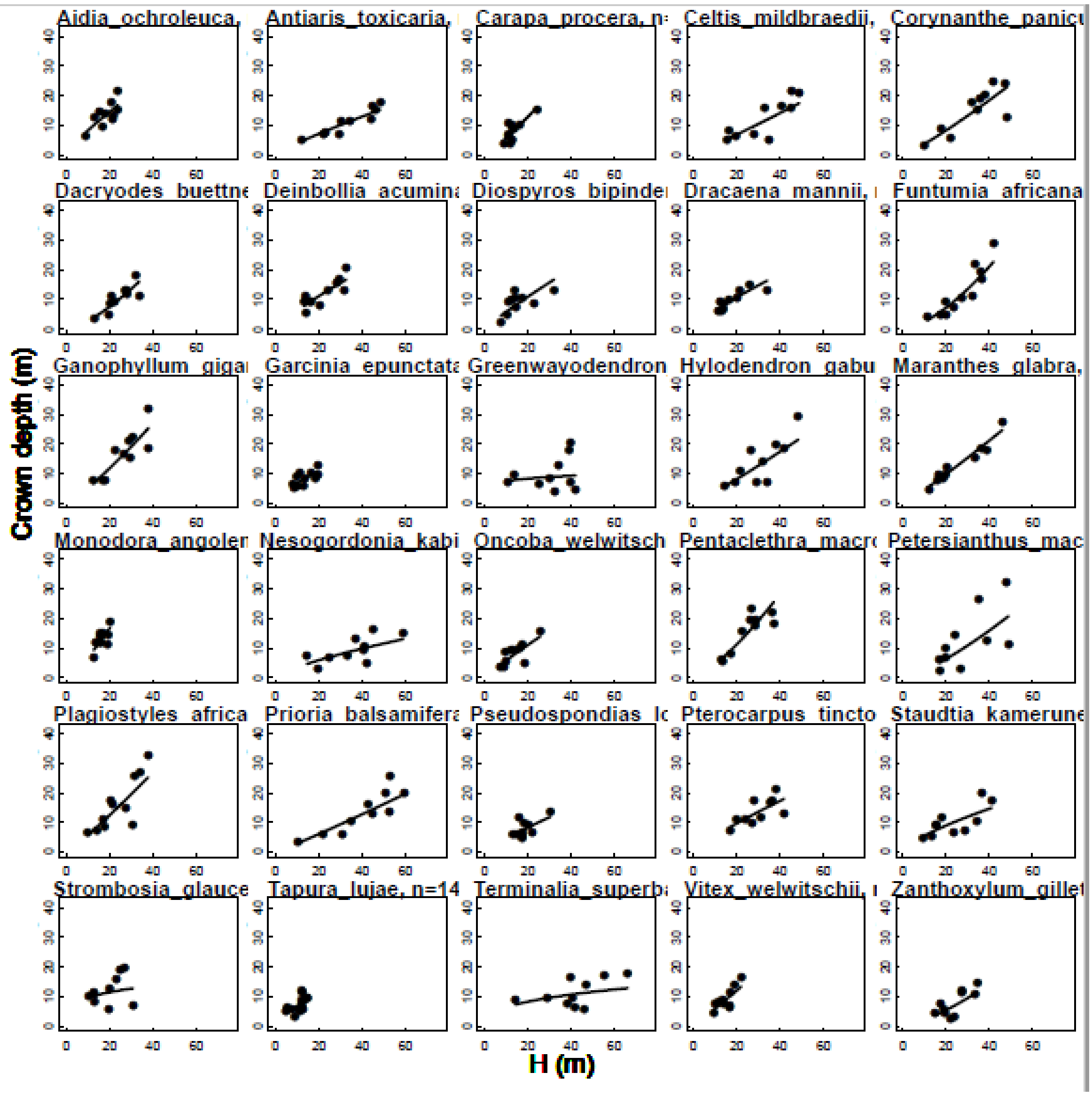
Appendix 1: Species specific H-D allometry and Hfut-D allometry



Apendix 2: Species specific Crown radius- Height allometry



Appendix 3: Species specific Crown depth -Height allometry



Appendix 4 : Selected species and their characteristics

	Species	Family	Reg Guild	Nbr of trees	Dmin (cm)	Dmax (cm)	H10 (m)	Hmax (m)	Cr10 (m)	CrMax (m)	Cd10 (m)	CdMax (m)	CEIjuv	WD (gcm-3)	AGB Mg ha-1	N
1	Aidia ochroleuca	Rubiaceae	SB	10	10,10	48,00	13,10	23,90	3,80	7,11	8,20	20,50	1,19	0,82	7,29	141
2	Antiaris toxicaria	Moraceae	P	10	12,60	124,30	16,30	48,40	2,00	15,19	3,90	17,10	1,32	0,39	5,88	25
3	Carapa procera	Meliaceae	SB	11	10,40	30,50	13,20	24,35	3,70	5,57	5,70	14,10	1,41	0,60	0,32	39
4	Celtis mildbraedii	Ulmaceae	NPLD	10	13,80	83,50	14,30	48,95	1,90	8,13	3,30	20,50	1,66	0,59	7,53	112
5	Corynanthe paniculata	Rubiaceae	SB	10	11,80	61,80	12,60	48,15	2,30	6,30	3,70	23,95	2,26	0,67	8,77	176
6	Dacryodes buettneri	Burseraceae	NPLD	10	13,00	153,80	17,80	33,90	3,90	15,57	2,70	17,15	1,58	0,51	7,96	42
7	Deinbollia acuminata	Sapindaceae	SB	11	14,00	48,80	12,20	32,65	3,50	9,84	6,20	19,80	1,30	0,66	2,11	35
8	Diospyros bipindensis	Ebenaceae	SB	10	11,10	29,70	12,10	32,15	3,90	5,24	5,80	12,10	1,59	0,83	3,17	61
9	Dracaena mannii	Liliaceae	SB	10	13,30	44,30	10,20	34,20	3,30	5,99	6,10	14,20	2,40	0,66	1,01	12
10	Funtumia africana	Apocynaceae	NPLD	11	11,40	65,20	12,80	42,05	3,30	8,03	2,40	28,00	1,71	0,42	0,30	7
11	Ganophyllum giganteum	Sapindaceae	NPLD	10	11,70	110,50	16,90	38,05	4,00	14,75	5,10	30,95	2,69	0,70	17,85	60
12	Garcinia epunctata	Clusiaceae	SB	12	10,90	29,30	9,80	19,60	4,32	6,42	6,90	11,75	1,22	0,84	0,55	34
13	Greenwayodendron suaveolens	Annonaceae	SB	10	11,00	49,10	14,50	42,15	3,36	5,66	7,50	19,60	1,35	0,66	3,92	118
14	Hylodendron gabunense	Caesalpinniaceae	NPLD	10	13,50	70,00	15,80	48,40	2,90	9,04	3,80	28,55	1,93	0,79	15,13	158
15	Maranthes glabra	Chrysobalanaceae	SB	10	12,90	57,10	11,80	46,10	2,60	10,36	4,50	26,25	1,30	0,88	3,39	51
16	Monodora angolensis	Annonaceae	SB	10	11,20	37,90	16,70	20,35	6,40	10,17	6,90	18,25	1,70	0,66	0,70	17
17	Nesogordonia kabingaensis	Sterculiaceae	SB	10	11,10	84,80	15,50	58,85	2,50	8,29	3,60	15,45	1,97	0,68	6,37	68
18	Oncoba welwitschii	Flacourtiaceae	P	10	10,90	24,80	13,30	25,85	3,70	5,25	5,90	14,65	2,12	0,66	0,30	23
19	Pentaclethra macrophylla	Mimosaceae	NPLD	10	12,60	71,50	13,30	37,15	3,80	9,69	4,50	22,55	2,22	0,84	3,89	25
20	Petersianthus macrocarpus	Lecythidaceae	NPLD	10	12,70	79,10	14,00	48,95	2,80	9,88	2,50	31,00	1,55	0,68	2,92	35
21	Plagiostyles africanum	Euphorbiaceae	SB	11	14,50	65,90	10,80	37,80	3,30	9,38	5,70	31,60	1,06	0,74	3,74	27
22	Prioria balsamifera	Caesalpinniaceae	NPLD	10	11,60	97,70	11,90	59,60	2,80	10,10	2,90	24,45	2,65	0,41	9,21	99
23	Pseudospondias longifolia	Anacardiaceae	NPLD	10	11,60	40,90	14,91	30,40	3,80	4,83	4,50	12,95	2,09	0,66	0,63	14
24	Pterocarpus tinctorius	Fabaceae	NPLD	10	10,60	56,50	18,70	41,90	3,30	8,53	5,40	20,25	2,08	0,60	2,63	37
25	Staudtia kamerunensis	Myristicaceae	SB	10	12,40	44,30	10,50	41,15	3,20	6,31	5,50	19,20	1,44	0,80	2,93	68
26	Strombosia glaucescens	Olacaceae	SB	10	11,30	39,50	12,80	30,85	3,30	7,78	9,60	18,75	1,39	0,83	0,47	17
27	Tapura lujae	Dichapetalaceae	SB	14	1,50	16,20	11,40	14,65	4,30	5,35	6,80	11,15	1,19	0,66	0,11	20
28	Terminalia superba	Combretaceae	NPLD	10	15,60	87,80	11,30	66,15	3,90	13,01	6,40	16,85	3,48	0,46	4,60	16
29	Vitex welwitschii	Lamiaceae	SB	10	13,70	45,00	11,70	22,25	2,10	9,73	5,90	15,70	2,04	0,45	0,50	14
30	Zanthoxylum gilletii	Rutaceae	P	10	13,60	38,70	14,20	34,55	1,95	6,95	2,10	13,55	2,04	0,69	1,19	26

Appendix 5 : CEI observation : (Moravie, 1999)

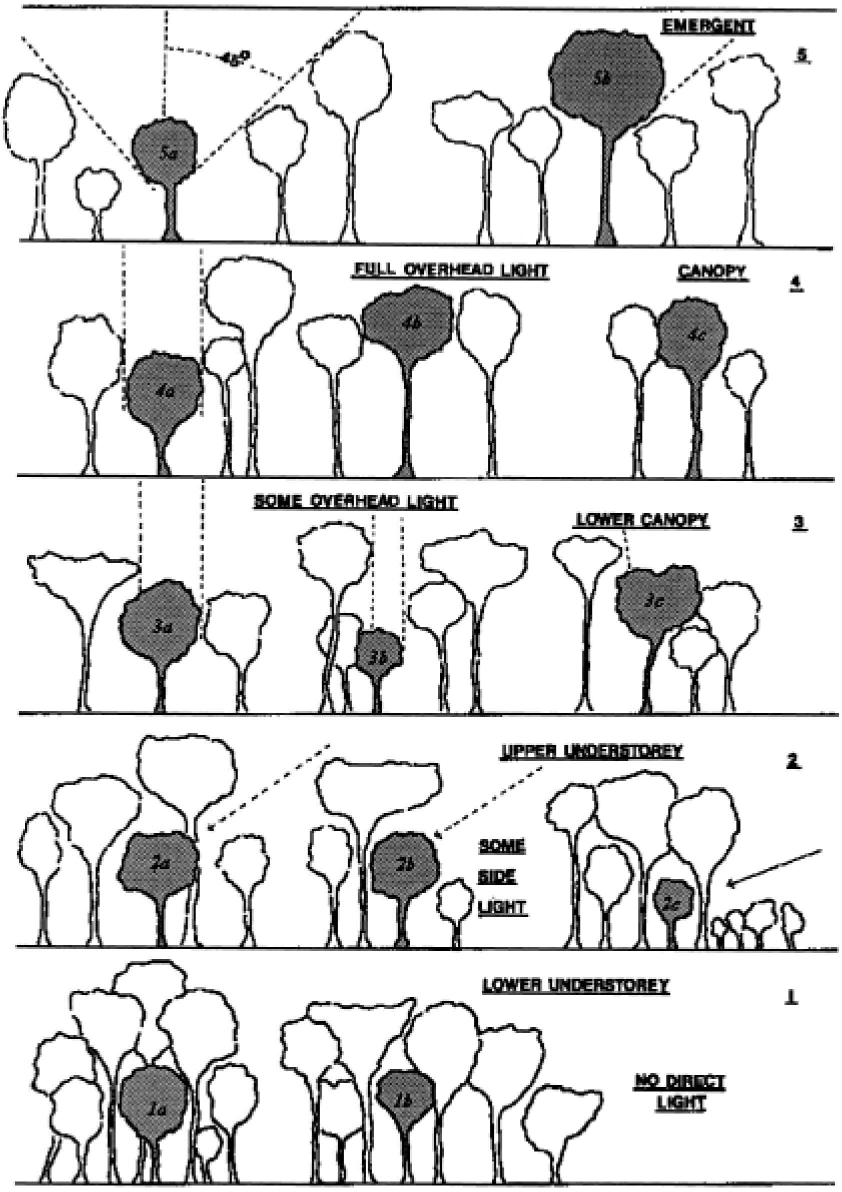
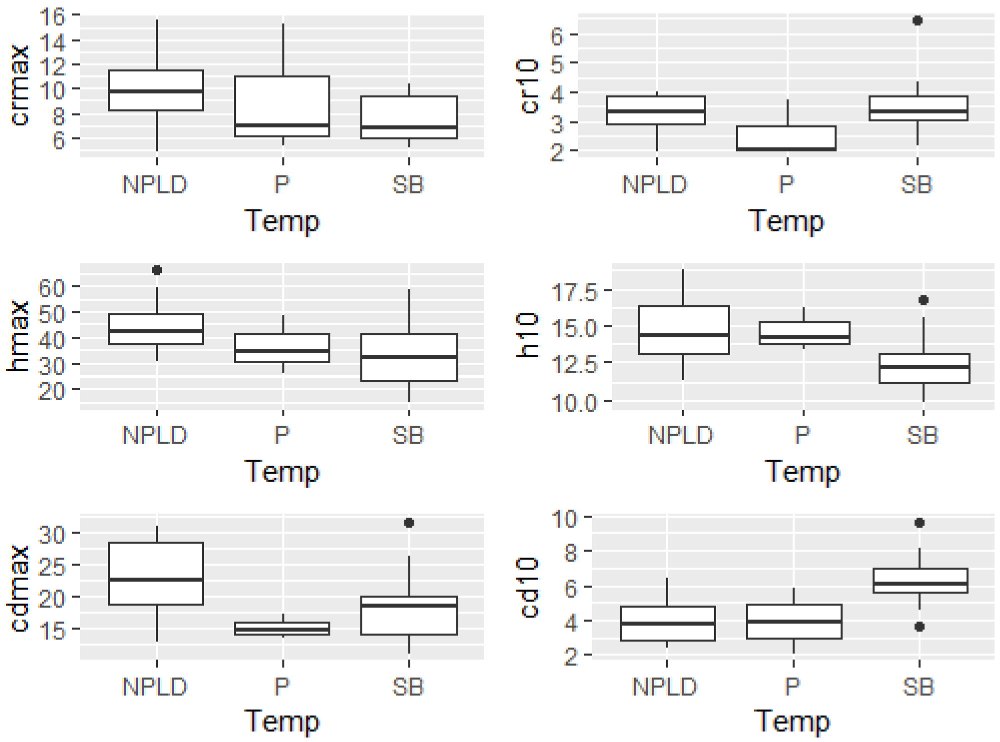
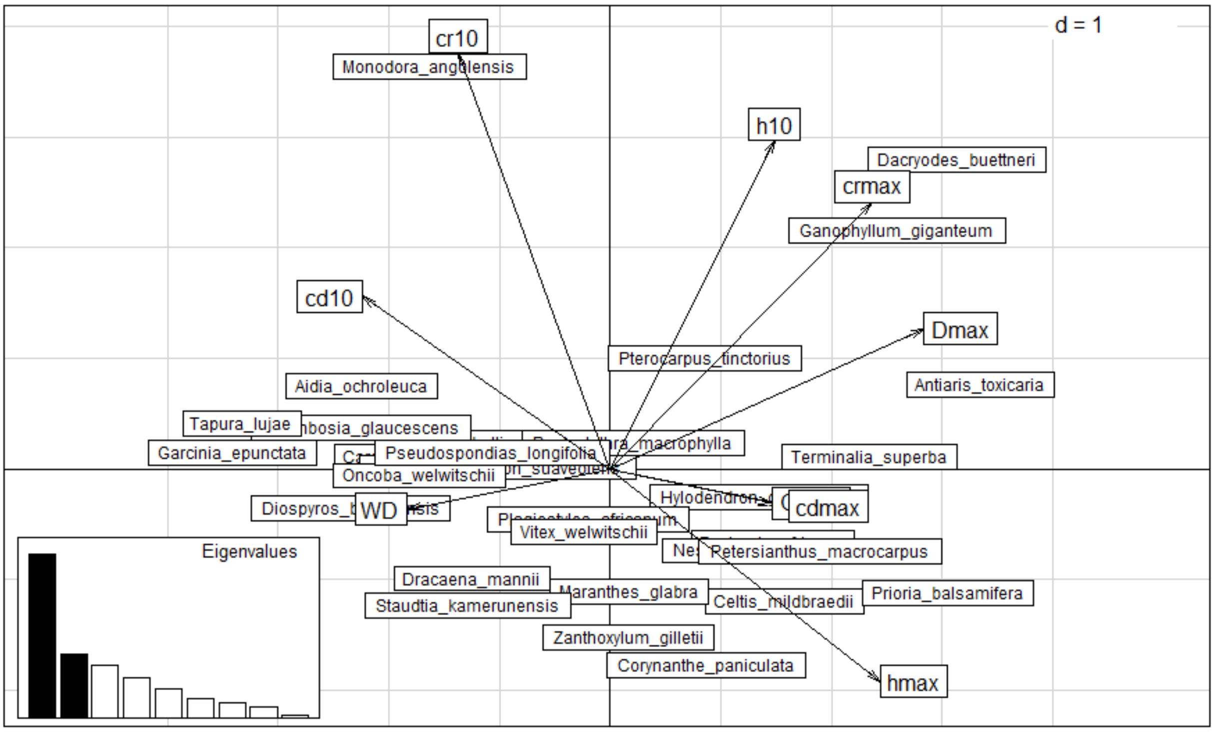


Fig. 3. Assessment of Dawkins code (from Synnott, 1979). The original classification of Dawkins (Dawkins, 1958), based on the tree crown position in canopy and on the proportion of crown exposed to light, distinguished five classes of trees: daw1, lower understorey trees, entirely shaded vertically and laterally by other crowns; daw2, upper understorey trees, entirely shaded vertically but with some direct side light; daw3, lower canopy trees, partly exposed and partly shaded vertically by other crowns; daw4, upper canopy trees, exposed in entire vertical plan but with other crowns laterally; daw5, emergent, entirely exposed, free from competition for light, at least within the 90 inverted cone in which the crown lies. Synnott (1979) using Dawkins code with five modalities to explain tree growth featured however 13 different situations. We used this sub-classification in 13 categories as it corresponds to difference in local light conditions we actually observed.

Appendix 6 : Boxplots of architectural traits against light regeneration guild.



Appendix 7 : Biplot from trait ordination showing both traits and species.



Appendix 8 : Example of the picture taken to evaluate the % of greenness of a tree community.