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Carbon storage and functional diversity of tropical rainforest in the Congo Basin

by

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Summary

Rainforests in the Congo Basin cover an area of over 300 million ha (FAO 2011), store approximately 57 Pg of carbon (FAO 2011) and represent a significant carbon sink (0.34 Pg C yr^{-1}; Lewis *et al*. 2009). As such, African tropical forests provide an important feedback to the global carbon cycle (Lewis *et al*. 2006 & 2009). In order to understand and quantify tropical forest carbon uptake and losses, accurate carbon stock reference data are needed (Huntingford *et al*. 2013). The accuracy of these reference data is essential for the implementation of climate mitigation policies to reduce emissions resulting from deforestation and forest degradation (UN-REDD, United Nations collaborative programme on reducing emissions from deforestation and forest degradation in developing countries, www.un-redd.org) (Gibbs *et al*. 2007; Somorin *et al*. 2012). However, central African tropical forests have been underrepresented in studies regarding both carbon storage and biodiversity. This dissertation aims to improving the accuracy of regional and basin-wide estimation of carbon storage in tropical forest of the Congo basin and increase our functional understanding of the forest community, providing useful information regarding ecosystem dynamics. In particular, we investigate the relationships between biodiversity, landscape composition and configuration and carbon storage in oldgrowth and intervened tropical forest (20 one-hectare inventory plots) in the Yangambi Biosphere reserve, as well as two other locations (Yoko and Yambela) in the Democratic Republic of the Congo. Both above and belowground carbon storage and its local variability are studied to improve local estimates for this region and the understanding of drivers behind this variability. Subsequently, we explore functional similarities between species to identify how or if biodiversity contributes to ecosystem functioning and stability.

Our research has shown consistently lower above ground biomass values for old-growth forest in Yangambi and surroundings (162 ± 20 Mg C ha^{-1}) compared to the outer regions of the Congo Basin (243-259 Mg C ha^{-1}, Lewis *et al*. 2009) due to a difference in tree height-diameter allometry. Consequently, the best available tree height–diameter relationships derived for Central Africa (Feldpausch *et al*. 2012; Banin *et al*. 2012) do not render accurate canopy height estimates for our study area. In addition, quantifying soil organic carbon (SOC) in old-growth forest in Yangambi, we found an equivalent of 68% of the above ground carbon stored within the first meter of soil. Yet, considerably lower SOC values (23%) were found at the Yoko site, although similar forest composition is present. We suggest that this large variability is related to differences in nutrient limitation, which drives differences in aboveground versus belowground carbon allocation. These findings have important consequences for the assessment of total carbon stored in tropical forests leading to different conclusions regarding the carbon storage capacity of the entire system. The large and unaccounted variability in SOC stocks introduces additional uncertainty in the response of tropical forest systems to climate change and its contribution to the current terrestrial carbon budget.

Predicting the future of the overall carbon budget of tropical forests is currently constrained by, amongst others, a proper understanding of how different species are limited by various resources (Prentice *et al*. 2007). Both light requirement and adult stature of tropical tree species are two traits, which capture a large portion of the variation in other functional traits (Loehle 2000; Turner 2001; Poorter *et al*. 2006). A classification using these two traits are also expected to form distinct groups within the leaf economics spectrum (Wright *et al*.

2004), contrasting inexpensive short-lived leaves vs. costly long-lived leaves. Our work however provides new insights to the current paradigm regarding these classifications. The site-specific classification of trees made in this study, irrespective of species identification, shows that these classifications do not show distinctly different trait values, mainly of leaf traits reflecting resource acquisition and stress tolerance.

Investigating functional similarity between species, we show that rare species are predominantly associated with extreme (leaf) traits. Although these results are well established in literature (Belyea & Lancaster 1999; Cornwell & Ackerly 2009; Kraft *et al.* 2008; Maire *et al.* 2012), our findings show that rare species show both unique and redundant functional traits, both of high importance for long-term stability of ecosystem functioning. In contrast, more common species mainly support redundant traits. Our study provides accurate descriptions of (rare) species composition and functional community structure related to the local environmental conditions of African tropical forests, which will allow us to better understand current and future species distributions and biodiversity in the African tropical forest.

In conclusion, the implications of our research range from basic research assessing the impact on the global carbon cycle over policy making through the REDD+ mechanisms (Somorin *et al*. 2012) to ecosystem conservation where functional understanding of the forest ecosystem using a trait based approach could allow us to better predict its resilience for land-use change and climate change (Pereira *et al*. 2010).

Samenvatting

Regenwouden in het Congobekken strekken zich uit over een enorm gebied van meer dan 300 miljoen ha (FAO 2011). Er zit een zeer grote hoeveelheid koolstof (57 Pg; FAO 2011) opgeslagen in die bossen en jaarlijks neemt dit toe met ~0,34 Pg C (Lewis *et al.* 2009). Om die reden zijn ze belangrijk voor de globale koolstofcyclus (Lewis *et al.* 2006 & 2009). Voor een beter inzicht in processen van koolstofopname en –afname zijn accurate referentiegegevens nodig van de hoeveelheid koolstof opgeslagen in het systeem (Huntingford *et al.* 2013). Bovendien dient het beleid betreffende klimaat mitigatie (bv. het UN-REDD programma; 'United Nations collaborative programme on reducing emissions from deforestation and forest degradation in developing countries'; www.un-redd.org) (Gibbs *et al.* 2007; Somorin *et al.* 2012) te steunen op nauwkeurige referentiegegevens van koolstofopslag. Echter, het Centraal Afrikaans tropisch regenwoud is ondervertegenwoordigd in studies met betrekking tot koolstofopslag en functionele diversiteit. Dit proefschrift is daarom gericht op het verbeteren van de nauwkeurigheid van schattingen van koolstofopslag in de tropische bossen in het Congobekken, en op het uitbreiden van onze kennis over het functioneren van de bosgemeenschap, met als doel nuttige informatie bij te dragen met betrekking op ecosysteemdynamiek. In het bijzonder onderzoeken we de relaties tussen biodiversiteit, landschapspatronen en verdeling en opslag van koolstof in pioniersbossen en volwassen tropisch bossen (20 percelen van 1 hectare) in het Yangambi reservaat, evenals twee andere locaties (Yoko en Yambela) in de Democratische Republiek Congo. Zowel boven- en ondergrondse koolstofopslag worden bestudeerd om de lokale schattingen voor deze regio te verbeteren en voor een beter begrip van de drijfveren achter deze variabiliteit. Vervolgens onderzoeken we de functionele gelijkenissen tussen boomsoorten om te bepalen hoe en of de biodiversiteit bijdraagt aan de werking en de stabiliteit van het ecosysteem.

In dit onderzoek wordt aangetoond dat de bovengrondse koolstofopslag systematisch lager is in de bossen van Yangambi en omgeving (162 ± 20 Mg C ha^{-1}) in vergelijking met gebieden aan de oost- en westkant van het Congobekken (243-259 Mg C ha^{-1}, Lewis *et al.* 2009) doordat de bomen doorgaans lager zijn. Hoogte-diameter relaties beschikbaar voor centraal Afrika in de literatuur (Feldpausch *et al.* 2012; Banin *et al.* 2012) laten niet toe accurate schattingen te maken van boomhoogte voor ons studiegebied. Vervolgens tonen we aan dat een equivalent van 68% van de bovengrondse koolstof opgeslagen is in de eerste meter van de bodem. In Yoko is dit veel lager, namelijk 23%, hoewel de floristische samenstelling dezelfde is. We suggereren dat deze grote variabiliteit te maken heeft met verschillen in beperkingen in bodemnutriënten, die vervolgens verschillen in de allocatie naar bovengrondse versus ondergrondse koolstof aandrijft. Deze bevindingen hebben belangrijke gevolgen voor de kwantificatie van de totale koolstof opgeslagen in tropische wouden, en kunnen leiden tot verschillende conclusies over de opslagcapaciteit van het gehele systeem. De grote variabiliteit in koolstofopslag in de bodem brengt extra onzekerheid met zich mee in onderzoek met betrekking tot de reactie van tropische bossen bij klimaatverandering en hun bijdrage aan de huidige terrestrische koolstof opslag.

Goede voorspellingen van veranderingen in de koolstof cyclus en opslag zijn gehinderd door, onder meer, onvoldoende kennis over de beperkende factoren voor boomgroei (Prentice *et al.* 2007). Zowel soort-specifieke lichtbehoefte en de hoogte van volwassen bomen van tropische boomsoorten zijn twee kenmerken die een groot deel van de variatie in andere functionele eigenschappen omvatten (Loehle 2000; Turner 2001; Poorter *et al*. 2006). Een classificatie van boomsoorten volgens deze twee eigenschappen zou verschillende groepen moeten opleveren met contrasterende bladeigenschappen (Wright *et al*. 2004). In dit werk zijn er echter geen duidelijke verschillen gevonden in bladeigenschappen voor wat betreft nutriënten opname en tolerantie aan stress.

Ons onderzoek naar de functionele gelijkenissen tussen boomsoorten heeft aangetoond dat zeldzame soorten voornamelijk worden geassocieerd met extreme (blad) kenmerken. Hoewel dit resultaat gekend is in de wetenschappelijke literatuur (Belyea & Lancaster 1999; Cornwell & Ackerly 2009; Kraft *et al*. 2008; Maire *et al*. 2012), kunnen we aantonen dat zeldzame soorten zowel unieke en overtollige functionele kenmerken hebben binnen hun gemeenschap, beide van groot belang voor de stabiliteit van het functioneren van het ecosysteem op lange termijn. Veel voorkomende soorten tonen echter voornamelijk redundante kenmerken. Onze studie biedt een nauwkeurige beschrijving van soortensamenstelling (inclusief zeldzame soorten) en de structuur van de functionele gemeenschap in relatie met de plaatselijke milieuomstandigheden van de Afrikaanse tropische bossen. Dit laat ons toe om de huidige en toekomstige soortensamenstelling en de biodiversiteit in het Afrikaans tropisch bos beter te begrijpen.

Concluderend, de implicaties van ons onderzoek reiken van fundamenteel onderzoek met betrekking tot de beoordeling van de impact op de mondiale koolstofcyclus, tot beleidsvorming aan de hand van het REDD+ mechanisme (Somorin *et al*. 2012). Ook wordt er aangetoond dat functioneel begrip van het bos ecosysteem essentieel is en ons toelaten om betere voorspellingen te maken van zijn veerkracht voor veranderingen in landgebruik en klimaatverandering (Pereira *et al*. 2010).

Résumé

Les forêts tropicales du bassin du Congo couvrent ±300 millions ha (FAO 2011), stockent jusqu'à 57 Pg de carbone (FAO 2011) et représentent un puits de carbone important (0,34 Pg C an^{-1} ; Lewis *et al.* 2009). En tant que telles, les forêts tropicales africaines fournissent un retour important de carbone pour le cycle global du carbone (Lewis *et al.* 2006 & 2009). Afin de comprendre et de quantifier les flux d’absorption et de perte de carbone en forêt tropicale, des données de référence précises sur les stocks de carbone sont nécessaires (Huntingford *et al.* 2013). L'exactitude de ces données de référence est essentiel pour la mise en œuvre des politiques d'atténuation du changement climatique de manière à réduire les émissions résultant du déboisement et de la dégradation des forêts (UN-REDD, ‘United Nations collaborative programme on reducing emissions from deforestation and forest degradation in developing countries’, www.un-redd.org) (Gibbs *et al.* 2007; Somorin *et al*. 2012). Cependant, les forêts tropicales d'Afrique centrale ont été le plus souvent sous-représentés dans les études concernant le stockage du carbone et la biodiversité. Cette thèse vise à améliorer la précision de l'estimation régionale et à l'échelle du bassin du stockage du carbone dans les forêts tropicales et d'accroître notre compréhension fonctionnelle de la communauté forestière, en fournissant des informations utiles sur la dynamique et la démographie des écosystèmes. En particulier, nous étudions les relations entre biodiversité, composition et configuration du paysage, et stockage de carbone dans les forêts tropicales anciennes et perturbées (20 parcelles d'un hectare) dans la réserve de biosphère de Yangambi, ainsi que sur deux autres sites (Yoko et Yambela) dans la République Démocratique du Congo. Tant le stockage du carbone aérien et souterrain, et sa variabilité locale sont étudiés pour améliorer les estimations locales dans la région et pour comprendre les facteurs à l'origine de cette variabilité. Par la suite, nous explorons les similitudes fonctionnelles entre les espèces afin de déterminer comment ou si la biodiversité contribue au fonctionnement des écosystèmes et à leur stabilité.

Nos recherches ont montré des valeurs de biomasse aérienne systématiquement plus faibles pour les forêts anciennes de Yangambi et de ses environs (162 ± 20 Mg C ha^{-1}) par rapport aux régions externes du bassin du Congo (243-259 Mg C ha^{-1} ; Lewis *et al.* 2009) en raison d'une différence d’allométrie hauteur-diamètre des arbres. Par conséquent, les meilleures relations hauteur-diamètre des arbres disponibles pour l'Afrique centrale (Feldpausch *et al.* 2012; Banin *et al.* 2012) ne permettent pas de représenter avec précision la hauteur de la canopée dans notre zone d'étude. En outre, en quantifiant le carbone organique du sol (SOC) des forêts anciennes de Yangambi, nous avons trouvé, dans le premier mètre de sol, un équivalent carbone de 68% du stock de carbone aérien. Néanmoins, des valeurs de SOC considérablement inférieurs (23%) ont été mesurées sur le site de Yoko, alors que des forêts de composition similaire y sont présentes. Nous suggérons que cette grande variabilité est liée à des différences de limitations en nutriments, ce qui entraîne des différences d’allocations du carbone dans les parties aériennes ou souterraines des arbres. Ces résultats ont des conséquences importantes sur l'évaluation de la quantité totale de carbone stockée dans les forêts tropicales, et mène à des conclusions différentes concernant la capacité de stockage de carbone de l'ensemble du système. Cette variabilité importante et inconnue des stocks de SOC introduit une incertitude supplémentaire dans la réponse des systèmes forestiers tropicaux au changement climatique et de leur contribution au budget actuel du carbone terrestre.

Les prédictions sur l'avenir du budget global de carbone des forêts tropicales sont actuellement limitée par, entre autres, une bonne compréhension de la façon dont les différentes espèces sont limitées par diverses ressources (Prentice *et al.* 2007). Tant les demandes en lumière et la stature des adultes des espèces d'arbres tropicaux sont des traits qui captent une grande partie de la variation d'autres traits fonctionnels (Loehle 2000; Turner 2001; Poorter *et al.* 2006). On s'attends aussi à ce qu'une classification utilisant ces deux traits forme des groupes distincts au sein du spectre économique de la feuille (Wright *et al.* 2004), opposant d'une part les feuilles éphémères et peu coûteuses et d'autre part les feuilles couteuses à longue durée de vie. Notre travail fournit cependant de nouvelles perspectives orthogonales au paradigme actuel concernant ces classifications. La classification spécifique aux sites des arbres réalisée dans cette étude, laquelle ne tient pas compte de l'identification des espèces, montre que cette classification ne montre pas de différences distinctes dans les valeurs des traits, principalement des traits foliaires reflétant l'acquisition de ressources et la tolérance au stress.

En étudiant les similitudes fonctionnelles entre espèces, nous montrons que les espèces rares sont surtout associées à des traits (de feuilles) extrêmes. Bien que ces résultats soit bien établis dans la littérature (Belyea et Lancaster 1999; Cornwell & Ackerly 2009; Kraft *et al.* 2008; Maire *et al.* 2012), nos résultats montrent que les espèces rares montrent à la fois des traits fonctionnels uniques et redondant, ce qui est d'une grande importance pour la stabilité à long terme du fonctionnement des écosystèmes. En revanche, les espèces les plus communes ne présentent principalement que des traits redondants. Notre étude fournit des descriptions précises de la composition d'espèces (rares) et de la structure des communautés fonctionnelles liée aux conditions environnementales locales des forêts tropicales africaines ce qui nous permettra de mieux comprendre la distribution actuelle et future des espèces et de la biodiversité dans la forêt tropicale africaine.

En conclusion, les implications de notre recherche vont de la recherche de base permettant l'évaluation de l'impact du cycle global du carbone à l'élaboration de politiques à travers les mécanismes REDD+ (Somorin *et al.* 2012), en passant par la conservation d'écosystèmes où la compréhension fonctionnelle de l'écosystème forestier en utilisant une approche basée sur les traits pourrait nous permettent de mieux prévoir sa résilience au changement d'utilisation des sols et les changements climatiques (Pereira *et al.* 2010).

Abbreviations

AfriTRON	African Tropical Rainforest Observation Network
AGB	Aboveground biomass
AGC	Aboveground carbon
AIC	Akaike information criterion
BA	Basal area
BELSPO	Belgian Federal Science Policy Office (Federaal Wetenschapsbeleid)
BS	Base saturation
CEC	Cation exchange capacity
COBIMFO	COngo Basin Integrated Monitoring for FOrest carbon mitigation and biodiversity
CoP	Conference of Parties
CPOM	Coarse particulate organic matter
DBH	Diameter at breast height
DCA	Detrended correspondence analysis
DRC	Democratic Republic of the Congo
ED2	Ecosystem Demography model
FAO	Food and Agricultural Organization of the United Nations
FD	Functional distinctiveness
FTS	Functional trait space
INEAC	Institut National pour l'Étude Agronomique du Congo
INERA	Institut National pour l’Etude et la Recherche Agronomiques
IPCC	Intergovernmental Panel on Climate Change
LAI	Leaf area index
LCC	Leaf carbon content
LDMC	Leaf dry matter content
LiDAR	Light Detection and Ranging
LNC	Leaf nitrogen content
LPC	Leaf phosphorus content
LES	Leaf economic spectrum
MAB	Man and Biosphere
NPLD	Non-pioneer light demanding
NPP	Net primary productivity
PCA	Principal component analysis
RAINFOR	Amazon Forest Inventory Network
REPCO	Régie des plantations de la colonie
RMCA	Royal Museum for Central Africa
RSE	Standard residual error
RWMax	Maximal ray width

RWMin	Minimum ray width
SD	Stem density
SLA	Specific leaf area
SOC	Soil organic carbon
SOTER	Soil and terrain
UPGMA	Unweighted pair group method using arithmetic averages
UN-REDD	United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in developing countries
UNESCO	United Nations Educational, Scientific and Cultural Organization
VD	Vessel density
VDm	Vessel diameter
VPDB	Vienna Pee Dee Belemnite
VSMOW2	Vienna Standard Mean Ocean Water
WD	Wood density
WES	Wood economics spectrum
WUE	Water use efficiency
YGB	Yangambi

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1

General introduction

1.1 Project rationale

Tropical forests represent a crucial carbon pool as they cover 7-10% of the global land area (Lewis *et al*. 2009) and, reportedly, store 40-50% of all terrestrial carbon (Houghton 2005; Lewis *et al*. 2006; IPCC 2007). These forests are an important component of the global carbon balance, with changes currently induced due to climate change (Pan *et al*. 2011) and anthropogenic disturbances (Harris *et al*. 2012). Increases in carbon storage over recent decades have been recorded in tropical forest indicating that they act as a carbon sink (Phillips *et al*. 1998; Baker *et al*. 2004a; Clark 2004; Lewis *et al*. 2009; Pan *et al*. 2011), specifically after major droughts (Phillips *et al*. 2009), with an increase of 1.3 Pg C yr^{-1} across all tropical forests (Lewis *et al*. 2009), although a more recent study showed a decline of this sink effect in the Amazon (Brienen *et al*. 2015). Accordingly, the relation between increasing carbon stock and the fertilization effect from increasing atmospheric CO_2 concentrations is still highly debated (Keenan *et al*. 2013; Battipaglia *et al*. 2015; van der Sleen *et al*. 2015). Conversely, anthropogenic activity in tropical forest has a large influence on this carbon balance, with tropical land-use change, mainly related to deforestation and forest degradation, introducing an important source of emissions (Harris *et al*. 2012).

Maintaining the positive side of this balance is of crucial importance, and the starting point of carbon mitigation policies. A major initiative is the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries program (UN-REDD, http://www.un-redd.org). This initiative started as RED (Reducing Emissions from Deforestation; 2000, CoP6, The Hague), but has been expanded to REDD including deforestation (2005, CoP11, Montréal), and later on REDD+ (2010, CoP16, Cancun) including afforestation, poverty alleviation, biodiversity conservation and improved forest governance. The UN-REDD concept is, at its core, a proposal to create a financial value for carbon stored in forest and offer incentives for developing countries to reduce national deforestation rates and associated carbon emissions below a baseline (Gibbs *et al*. 2007; UN-REDD). This framework could simultaneously mitigate climate change, conserve biodiversity and protect other ecosystem services (Gibbs *et al*. 2007). Climate change mitigation through the sequestration of carbon and the protection of biodiversity have both been high priorities in the scientific, governmental, and civil society agendas of the last few years, but they have rarely been considered in conjunction (Díaz *et al*. 2009). Biodiversity is generally described as a potential “co-benefit” of forest carbon sequestration, but components of forest biodiversity may overlap to different degrees, trade off with, or be largely independent from those that intervene in carbon sequestration potential (Díaz *et al*. 2009). Additionally, diversity can also carry an important role in maintaining ecosystem functioning, stability and services (Hector & Hooper 2002).

These two main aspects – carbon and biodiversity – form the base of this dissertation. The tropical forests of the Congo Basin have namely been underexplored compared to the Amazon and, to a lesser extent, Southeast Asia, with both research on carbon dynamics and biodiversity lagging behind (Verbeeck *et al*. 2011). Intensive study on these two topics in the Congo Basin is of major importance to allow for a better and more informed implementation of climate mitigation and conservation policies. My main focus was to address different aspects of carbon storage and tree species diversity. First, I set-up baseline reference data on above and belowground carbon storage in pristine and intervened dense tropical forests in the Yangambi Biosphere reserve, and addressed local and regional variability. Secondly, I investigate the diversity aspect through assessment of functional diversity of tree species within the forest based on a detailed data-driven functional trait approach with a strong focus on resource acquisition and carbon allocation traits.

1.2 The carbon aspect

Aboveground carbon storage in tropical forests

In order to understand and quantify tropical forest carbon uptake and losses, accurate carbon stock reference data are needed (Huntingford *et al*. 2013), as well as estimates of carbon fluxes resulting from both natural processes and land-use changes (IPCC 2007; Gourlet-Fleury *et al*. 2011), at different spatial scales. Studies concerning estimation of tropical forest carbon storage and its spatial variability are based on remote-sensing techniques (Saatchi *et al*. 2011; Baccini *et al*. 2012) and spatially extensive ground-based inventory networks (Phillips *et al*. 1998; Lewis *et al*. 2013), both of which are associated with uncertainties. Carbon stock estimations from inventory data rely on the accuracy of allometric models (e.g. Brown *et al*. 1989; Chave *et al*. 2005) incorporating diameter at breast height (DBH), tree height and wood density in its estimation. However, inventory data most generally only consists of DBH measurements and taxonomic information for the trees, from which tree height and wood density are inferred. Error propagation and uncertainties associated with ground-based carbon stock estimation are therefore essential (Chave *et al*. 2004; Clark & Kellner 2012; Molto et al. 2013), especially when this data is used (directly or as a validation tool) to estimate regional scale carbon stocks (through spatial interpolation, spatial modelling or satellite signal treatment). The uncertainty associated with these data is thus high and there are still large gaps in our knowledge with respect to the actual amount of carbon stored in tropical forests and the stability of this pool (Huntingford *et al*. 2013). Additionally, the spatial variation of biomass in these forests remains poorly understood (Malhi *et al*. 2006), with little agreement regarding ecological drivers (Baraloto *et al*. 2011).

An even spatial coverage of tropical forest is important for biomass studies to quantify spatial variability and its drivers. Large spatial variability in aboveground biomass (AGB) with broad environmental gradients has been reported, with climate, soil and forest structure as major explanatory factors (Laurance *et al*. 1999; de Castilho *et al*. 2006; Baraloto *et al*. 2011). Several studies show a similar relationship with rainfall and the dry season length, with the highest biomass found in moist climates with short dry or no dry season (Chave *et al*. 2004; Malhi *et al*. 2006; Quesada *et al*. 2009). However, no clear general relationship has been established between forest carbon stocks and soil properties, and the available results are contradictory (Laurance *et al*. 1999; Clark & Clark 2000; Gourlet-Fleury *et al*. 2011, Quesada *et al*. 2012). For example, some studies report a positive effect of soil fertility on AGB suggesting a limiting effect of nutrient availability on biomass (Laurance *et al*. 1999; DeWalt & Chave 2004), while others report a negative relationship with higher biomass on infertile soils related to lower turnover rates in these forests (Quesada *et al*. 2009). Strong relationships have also – not surprisingly – been found between AGB and forest structure and composition, namely with basal area, stem density and diameter distributions (Chave *et al*. 2004; DeWalt & Chave 2004; Rutishauser *et al*. 2010; Slik *et al*. 2010). Less consistency is found for the relationship between AGB and wood density. For example, Baker *et al*. (2004b) related the spatial patterns in AGB across the Amazon Basin with variation in wood density, although the study by Stegen *et al*. (2009) did not support this relationship.

A strong relationship between AGB and forest structure is not unexpected, as the predictors, generally stem diameter, wood density and tree height, used to calculate aboveground biomass through allometric relationships are also associated to forest structure (Brown *et al*. 1989; Chave *et al*. 2005). Insight in spatial variation in allometry (i.e. the tree height and biomass supported for a given tree diameter) can therefore improve the knowledge on spatial variability in aboveground biomass. Some variability is already incorporated in pan-tropical allometric relationships, by distinguishing relationships according to a precipitation-based forest classification (dry, moist, or wet) (Brown *et al*. 1989; Chave *et al*. 2005). One major issue with allometric relationships for biomass estimation is related to architectural differences in tropical trees and the importance of including tree height. Numerous studies indicate that tree height-diameter allometry depends on both physiological and environmental factors (Falster & Westoby 2005; Ryan *et al*. 2006; Niklas 2007; Kempes *et al*. 2011). These include climatic conditions and altitude (Aiba & Kitayama 1999; Nogueira *et al*. 2008a; Lines *et al*. 2012), local edaphic conditions (Aiba & Kitayama 1999; Kempes *et al*. 2011), competition for resources (Henry & Aarssen 1999; Harja *et al*. 2012; Antin *et al*. 2013) and evolutionary, architectural and hydraulic constraints (King 1990a; Ryan & Yoder 1997; Koch *et al*. 2004; Falster & Westoby 2005). Accordingly, significant variation in tropical tree allometry has been reported across plots, regions and continents (Feldpausch *et al*. 2011; Banin *et al*. 2012). Accounting for differences in height-diameter allometry and including tree height into biomass estimation is thus important to assess biomass variability and has been shown to reduce bias of the estimate (Chave *et al*. 2004; Feldpausch *et al*. 2012). However, tree height is often not included because measuring tree height accurately is difficult in closed-canopy forests (Hunter *et al*. 2013; Larjavaara & Muller-Landau 2013; Chave 2014), and very time-consuming. Recently, Feldpausch *et al*. (2011) addressed this problem by developing a set of region-specific height-diameter relationships to account for regional variability and reduce bias when studies do not have height measurements available (see also Banin *et al*. 2012). Nevertheless, the analysis of large-scale variation in tree allometry has only recently begun (Moles *et al*. 2009; Feldpausch *et al*. 2011; Banin *et al*. 2012; Lines *et al*. 2012). The quality of allometric relationships, both for tree height and biomass estimation, represents one of the most important limitations in assessing AGB stocks in tropical forests (Chave *et al*. 2004; Baccini & Asner 2013), and further exploration regarding the variation of tree allometries is needed.

Belowground carbon storage in tropical forests

Belowground storage of carbon represents a large pool with an estimated 36-60% of tropical forest carbon stored in soil (Don *et al*. 2011; Pan *et al*. 2011). However, this pool is a large source of uncertainty for the total amount of carbon stored in this ecosystem, with spatial distribution and variability of soil carbon stocks practically unknown (Batjes 2008). Additionally, few data on changes in soil carbon stocks in tropical land-use systems exists (e.g. Guo & Gifford 2002; Minasny *et al*. 2010; Powers *et al*. 2011; Wasige *et al*. 2014) and currently there is no consensus on how much soil carbon is lost by tropical land-use change (e.g. Ramankutty *et al*. 2007; Van der Werf *et al*. 2009). Land-use change and deforestation have significant potential effects on soil carbon and the global carbon cycle (Guo & Gifford 2002; Ogle *et al*. 2005; Ramankutty *et al*. 2007; Allison *et al*. 2010; Craine *et al*. 2010), and quantification of spatial and temporal variability of soil organic carbon (SOC) pools is essential.

Quantification of current carbon stocks in tropical soils and future changes in this pool is of major importance for climate mitigation initiatives. Some attempts have been made to quantify soil carbon stocks in Central Africa at a large scale. Batjes (2008) presented SOC estimates per agro-climate zone and soil type for Central Africa based on the soil and terrain (SOTER) database. However, for large regions no soil analytical data were available and gaps were filled using expert rules and taxonomy-based pedotransfer functions for similar groups of FAO (1988) soil types, providing a first, although coarse-scale, approximation of SOC stocks for Central Africa. This approach is nevertheless not sufficient to address questions concerning spatial variability, and a better spatial coverage is needed to gain more insight in drivers for this variability including soil, climate, land-use and management history.

1.3 The diversity aspect

Tropical forests are characterized by a high biodiversity and genetic diversification (Hubbell & Foster 1983; Parmentier *et al.* 2007; Slik *et al.* 2015), regarding both fauna and flora. Biodiversity, however, is a complex term which in the broad sense can be defined as the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system (Díaz *et al*. 2006). The study of biodiversity, specifically in tropical forests, is a challenge namely due to the high number of species present, the spatial variability of the ecosystem and changes it is undergoing related to climate and land-use change.

Functional groups

The high tree species diversity in tropical forests creates difficulties for ecological analysis. In order to simplify this diversity, species can be classified into functional groups that have similar functions in the ecosystem (Swaine & Whitmore 1988). Such classifications allow us to better understand the origin and the functioning of species-rich ecosystems (Gitay *et al*. 1999), or to model the dynamics of such ecosystems (Köhler *et al*. 2000; Picard *et al*. 2009 & 2012; Fyllas *et al*. 2012). Numerous different motivations to classify species, each with different criteria for their classification, have produced a diversity of functional classifications (Köhler *et al*. 2000; Picard and Franc 2003). Additionally, many techniques have been used for classification, either expert knowledge-based or data-driven (Gitay *et al*. 1999; Gourlet-Fleury *et al*. 2005; Souza *et al*. 2014), aiding in the diversity of the different classifications suggested.

A classic example of functional groups in tropical forests is the dichotomy between pioneers and climax species (Swaine & Whitmore 1988), mainly based on a species' requirement for full light for both germination and establishment. The pioneer group showed high correlations with a whole syndrome of characters (Swaine & Whitmore 1988; Turner 2001), while the non-pioneer group is more heterogeneous. Refined of these groups have been proposed associated with other characters such as or maximum height (Poorter *et al*. 2006), and wood density (Köhler *et al*. 2000).

Plant functional traits and functional diversity

In this study, we focus on a specific type of diversity, namely functional diversity defined as the value, range, distribution and relative abundance of functional traits of the organisms that make up an ecosystem (Díaz *et al*. 2007). Functional diversity is thus a component of biodiversity that generally concerns the range of things that organisms do in communities and ecosystems (Petchey & Gaston 2006), and as the definition shows, it is generally assessed through the use of traits. Plant functional traits are characteristics of an individual organism (Garnier & Navas 2012), usually measured at the tissue-level like at the leaves, that bear some relationship to plant functioning (Lavorel *et al*. 2007). More precisely, functional traits are physiological, structural, behavioral, or phenological characteristics associated to the response of organisms to the environment and their effects on the functioning of the ecosystems in which they live (Díaz *et al*. 2007). These traits are the cornerstone of functional ecology (Calow 1987; Keddy 1992a), where species are not only described by their taxonomic identity but also by their biological characteristics, generally described through the measurement of functional traits (Lavorel *et al*. 1997; Violle *et al*. 2007). The functional characterization of biodiversity that traits make possible, enables us to bring insights which go well beyond what is possible through generic species identification. Specifically in species-rich tropical forest, a functional assessment of the community enables to address questions without prior knowledge on all species present.

The set of traits values belonging to an individual (tree) result from trade-offs between different plant functions (Díaz & Cabido 1997) and from responses to its environment. The concept of functional trade-offs have led to the identification of major axes of variation in traits, that are consistent across environments, biogeographic regions and major plant taxa (Grime 1977; Díaz *et al*. 2004), generally known as ‘economics spectra’ (Wright *et al*. 2004; Chave *et al*. 2009). An important breakthrough was the description of the leaf economic spectrum (LES) which operates largely independently of growth form, plant functional type or biome (Wright *et al*. 2004). This spectrum represents a continuum of carbon and nutrient investment strategies at the leaf level (Reich *et al*. 1997; Wright *et al*. 2004), which is essentially a fast - slow continuum of resource acquisition and stress tolerance (Grime 1977; Reich 2014). The existence of a wood economics spectrum (WES) along an axis of variation related to wood traits has also been suggest (Chave *et al*. 2009), although not as widely confirmed as the LES. Efforts have been made to expand these spectra to a whole-plant approach. Integrated studies of stem and leaf traits of Neotropical tree species showed that stem and leaf economic spectra are not only independent (Wright *et al*. 2007), but also orthogonal (Baraloto *et al*. 2010b), indicating that functional trade-offs operate independently at these levels. Fortunel *et al*. (2012) subsequently expanded this approach by integrating root structural traits, and showed that these traits are closely related to wood traits, but not to leaf traits. Two other dimensions are widely accepted as important to plant functioning and ecological strategies (Westoby *et al*. 2002), namely potential height and seed size (see Garnier & Navas 2012). Potential plant height represents several trade-offs and captures multiple constraints such as the density and height of shading competitors, water economy, and response to disturbance (Schenk & Jackson 2002; Violle *et al*. 2009). Seed size and mass represents the trade-off with fecundity, and addresses establishment probabilities (Muller-Landau *et al*. 2008).

Environmental filtering and niche differentiation

The identification of these economics spectra and main axes of variation have led to improved insights into species composition and the processes controlling species distributions. Conceptualization of species by functional traits reflecting strategies along these axes of variation related to resource acquisition, regeneration niche, environmental tolerance and life history (Westoby *et al*. 2002; Westoby & Wright 2006; Poorter *et al*. 2008), opened the door for a better understanding of species assembly processes, species coexistence and aid in explaining the high diversity of tropical forests (Kraft *et al*. 2008). By investigating the distribution of trait values of all individuals in a community, insight can be gained on the balance between processes related to environmental filtering and those leading to niche differentiation between individuals, as hypothesized by the assembly rule theory (e.g. Belyea & Lancaster 1999). Environmental filtering is a widely accepted ecological process shaping community assembly (Harper 1977), which results from the interaction of plants with their abiotic environment, i.e. environmental conditions, resource availability and disturbance. This mechanism is based on filtering out species that lack specified combinations of traits needed to survive in a specific environment (Keddy 1992a & b). Environmental filtering can be deducted from trait ranges in a community, as it generally leads to convergence of resource-use related trait values due to adaptation to the physical environment (Cornwell & Ackerly 2009; de Bello *et al*. 2009). The importance of environmental filtering for species assembly in tropical forests has been demonstrated by numerous studies using functional traits (ter Steege *et al*. 2006; Kraft *et al*. 2008; Paine *et al*. 2011; Ding *et al*. 2012; Fayolle *et al*. 2012; Katabuchi *et al*. 2012; Fortunel *et al*. 2014; Lasky *et al*. 2014). Similarly, a dispersal filter can act as a determinant of community assembly, favoring the convergence of dispersal traits (Weiher & Keddy 1995; Grime 2006). Alternatively, niche differentiation, the evolutionary partitioning of niche conditions by species, limits coexistence of similar plants (limiting similarity principle; Macarthur & Levins 1967), and leads to the divergence of trait values (Wilson 2007; Cornwell & Ackerly 2009). Niche differentiation results from interactions among neighboring individuals and is influence by both resource competition and shared natural enemies (Chase & Leibold 2003). Kraft *et al*. (2008) provided evidence for processes that simultaneously drive convergence and divergence. Their results showed that strategy differentiation among species contributes to the maintenance of diversity in the Amazon tropical forest.

Community-level means and functional diversity

Two main component are important in describing the functional structure of communities, namely the value and range of traits, which correspond to two types of quantitative variables, namely community-level means and functional diversity. The community-weighted mean is a useful variable as a functional description of a community for understanding the links between climatic factors, vegetation types and ecosystem services (Wright *et al*. 2005; Cornwell *et al*. 2008; Malhado *et al*. 2009). The significance of this variable is related to the mass–ratio hypothesis (Grime 1998), which proposes that the controls on function by species are proportional to their abundance in the community. On the other hand, functional diversity aims at describing the functional dissimilarity among the species present in the communities. Functional diversity is a rather complex idea consisting of different dimensions, and numerous indices have been proposed to best describe these dimensions (reviewed in Petchey

& Gaston 2006). According to Mason *et al.* (2005) and Villéger *et al.* (2008), at least three different indices are needed to capture these different dimensions, namely functional richness, functional evenness and functional divergence. Functional richness is defined as the amount of niche space filled by species in the community, thus describing trait dissimilarity. Functional evenness is the evenness of abundance distribution in filled niche space. Functional divergence is the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community. Among these indices, functional divergence relates most to the divergence versus convergence aspect as discussed above, revealing the complementarity or similarity in species traits within a community (Garnier & Navas 2012).

1.4 Thesis aims and objectives

The overall aim of my study was improving the accuracy of regional and basin-wide estimation of carbon storage in tropical forest and increase our functional understanding of the forest community, providing useful information regarding ecosystem dynamics and demographics.

Six specific objectives are formulated for this thesis:

Objective 1: To provide baseline reference data for above and belowground carbon storage of old-growth tropical forest in a central area of the Congo Basin.

Objective 2: To identify regional and local variability and its drivers in above and belowground carbon storage of old-growth tropical forest in a central area of the Congo Basin.

Objective 3: To identify the effect of deforestation for agricultural purposes and subsequent forest regrowth on carbon storage, both above and belowground, and on the functional community structure.

Objective 4: To quantify the functional structure of prevailing forest types of the study area, and to identify the main processes shaping this structure.

Objective 5: To determine the contribution to functional diversity (based on resource acquisition and carbon allocation traits) and carbon storage of different species in this tropical forest.

Objective 6: To identify species with similar functional traits and classify them into plant functional types.

1.5 Chapter overview

This thesis consists of 9 chapters: the introduction (*Chapter 1*), description of the study site (*Chapter 2*), six research chapters (*Chapters 3-8*) and the general conclusions (*Chapter 9*). The research chapters have been divided into two main topics, namely (1) carbon storage and (2) plant functional traits and functional diversity, as was this introduction.

As all research chapters focus on the same site, the Yangambi Biosphere reserve (DRC), a detailed description of the site and its history is provided in *Chapter 2*, including the methodology used for the forest inventory in the framework of the COBIMFO project, which is the starting point of each research chapter. The Yangambi Biosphere reserve is located in a central, unexplored area of the Congo Basin, and it presents a unique opportunity to collect and quantify baseline carbon storage estimates for this region. This is the main topic of *Chapter 3*, where aboveground and soil carbon storage of pristine and intervened forests are presented. Our estimation on aboveground carbon storage in Yangambi is compared to two regions in the East and West of the Congo Basin in order to validate biomass variability found in literature. This chapter raised questions regarding both tree allometry (height-diameter relationships) and soil carbon storage in this region. I therefore increased our study area to further explore these questions. In *Chapter 4*, tree allometry was investigated in two additional study sites, Yoko and Yambela, to assess local variability in allometry and evaluate the generality of the results found in *Chapter 3* for this region. In *Chapter 5*, a comprehensive comparison is made of soil carbon storage between the Yangambi and Yoko study area. A large difference in soil carbon storage is found, and I investigate several current hypotheses offering possible explanations on the underlying reasons and mechanisms for these findings.

The following three research chapters are related to functional diversity and community structure. These chapters are all based on an extensive trait dataset set up for the Yangambi Biosphere reserve, covering 15 leaf and wood traits related to resource acquisition and carbon allocation, for 123 species.

The high species diversity in tropical forests has led to the frequent need and use of classifications of species. In *Chapter 6*, I identify a site-specific classification of individual trees found in the Yangambi Biosphere reserve incorporating intra-species variability. Subsequently, the obtained classification is compared to frequently used knowledge-based classifications, and an attempt is made to better describe the relation of these classifications with ecological strategies. In *Chapter 7*, I focus on the functional structure of three forest types in Yangambi, namely the regrowth forest dominated by *Musanga cecropioides*, an old-growth forest type dominated by *Gilbertiodendron dewevrei*, and mixed old-growth forest. I investigate how functional diversity and community structure are influenced by persistent monodominance, and assess their change along a successional gradient with non-persistent monodominance. In *Chapter 8*, I aim to identify a relation between the abundance of a species and the distinctiveness of its traits in the community, and quantify the species-specific contributions to functional diversity for both the mixed and monodominant forest type. Subsequently, I aim to identify species that are more influenced by environmental filtering or by niche differentiation. Finally, in *Chapter 9*, I summarize the cross-cutting findings and discuss how the results of this thesis contribute to current knowledge.

2

Yangambi

UNESCO Man and Biosphere reserve

Abstract

All scientific chapters in this thesis focus on research in the same study area in the Man and Biosphere reserve of Yangambi. Yangambi was selected within the COBIMFO project as main study area because of its central location in the Congo Basin and its long-standing tradition in forest research and experimental silvicultural treatments, some of them dating back to 1930. Within this chapter, an overview is provided of this study area concerning its location, climate, prevailing vegetation types and some historical background is given. Additionally, as all chapters focus on the same initial inventory made, the methodology of the inventory and an overview of the plots is provided.

2.1 The Yangambi reserve

The Yangambi Biosphere Reserve is situated within the Congo River Basin, approximately 100 km west of the city Kisangani in the Democratic Republic of the Congo (DRC) (Figure 2.1). The reserve covers an area of 6297 km^2 (Ebuy *et al*. 2011), just north of the Congo River. Nevertheless, the boundaries of the reserve are not clearly defined and the reserve is surrounded by small villages. Although there are no figures on the number of inhabitants of the area, some economic activities take place within the biosphere reserve boundaries such as agriculture, hunting, fishing, the production of canoes as well as some gold extraction.

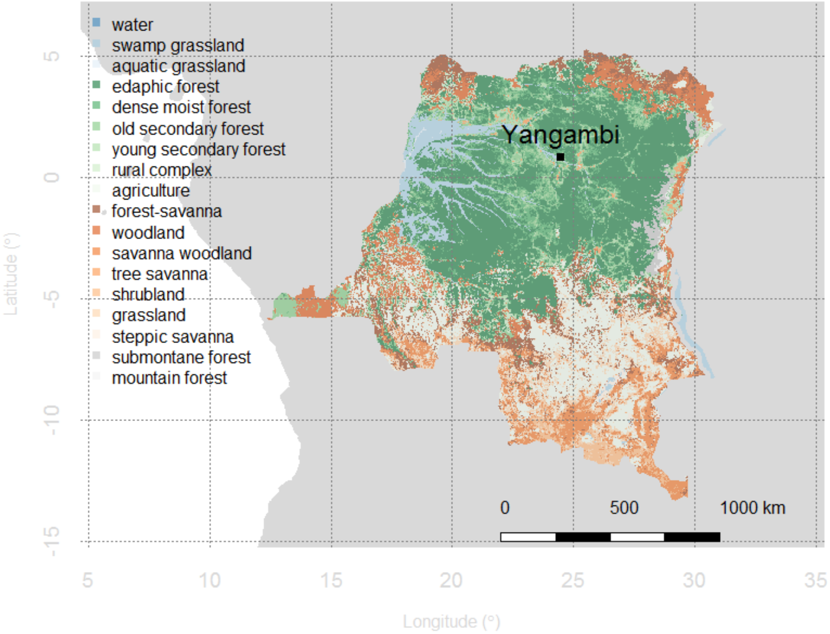

Figure 2.1: Location of the Yangambi reserve on a land cover map of DRC (Verhegghen *et al*. 2012).

A biogeographic analysis of forest composition across tropical Africa shows that the forest in this region belongs to 'moist Central Africa' (Fayolle *et al*. 2014b). Vegetation in the reserve is nevertheless characterized by both old-growth and intervened forest (Gilson *et al*. 1956). Forest disturbance is mainly in the form of slash-and-burn agricultural activities followed by abandonment allowing the forest to regenerate. The pioneer stage of forest recolonization presents itself as very dense thickets dominated by *Vernonia conferta*, *Macaranga spinosa* and *Harungana madagascariensis*. During the next stage of regrowth, most frequently a dominance of *Musanga cecropioides* in the canopy is established. In the following stages of regrowth, a large floristic diversity can be attained, generally combined with a heterogeneous canopy and tangled stratification with a lush undergrowth. These forests are generally characterized by species with a fast growth rate and low wood density, including

Ricinodendron heudelotii, *Combretodendron africanum*, *Pentaclethra macrophylla*, *Albizzia ealaensis* and *Irvingia grandifolia*. Two stages have been identified, namely a younger stage with *Myrianthus arboreus* and an older stage with *Alstonia boonei*. Two main old-growth forest types are found in the Yangambi reserve. The first is the moist semi-deciduous rainforest, characterized by a closed canopy and a thin undergrowth. Its floristic composition is strong variable, however, *Scorodophloeus zenkeri* is present almost everywhere and strong local dominance arises. The second type of old-growth forest is the moist evergreen rainforest dominanted by *Gilbertiodendron dewevrei*, who forms a continuous forest canopy under which only sparse understory is present (Gilson *et al*. 1956).

Soils on the Yangambi plateau are ferralsols primarily formed from eolian sediments, composed mostly of quartz sand, kaolinite clay and hydrated iron oxides (Gilson *et al*. 1956; Van Ranst *et al*. 2010). The slope on the plateau rarely exceeds 2-3%. Kellogg & Davol (1949) has classified the soils of the region in the 'reddish-yellow latosols' and identified the following essential characteristics for these latosols: low silica/sesquioxide, low to average exchange capacity for the mineral fraction, low activity of clay, few primary minerals, few soluble materials, a fairly high degree of consistency of structural aggregates and a red to reddish color of the soil.

The region has an Af type tropical rainforest climate (following Köppen-Geiger; Peel *et al*. 2007). As measured in the Yangambi reserve, the regions receives an annual precipitation of 1762 ± 295 mm (1961 - 2012) with an average dry season length of 3.3 ± 1.3 months with monthly precipitation lower than 100 mm, during December – February (Figure 2.2). A smaller dry season occurs from June to August with monthly precipitation lower than 150 mm. Temperatures are high and constant throughout the year with a minimum of 24.2 ± 0.4 °C in July and a maximum of 25.5 ± 0.6 °C in March.

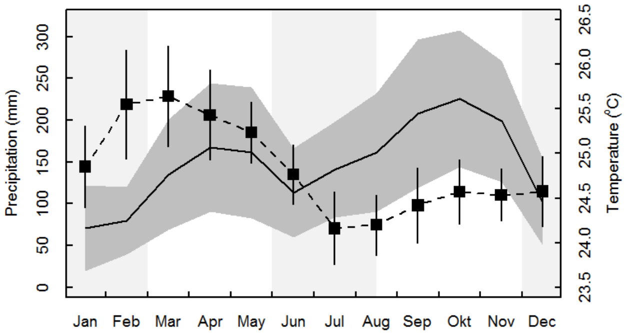

Figure 2.2: Meteorological characteristics of the Yangambi site (1961 - 2012). Monthly mean precipitation (mm) is indicated as a full black line with standard deviation indicated as a dark grey envelope, monthly mean temperature (°C) as black squares and dashed lines. Variability of the temperature is indicated as ± 1 SD vertical segments. Light grey background areas indicate the wet seasons. The large (Dec - Febr; < 100 mm) and small (Jun - Aug; < 150 mm) dry season of the Yangambi site are indicated with a light grey background.

2.2 Historical background

The Democratic Republic of the Congo (DRC) is a very large country with a total surface of 2,345,408 km^2, i.e. the largest country in Sub-Saharan Africa. The country was colonized by Belgium from 1908 till 1960 (Belgian Congo); from 1877 till 1908, it was the so-called 'Congo Free State' ruled by Leopold II, King of Belgium. After independence, the country was renamed several times - from 1960 onwards - as Congo-Léopoldville, Congo-Kinshasa, Zaire and finally the DRC.

During the colonial rule of Congo by Belgium (Belgian Congo), the Yangambi research facility, among 31 other facilities, was established under the supervision of the 'Régie des plantations de la colonie' (REPCO) and later in 1933 taken over by the 'Institut National pour l'Étude Agronomique du Congo' (INEAC). INEAC was a very large research institution, specialized in all aspects of agriculture, and thus of major importance for agricultural development of the colony. Through the establishment of the principal research station in Yangambi, and many small research centers elsewhere in the country, their goal was to establish a plan for a rational agriculture organization with a focus on fundamental research. The methods developed in these agricultural research institutes could then be used on all farms in the colony.

The Yangambi research institute grew to be the largest of its kind in Belgian Congo, with homes, offices, a library and modern laboratories (Figure 2.3). By mid-1950s, about half of the European Personnel in Africa of the INEAC were stationed in Yangambi and the research institute employed numerous specialists from various fields. The INEAC in Yangambi focused on the selection of seeds and crops and on the promotion of a scientific agriculture. Multiple scientific departments and laboratories were established, including departments of Oil Palm, Hevea, Coffee and Cocoa Trees, Food Crops, Botany, Phytopathology and Insects, Agricultural Chemistry, Forestry, Agrology, Genetics, Climatology, Plant Physiology, Agricultural Mechanics and Farm Building, Animal Husbandry, Hydrobiology for Pisciculture, Biometrics, Diverse Cash Crops, and Agricultural Economics and Sociology.

The independence of the Belgian Congo in 1960 brought an abrupt end to the accumulated expertise of the INEAC, and the institution was disbanded in the following years. Today, the traces of this institution remain limited to a few (repealed) agricultural centers in DRC, an impressive library and archive documents that are stored in the State Archives of Belgium.

Figure 2.3: In the left panel the library of the former INEAC, and in the right panel an abandoned warehouse of the Agricultural Mechanics and Farm Building Division.

After the independence, the INEAC was replaced by the Congolese institution: ‘Institut National pour l’Etude et la Recherche Agronomiques’ (INERA). The INERA has similar objectives as the former INEAC, although the same status of expertise has not been reclaimed.

In 1976, the Yangambi reserve was declared a Man and Biosphere by UNESCO.

2.3 Plot inventory within the COBIMFO project

The COBIMFO project aims to identify relationships between carbon storage and biodiversity, and sites needed to be selected along a gradient in forest productivity with high differentiation in forest structure, species composition and disturbance.

A preliminary classification of the study area was made using SPOT-4 HRVIR, Landsat and geo-eye satellite images (UCL 2012) using an object-based classification approach. A vegetation map of the Yangambi reserve was prepared mainly focussing on the SPOT-4 image of 20 m resolution. A detailed forest type classification was made using the Nearest-Neighbour classification algorithm of eCognition software, and the comparison with the INEAC vegetation map of Yangambi from 1953 (Gilson *et al*. 1956) allowed defining the different land cover classes. Final adjustments of the classification were made by visual reinterpretation. An array of possible study sites were proposed covering the various forest types, allowing for an unbiased selection of plot location (Phillips *et al*. 2010). The final selection of plot location was based on the correct validation of forest type in the field and the accessibility of the plot.

Permanent inventory plots of 1 ha (Phillips *et al*. 2010; Picard *et al*. 2010) have been installed in the beginning of 2012. Squared or rectangular plots were realized on the ground without a projected area as the topography of the region is gentle. A standardized international inventory protocol for tropical forest was used (Phillips *et al*. 2010; RAINFOR) to assure comparability with other studies. All live tree stems with a diameter larger than 10 cm were tagged, measured for diameter at breast height at 1.3 m and identified up to species level. Buttressed trees, although a rarity in the region, and stilt-rooted trees are measured 50 cm above the highest root, where the trunk shape is cylindrical. When a deformity is present at breast height, the diameter is measured 2 cm lower. Preliminary species identification was done with the help of local botanists of the INERA. The identification of species has been double checked by a team of botanist of the Botanic Garden Meise (Belgium), and botanical specimens were collected for all individuals for which uncertainty remained. Final identification was then based on a comparison with herbarium material and DNA sequencing when necessary.

In total, 20 plots have been installed in old-growth and intervened forest along various successional stages in the south-western (N00º47’; E24º30’) and north-western part (N00º59’; E24º32’) of the reserve, with an imbalanced stratified sampling related to the different investigated forest types. Accordingly, a higher number of plots have been installed in the old-growth forest which cover a larger area in the reserve compared to the intervened forest. Seven plots have been installed in regrowth forest in different stages of regrowth after abandonment of slash-and-burn agricultural activities, namely young *Musanga* regrowth forest (n = 3; age since disturbance ± 7 years), old *Musanga* regrowth forest (n=3; age since disturbance ± 20 years) and old mixed regrowth forest (n = 1; age since disturbance not known). The disturbance history was estimated based on communication with local farmers.

The two *Musanga* regrowth forest types both show a monodominance of *Musanga cecropioides* R.Br. ex Tedlie, but differ in age since disturbance. Subsequently, thirteen plots have been included in old-growth forest. The terminology ‘old-growth’ is used to indicate that these forest have not undergone major anthropogenic disturbance. However, it should be noted that anthropogenic activity does take place, for example in the form of hunting and collecting wood for housing; with villages surrounding the forest. These forest can therefore not be defined as majestic or pristine. Two types of old-growth forests are investigated, namely old-growth mixed semideciduous forest (n = 8) and monodominant forest of *Gilbertiodendron dewevrei* (De Wild.) J. Leonard (n = 5). Location and details of each plot can be found in Figure 2.4 and Table 2.1. Within the COBIMFO project, 5 plots have also been installed at the edge of the forest, with one side of the plot bordered by a recent clear cut of the forest for slash-and-burn agricultural activities. These plots are not included in this dissertation.

Table 2.1: Plot characteristics of the 24 one-hectare plots in Yangambi. Stem density (SD), basal area (BA) and species richness (S; number of species found per hectare). It has been indicated in which of the research chapters the plots have been used.

Site	**Coordinates**	**SD (ha^{-1})**	**BA ($m^2 ha^{-1}$)**	**S (ha^{-1})**	**Chapter**
Fallow-1	N 00°47'48.7" E 24°29'39.2"	350	5.39	26	3,6,7
Fallow-2	N 00°47'34.8" E 24°29'51.1"	132	2.06	22	3,6,7
Fallow-3	N 00°47'40.5" E 24°28'55.8"	361	6.67	40	3,7
Young regrowth-1	N 00°47'20.4" E 24°31'1.5"	322	20.44	40	3,6,7
Young regrowth-2	N 00°47'43.1" E 24°29'32.5"	447	16.63	25	3,6,7
Young regrowth-3	N 00°47'36.9" E 24°29'26.0"	313	17.80	43	3,6,7
Old regrowth-1	N 00°52'56.8" E 24°19'46.1"	384	19.48	92	3
Mixed-1	N 00°48'50.6" E 24°30'47.2"	563	34.81	83	3,4,5,6,7,8
Mixed-2	N 00°46'51.1" E 24°31'14.2"	403	35.25	78	3,4,5,6,7,8
Mixed-3	N 00°47'14.5" E 24°31'24.7"	367	30.69	75	3,4,5,6,7,8
Mixed-4	N 00°48'52.2" E 24°29'38.9"	432	33.01	84	3,4,5,6,7,8
Mixed-5	N 00°48'11.0" E 24°29'16.5"	329	25.2	80	3,4,5,6,7,8
Mixed-6	N 00°59'33.2" E 24°32'20.6"	490	32.63	86	3,4
Mixed-7	N 00°59'23.3" E 24°32'18.7"	598	31.47	92	3,4
Mixed-8	N 00°59'11.8" E 24°32'18.8"	556	29.20	90	3,4
Monodominant-1	N 00°49'38.7" E 24°31'21.2"	344	31.80	48	3,6,7,8
Monodominant-2	N 00°49'39.9" E 24°31'56.7"	436	32.06	55	3,6,7,8
Monodominant-3	N 00°47'51.1" E 24°29'52.6"	376	30.57	62	3,6,7,8
Monodominant-4	N 00°48'22.7" E 24°31'47.3"	374	27.69	46	3,6,7,8
Monodominant-5	N 00°52'4.1” E 24°27'25.2"	217	27.19	46	3,6,7,8

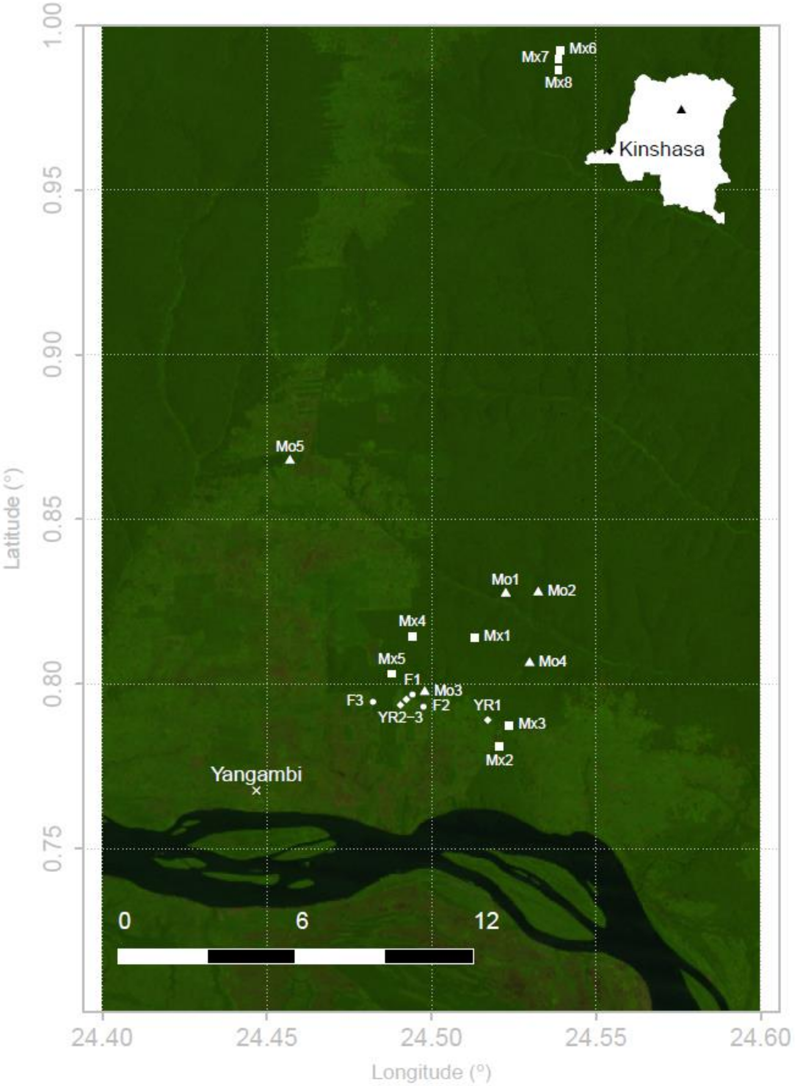

Figure 2.4: Site location of the Yangambi field sites within the Democratic Republic of the Congo (DRC): fallow (F 1-3; circles), young regrowth (YR 1-3; diamonds), mixed old-growth forest (Mx 1-8; squares) and monodominant old-growth forest (Mo 1-5; triangles) plots. A cloud free Landsat composites false color map of the study area. The location of this map within DRC is delineated by a black triangle in the top left inset. The scale bar is in kilometers.

PART I

The carbon-side of the story

3

Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin

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Abstract

Policies to reduce emissions from deforestation and forest degradation largely depend on accurate estimates of tropical forest carbon stocks. Here we present the first field-based carbon stock data for the central Congo Basin in Yangambi, DRC. We find an average aboveground carbon stock of 162 ± 20 Mg C ha^{-1} for intact old-growth forest, which is significantly lower than stocks recorded in the outer regions of the Congo Basin. The best available tree height-diameter relationships derived for Central Africa do not render accurate canopy height estimates for our study area. Aboveground carbon stocks would be overestimated by 24% if these inaccurate relations were used. The studied forests have a lower stature compared to forests in the outer regions of the basin, which confirms remotely sensed patterns. Additionally, we find an average soil carbon stock of 111 ± 24 Mg C ha^{-1}, slightly influenced by current land-use change.

3.1 Introduction

Tropical forests represent a crucial carbon pool since they, reportedly, store 40-50% of all terrestrial carbon (Lewis *et al.* 2006; IPCC 2007) and influence the global carbon balance when changes are induced due to climate change (Pan *et al.* 2011) and anthropogenic disturbances. In order to understand and quantify tropical forest carbon uptake and losses, accurate carbon stock reference data are needed (Huntingford *et al.* 2013), as well as estimates of carbon fluxes resulting from both natural processes and land use changes (IPCC 2007; Gourlet-Fleury *et al.* 2011). The accuracy of these reference data is essential for the implementation of climate mitigation policies to reduce emissions resulting from deforestation and forest degradation (REDD, UN Framework Convention on Climate Change, www.un-redd.org) (Gibbs *et al.* 2007; Somorin *et al.* 2012). Currently, the uncertainty associated with these data is high and there are still large gaps in our knowledge with respect to the actual amount of carbon stored in tropical forests and the stability of this pool (Huntingford *et al.* 2013).

In African tropical forests, in particular, there are major challenges with respect to estimating carbon stocks and fluxes. Saatchi *et al.* (2011) developed a benchmark map of carbon stocks across the tropics, predicting a gradient in Central Africa with highest stocks in western and eastern parts of the Congo Basin. This gradient is not always predicted (Baccini *et al.* 2012), and more data is needed for effective mapping which is dependent on spatially extensive ground-based measurements to reduce regional uncertainties. To date, African tropical forests have been underrepresented in carbon research mainly due to a lack of resources for scientific research, limited logistical support, poor infrastructure, and periodic political instability (Verbeeck *et al.* 2011; Baccini *et al.* 2012). Only a limited number of inventoried and permanent monitoring plots have been established given the considerable extent of the African tropical forest (Lewis *et al.* 2009). The few available inventoried plots are unevenly distributed, with a high concentration in the outer regions of the Congo Basin, leaving the center of the basin unexplored (Lewis *et al.* 2009; Verbeeck *et al.* 2011). Biomass estimates for these plots have been extrapolated to the entire African tropical forest based on pan-tropical allometric equations (Brown *et al.* 1989; Chave *et al.* 2005). These equations are generally parameterized without data from the African continent due to the lack thereof (Chave *et al.* 2005). Only the study of Feldpausch *et al.* (2012) has recently expanded the frequently used pan-tropical Chave *et al.* (2005) equation with African data from the western Congo Basin. The robustness and accuracy of this equation has been noted for some African regions (Djomo *et al.* 2010; Henry *et al.* 2010), with its strength lying in the large sample size of tropical trees compared to the other equations. Nevertheless, the use of pan-tropical equations (Brown *et al.* 1989; Chave *et al.* 2005) in unstudied areas needs to be done with care since it could produce systematic errors in carbon stock estimates, specifically if not all variables, namely diameter, wood density and tree height, are accounted for.

Here we report the first inventory-based carbon data obtained from a central location in the Congo Basin, situated in the UNESCO Man and Biosphere reserve at Yangambi, DRC (Figure 3.1), with estimates for both aboveground live tree and soil carbon stocks in intact old-growth forest and in regrowth forest. A comparison of aboveground carbon stocks in old-growth forests is made with AfriTRON sites (Lewis *et al.* 2009) in western and eastern Congo Basin, in order to assess whether our first ground-based observations for this important region confirm the spatial trends observed by remote sensing (Saatchi *et al*. 2011; Baccini *et al*. 2012) and to quantify possible intrinsic differences in carbon stocks.

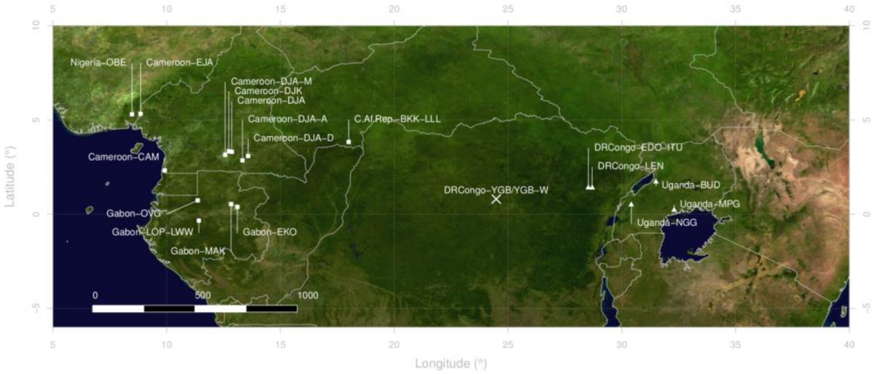


Figure 3.1: Site locations. MODIS composite (NASA, Blue Marble) with the Yangambi study site and AfriTRON sites superimposed (Lewis *et al*. 2009). The sites are separated into different regions: squares indicate western Congo Basin sites, circles indicate eastern Congo Basin sites, and the cross indicates the central Congo Basin site in Yangambi. In the scale bar, one block equals 250 km.

3.2 Methods

Study area

This study was carried out in 20 inventory plots in Yangambi (DRC) of which a detailed description can be found in *Chapter 2*. This study focusses on thirteen one-hectare plots in intact old-growth forest, including two forest types namely, mixed semi-deciduous (n = 8) and riparian monodominant evergreen *Gilbertiodendron dewevrei* (n = 5) forests. In addition, to assess the effect of deforestation and regrowth at local scales, seven plots of one hectare are included in previously deforested areas of mixed semi-deciduous forests, with varying regrowth ages after slash-and-burn agriculture, namely young *Musanga* (n = 3; age since disturbance ± 7 years), old *Musanga* regrowth forest (n = 3; age since disturbance ± 20 years) and old mixed regrowth forest (n = 1; decades since disturbance).

Height measurements

All tree individuals were classified in the field into diameter classes (i.e. 10-20 cm, 20-30 cm, 30-50 cm, > 50cm) and all species contributing to a cumulative 95% of the basal area of the plot were selected for further measurement. For each of these species, 2 individuals were selected within each diameter class. These individuals were measured for tree height using a Nikon Laser Rangefinder Forestry Pro hypsometer. The top of the tree is determined from different view angles and multiple measurements are made to account for over- or underestimation. When the top of an individual is not visible, a different individual using the same selection criteria is selected.

Wood density measurements

The same individuals selected for tree height measurements are selected for wood sampling to determine species wood density, defined as the ratio of oven dry weight and fresh volume. Wood samples with an average size of 5 x 5 x 5 cm are taken under the bark. For those species with no wood density data, a genus-average was taken or when genus data is unavailable, a family-average was used. For a few remaining species from which the family did not occur elsewhere in the plot and for the remaining unidentified individuals, a site-average was used. Mean wood density for each plot was weighted by basal area.

Height-diameter regressions

Stand-specific height-diameter regression models were developed for each forest type, irrespective of tree species. All trees known to be broken, damaged or leaning more than 10% were excluded from analysis. Weibull, Chapman-Richards, logistic, power and 2- and 3-parameter exponential models were compared. The optimal model was selected based on the Akaike Information Criterion (AIC) and the residual standard error (RSE) and was further used to determine tree heights for aboveground carbon stock estimation. No tree height measurements are available for old mixed regrowth forest (n = 1), and the model for mixed semi-deciduous forest was used since similar species were present.

Allometric equations

The relation of Chave *et al*. (2005) for moist tropical forest including height and wood density was selected for aboveground carbon stock estimation, with biomass assumed to be 50% carbon.

Soil carbon storage

Soil carbon stocks to a depth of 100 cm are quantified for all forest types except for the old mixed regrowth forest. Soil cores were collected using five depth increments: 0-10, 10-20, 20-30, 30-50 and 50-100 cm. From each replicated plot per forest type a composite soil sample (n = 10) was prepared per depth. Composite samples were oven-dried at 50°C. Carbon content was determined via element analyses using continuous flow EA-IRMS. For each depth increment, carbon stocks (Mg C ha^{-1}) were determined as a product of bulk density (g cm^{-3}), carbon concentration (%) and thickness of the increment layer (cm). Soil texture was determined by means of the percentage of sand, silt and clay. Analyses were performed on air-dried soil fractions (< 2 mm). The sand fraction (> 63 µm) was separated by wet sieving; the silt and clay fractions were determined by the pipette method of Köhn after dispersion with sodium hexametaphosphate (Pansu & Gautheyrou 2006).

Comparison with AfriTRON sites

The estimations of aboveground carbon stocks in old-growth forests in Yangambi are compared to those for the AfriTRON sites (Lewis *et al*. 2009) in western and eastern Congo Basin. One-way Anova is used followed by a Tukey HSD test to compare the means of the AfriTRON sites (Lewis *et al*. 2009) and the Yangambi sites. To compare the carbon stocks of the different forest types in Yangambi, Fisher's LSD test is used.

3.3 Results

Yangambi aboveground carbon stocks are lower

With an aboveground carbon stock in live free-standing woody stems (minimum diameter 10 cm) in old-growth forest at Yangambi of 162 ± 20 Mg C ha^{-1}, our estimates are 19% lower and significantly different ($p < 0.001$, Df = 2) from estimates at the AfriTRON sites (Lewis *et al*. 2009) (Figure 3.2) in the Congo Basin. Lewis *et al*. (2009) report an average of 202 Mg C ha^{-1} for African tropical forest, and an even higher average in the Congo Basin, with 243 Mg C ha^{-1} for the western Congo Basin and 259 Mg C ha^{-1} for eastern Congo Basin sites (Figures 3.1 and 3.2). Although the AfriTRON data show a large degree of variability within each geographic region, most AfriTRON sites have a significantly higher carbon stock than those estimated for Yangambi (Figure 3.2). The lower aboveground carbon stock at Yangambi is very remarkable and can be attributed to a different forest structure, where trees do not reach the same height for a given tree diameter as in the western or eastern Congo Basin (Figure 3.3). When comparing tree height-diameter regression curves developed for Central Africa (Lewis *et al*. 2009; Banin *et al*. 2012; Feldpausch *et al*. 2012) with those based on the Yangambi dataset, we found an asymptotic height difference of 9.4 ± 0.9 m (Figure 3.3, Table 3.1) resulting in an overestimation in aboveground carbon stocks of 12 up to 25% (median 24%) equivalent to 29 - 62 Mg C ha^{-1} (median 53 Mg C ha^{-1}). This results in an overestimated mean carbon stock of 212 ± 24 Mg C ha^{-1} (Figure 3.2, red points). This is a first indication that height-diameter allometry in some regions in central Africa can differ from general regressions for central Africa (Banin *et al*. 2012; Feldpausch *et al*. 2012), and that more localized height-diameter allometry is required.

Tree height is the determining structural factor

To explore in more detail the forest structural parameter responsible for the observed lower aboveground carbon stocks, we compared our data in more detail with datasets from sites in the Dja Faunal Reserve in Cameroon in the West of the Congo Basin and in the Ituri Dynamics Plots in the East, with a distinction of mixed and monodominant *Gilbertiodendron dewevrei* forest types (Table 3.2). For these areas carbon stocks, basal area, stem density and wood density were available from literature, but explicit height data is lacking. In addition, data on soil and climate is available. By comparing mixed and monodominant plots separately, we were able to get a better view on structural parameters driving the biomass differences.

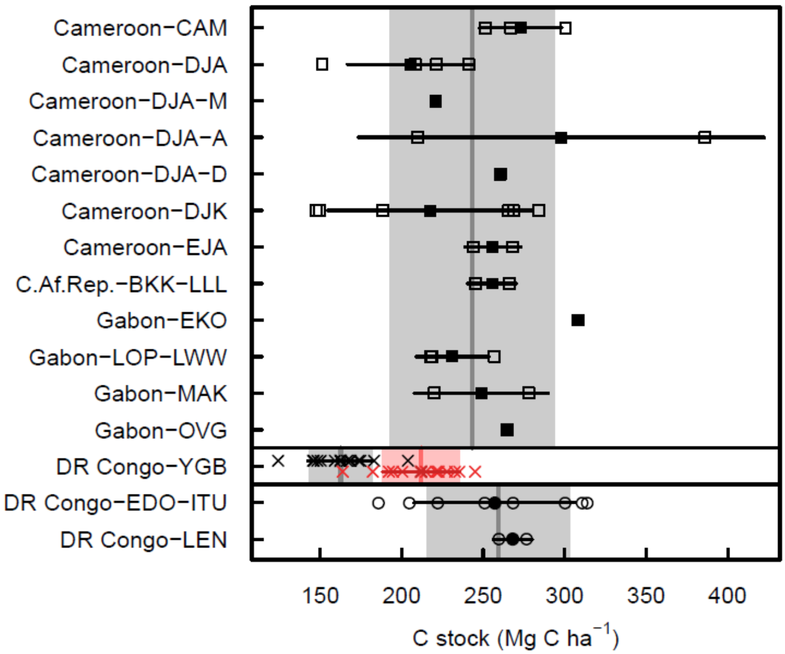


Figure 3.2: Comparison between aboveground carbon stock at Yangambi and sites from the AfriTRON network. Sites from the AfriTRON network (Lewis *et al*. 2009) are grouped according to location, respectively West Congo Basin (squares) and East Congo Basin (circles). All acronyms refer to the applied site names in the AfriTRON network. Aboveground carbon stocks at Yangambi (YGB) are incorporated as a separate region, central Congo Basin (crosses). All carbon stocks are based on the same allometric equation for biomass (Chave *et al*. 2005). For the Yangambi site, a distinction is made between carbon stocks estimated using a site-specific height-diameter relationship (grey) and a height-diameter relationship proposed for central Congo Basin (Feldpausch *et al*. 2012) (red). The overall mean carbon stocks for the separate regions – West Congo Basin, central Congo Basin and East Congo Basin – are indicated by a grey line. The light grey box indicates standard deviations along this mean. The significantly lower carbon stocks at Yangambi are emphasized, and the possible overestimation using the generalized height-diameter relationship for central Congo Basin of Feldpausch *et al*. (2012) is indicated in red. Within each region, a detailed representation of the same data grouped into clusters with plot locations close together (Lewis *et al*. 2009) is shown indicating the large heterogeneity associated with carbon stock estimates, with open symbols all individual plot estimates and filled symbols the mean of the cluster including standard deviation.

Table 3.1: Coefficients for height-diameter relationship in a three-parameter exponential regression model. Regression model: ($H = a – b.e^{-cD}$). A, b and c are the optimized parameters for the individual equations per forest type, which represent, respectively, the maximum asymptotic height, the difference between minimum and maximum height, and shape of the curve (Banin *et al*. 2012). Standard residual error (RSE), Akaike information criterion (AIC) and number of trees (n) are given for each forest type.

Forest type	**a**	**b**	**c**	**AIC**	**RSE**	**n**
Mixed	36.3576	31.6591	0.0221	1085.653	4.221	487
Monodominant	35.0437	30.4327	0.0246	2552.917	4.053	452
Old *Musanga* regrowth forest	21.0279	19.5718	0.0564	786.6445	2.585	167
Young *Musanga* regrowth forest	14.6846	10.4496	0.0547	1952.425	1.824	482
Africa (Banin *et al*. 2012)	45.1	42.8	0.025			

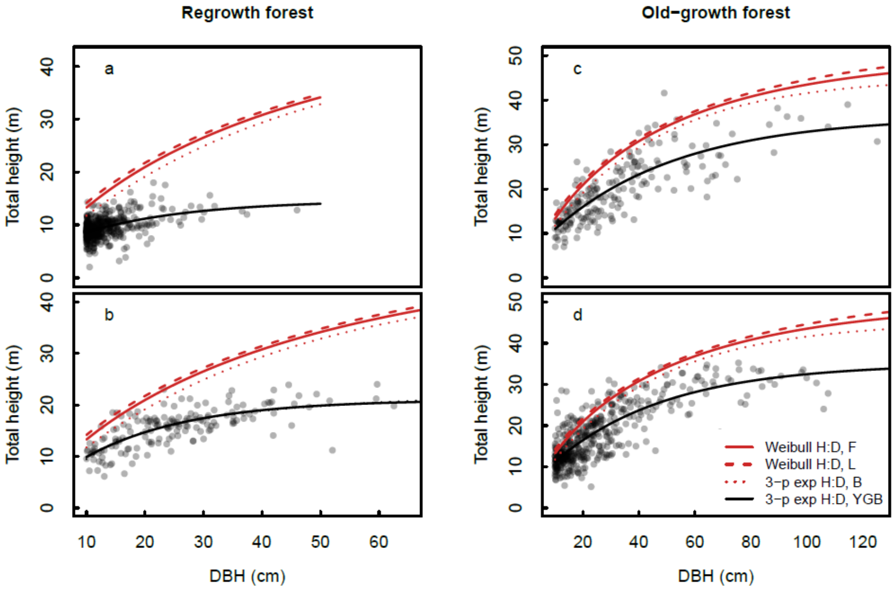


Figure 3.3: Height-diameter models for different inventoried forest types at the Yangambi reserve in the central Congo Basin. Comparison is made between regrowth and old-growth forests using different scales. a = Young *Musanga* regrowth forest; b = Old *Musanga* regrowth forest; c = Mixed old-growth forest; d = Monodominant old-growth forest. In black: the 3-parameter exponential height-diameter (H:D) model optimized for the Yangambi (YGB) site. In red: regional models for Central Africa. Weibull H:D, F = Feldpausch *et al.* (2012) model; Weibull H:D, L = model used by Lewis *et al*. (2009) (dashed); 3-p exp H:D, B = Banin *et al*. (2012) model (dotted). The use of regional models results in an overestimate of tree heights and biomass estimates are thus affected.

For mixed forests in these three sites, aboveground carbon stocks do not follow the same spatial gradient as generally seen for the Congo Basin (Saatchi *et al.* 2011), with the Dja mixed forests showing smaller stocks, similar to the Yangambi ones. In the Dja reserve, a lower ($p < 0.03$) basal area is found while both stem density and wood density are not significantly different from the Yangambi mixed forest ($p = 1$). The combination of a lower basal area with the same amount of trees in the plots in Dja, indicates that the average tree diameter is lower than in Yangambi. In order to reach a similar carbon stock as in Yangambi, for a specific diameter, trees need to grow taller. This shows that differences in height-diameter relationships are a driver for the amount of carbon stored in these sites.

Mixed forests in Ituri represent a significantly ($p = 0.01$) larger carbon stock than in Yangambi. Comparison of the structural parameters shows that a higher mean wood density ($p < 0.001$) is found in Ituri than in Yangambi with other variables (Table 3.2) statistically indistinguishable ($p > 0.6$). This shows that the species composition is an important factor determining the larger carbon stock in Ituri, with a tendency for species with a higher wood density. This does not preclude that additional differences in height-diameter relationships could be present. In the mixed forests of these two regions, both basal area and stem density are similar. This indicates that the average tree diameter in both regions is similar and that a different maximal tree height attained in these forests could be the driver for the difference in carbon stock.

By considering the monodominant *Gilbertiodendron dewevrei* forests for the three regions, we exclude the influence of species composition on carbon stock. A significantly lower ($p < 0.001$) carbon stock is found in Yangambi, while all other forest stand variables are similar (Table 3.2). The basal area in Yangambi is slightly lower ($p = 0.04$) than in Ituri, but similar to the values in Dja. With stem density being not significantly different for all regions, this indicates that monodominant forests in Yangambi do not have a lack of trees with a large diameter compared to the other regions. Mean wood density is slightly lower in Yangambi, although not significantly ($p = 0.1$). Consequently, the remaining determinative variable for the estimation of carbon stock is the total tree height reached in these monodominant forests, which clearly confirms our overall conclusion that that tree height is largely explaining the significantly lower stock in Yangambi.

Table 3.2: Aboveground carbon stock in relation to structural and climate parameters for study sites. A distinction is made between mixed and monodominant forests. Dominance of *Gilbertiodendron dewevrei* is expressed both in terms of basal area (BA) and aboveground carbon (AGC) stock. Soil information for depths 0-30 cm in Dja and Yangambi, 0-20 cm in Ituri. Months with precipitation lower than 100 mm are regarded as dry. N.a. data is not available. For each parameter, significance from Tukey HSD is provided between brackets comparing forest types for the three regions, with uppercase letters for the monodominant forest and lowercase letters for the mixed forest.

	Yangambi		**Dja**			**Ituri**		
	Mixed	**Monodominant**	**Mixed**	**Monodominant**	**Ref**	**Mixed**	**Monodominant**	**Ref**
Aboveground C stock (Mg C ha^{-1})	160.5 ± 23.8$^{(a)}$	165.5 ± 14.3$^{(A)}$	161.9 ± 22.9$^{(a)}$	272.6 ± 9.9$^{(B)}$	*	226.3 ± 33.5$^{(b)}$	292.1 ± 23.3$^{(B)}$	*
Stem density (ha^{-1})	467.1 ± 99.6$^{(a)}$	349.4 ± 81.2$^{(A)}$	437.3 ± 43.5$^{(a)}$	342.7 ± 25.2$^{(A)}$	#	470.8 ± 19.8$^{(a)}$	345.2 ± 25.4$^{(A)}$	‡
Basal area (m^2 ha^{-1})	31.5 ± 3.3$^{(a)}$	29.9 ± 2.3$^{(A)}$	25.0 ± 1.7$^{(b)}$	32.6 ± 1.1$^{(AB)}$	#	28.9 ± 3.6$^{(ab)}$	35.7 ± 3.4$^{(B)}$	‡
Wood density (g cm^{-3})	0.62 ± 0.03$^{(a)}$	0.67 ± 0.01$^{(A)}$	0.62 ± 0.02$^{(a)}$	0.71 ± 0.00$^{(A)}$	**	0.7 ± 0.02$^{(b)}$	0.7 ± 0.02$^{(A)}$	**
Dominance (% AGC)	-	71.9 ± 8.4$^{(A)}$	-	85 ± 12 $^{(A)}$	##	-	n.a.	
Dominance (% BA)	-	64.1 ± 9.6$^{(A)}$	-	n.a.		-	63.2 $^{(A)}$	◊
Soil properties					#			Δ
Proportion of clay (%)	13.1 ± 1.0$^{(a)}$	12.5 ± 2.6$^{(A)}$	27.2 ± 10.4$^{(b)}$	21.5 ± 8.1$^{(A)}$		n.a.	n.a.	
Proportion of silt (%)	1.9 ± 0.2$^{(a)}$	3.0 ± 0.2$^{(A)}$	31.0 ± 4.4$^{(b)}$	35.2 ± 7.6$^{(B)}$		n.a.	n.a.	
Proportion of sand (%)	85.1 ± 1.0$^{(a)}$	84.4 ± 2.6$^{(A)}$	41.8 ± 14.4$^{(b)}$	43.3 ± 7.7$^{(B)}$		64.4$^{(c)}$	71.7$^{(C)}$	
Bulk density	1.30 ± 0.05$^{(a)}$	1.26 ± 0.06$^{(A)}$	1.01 ± 0.20$^{(b)}$	0.87 ± 0.02$^{(B)}$		n.a.	n.a.	
C (%)	1.3 ± 0.4$^{(a)}$	1.8 ± 0.5$^{(A)}$	1.89 ± 0.20$^{(b)}$	2.03 ± 0.66$^{(A)}$		1.11 ± 0.44$^{(a)}$	0.98 ± 0.37$^{(B)}$	
N (%)	0.10 ± 0.03$^{(a)}$	0.13 ± 0.03$^{(A)}$	0.16 ± 0.01$^{(b)}$	0.15 ± 0.03$^{(AB)}$		0.09 ± 0.04$^{(a)}$	0.09 ± 0.03$^{(A)}$	

* Lewis *et al.* (2009); # Peh *et al.* (2011a); ** Lewis *et al.* (2013); ## Peh *et al.* (2012); & Hijmans *et al.* (2005); ‡Hart *et al.* (1989); ◊ Makana *et al.* (2004a); Δ Conway (1992)

Table 3.2 continued

	Yangambi		Dja			Ituri		
	Mixed	**Monodominant**	**Mixed**	**Monodominant**	**Ref**	**Mixed**	**Monodominant**	**Ref**
Climate data					&			&
Precipitation (mm yr^{-1})	1764 ± 512(a)		1636 ± 900(a)			1757 ± 510(a)		
Dry season length (months)	2		4			3		
Number of dry seasons	1		2			1		
Average daily temp	24.6 ± 4.3(a)		23.3 ± 5.6(a)			24.3 ± 4.3(a)		
Coordinates					*			*
Latitude	0.800000		3.146250			1.388833		
Longitude	24.48229		13.03613			28.51333		
Altitude (masl)	473		654			788		

* Lewis *et al*. (2009); # Peh *et al.* (2011a); ** Lewis *et al*. (2013); ## Peh *et al.* (2012); & Hijmans *et al*. (2005); ‡Hart *et al*. (1989); ◊ Makana *et al*. (2004a); Δ Conway (1992)

Land use change effect on above and belowground carbon stock

We estimated that aboveground carbon stocks in live trees with a minimum diameter of 10 cm in intact old-growth forest average 162 ± 20 Mg C ha^{-1}, with no significant differences between the different old-growth forest types examined (Figure 3.4). For previously deforested plots, a lower aboveground carbon stock is found, varying according to land use type and the age of any regenerated forest patch, with higher values for older plots with forest regrowth. There is, however, no corresponding difference in soil carbon stocks between intact and degraded forest plots. Soil carbon stocks to a depth of 100 cm in intact forest averaged 111 ± 24 Mg C ha^{-1} and were equivalent to 68% of the aboveground stock. A significantly higher stock is found in monodominant forests with an average of 128 ± 27 Mg C ha^{-1}, compared to 95 ± 11 Mg C ha^{-1} in mixed forests (Figure 3.4). Even after forest clearing of mixed forest sites, the soil carbon stock remains high, although a gentle gradient is observable. Soil carbon stocks in young *Musanga* regrowth forest plots average 74 ± 8 Mg C ha^{-1} and increase significantly with regrowth age as *old Musanga regrowth* forest shows an average of 101 ± 22 Mg C ha^{-1} and thus return to the amount of soil carbon stock of the mixed forest from which they originate (Supplementary Table S3.1).

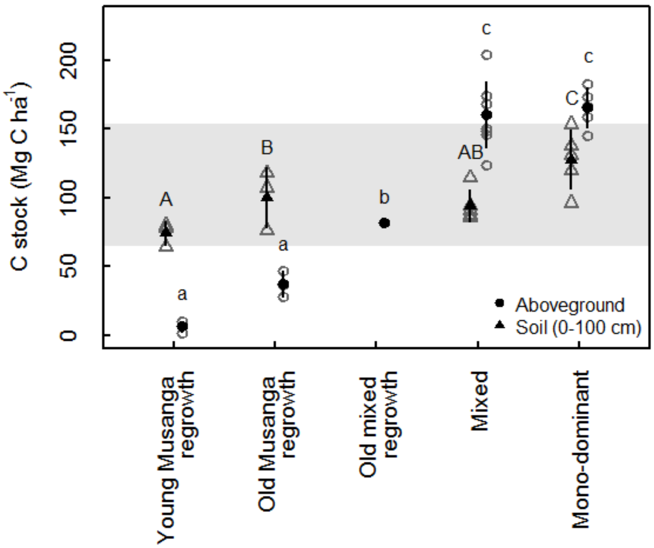


Figure 3.4: Aboveground and soil carbon stock per forest type for inventory plots in the Yangambi reserve. Forest types are arranged from degraded to old-growth forest and show the impact of deforestation on aboveground carbon stock (circles) and soil carbon stock (triangles). The grey box indicates the variability range for soil carbon stocks. Significance from Fisher's LSD test is visualized, with uppercase letters for the soil carbon stock and lowercase letters for the aboveground carbon stock.

3.4 Discussion

Our observations, of lower aboveground carbon stocks for the central Congo Basin, confirm patterns found by remote sensing (Saatchi *et al*. 2011), indicating that the western Congo Basin in Gabon and southern Cameroon, and eastern DRC support higher carbon stocks. We attribute this low stock mainly to a difference in diameter-height relationships.

The lower carbon stocks and reduced canopy height at Yangambi could be related to climate and soil properties, the local available species pool, or past natural and anthropogenic disturbances (Clark & Clark 2000; Malhi *et al*. 2006; Saatchi *et al*. 2007 & 2011; Quesada *et al*. 2012). Disturbances due to past selective logging can have a substantial impact on forest structure (Makana *et al*. 2006) and therefore on carbon stocks. Nevertheless, based on our own field observations, analysis of the species composition (Supplementary Figure S3.1), communication with local foresters and an assessment of historical archives of the Yangambi station, we found no single indication that selective logging activities have been conducted in the study area in the last 150 years. Disturbance due to edge effects (Laurence 2004; Harper *et al*. 2005) could be a factor for some plots close to the edge (Supplementary Figure S3.2), but this effect remains negligible since we did not observe a significant difference between these plots and the plots at a longer distance from the edge. Relatively high average air temperatures in this lowland study area could explain the lower standing biomass because it may cause increased turnover rates and photosynthetic inhibition (Lloyd & Farquhar 2004). This could be an important factor, but in itself cannot explain the significantly lower carbon stock in Yangambi since the mean annual temperatures in Ituri and Dja are similar to Yangambi. The effect of soil conditions is probably more important here. Soils in our study area are sandier compared to those in Dja and Ituri (Table 3.2), with sandy soils generally characterized by lower fertility and more limited water retention. The low N content and the high sand fraction in Yangambi indicate resource-poor soils, both in terms of nutrients and water availability. This low N content is also found in Dja and Ituri, but the sand fraction in these soils is lower providing a higher water holding capacity, specifically in Dja. Additionally, the higher bulk density for the more sandy soils in Yangambi indicates more compaction, which influences root penetration and reduces water infiltration. These soil properties can have an effect on height-diameter relationships (Oliviera-Filho *et al*. 2001) through nutrient limitations or a reduced water holding capacity, both of which influence the amount of carbon stored in biomass. In addition, there may be issues with mechanical instability in sandy soils (Quesada *et al*. 2012), increasing natural disturbances and leading to a lower standing biomass, or favoring smaller trees. This soil effect could be a driver for the differences in carbon stocks between Yangambi and Dja, with height-diameter relationships being the main structural difference between these sites, both for mixed and monodominant forests. A lower maximal tree height is reached on resource-poor and less stable soils in Yangambi. Also in the monodominant forests of Ituri tree height is a major factor driving the higher biomass, but the comparison with mixed forests in Ituri highlights wood density as an additional factor. In these forests, a higher mean wood density is found compared to the Yangambi sites, with the Ituri sites on more sandy soils. In the study of Gourlet-Fleury *et al*. (2011) the contrary was shown, with higher carbon stocks in less fertile regions due to a tendency to support slow-growing species with a higher wood density and possibly due to a slower turnover rate (Galbraith *et al*. 2013). Nevertheless, we show that when eliminating differences in the species pool, via the analysis of monodominant forests, a lower aboveground carbon stock on less fertile soils of Yangambi is explained through a lower maximal tree height.

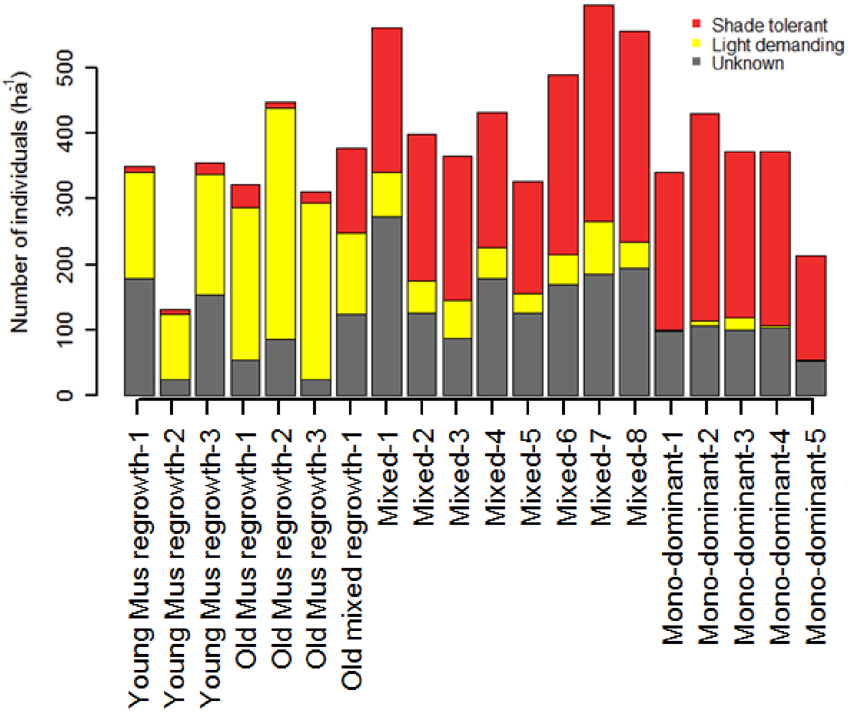
To date, no clear general relationship has been established between forest carbon stocks and soil properties, and the available results are contradictory (Laurance *et al.* 1999; Clark & Clark 2000; Gourlet-Fleury *et al.* 2011, Quesada *et al.* 2012). If soil texture or other soil properties are indeed related to forest structure, applying equations developed from trees on a different soil type could give rise to highly inaccurate carbon stock estimates across the Congo Basin. Regressions based on large sub-continental regions that are used (Banin *et al.* 2012; Feldpausch *et al.* 2012), may need to be replaced with a regional approach or an approach based on climatic or soil classifications.

However, the spatial distributions of soil type, forest structure and carbon stocks in tropical Africa are poorly known (Batjes 2008; Saatchi *et al.* 2011) and quantification of the carbon emission and storage potential of these forests remains challenging. At local scales, emissions resulting from deforestation, degradation and regrowth can be determined by measuring forests in different stages of degradation (Gibbs *et al.* 2007). Looking at different regrowth stages in our study area, we made two main observations. Firstly, within the first few decades of regrowth, the aboveground carbon stock did not return to its initial state. This trend could persist, since tree species composition has changed and there is a tendency towards species with a lower wood density (Supplementary Table S3.2), hence decreasing the total carbon stock of this type of disturbed forest. Secondly, soil carbon stocks remain high even after degradation of the forest (Figure 3.4), but do show sensitivity to land-use change. An initial non-significant soil carbon decline is observed due to forest clearing for agricultural use. However, the stock rapidly increases to a significantly higher level after two decades of regrowth. Because of the large amount of carbon stored in the soil it will be crucial to quantify the impact of possible future agricultural intensification, since land use after deforestation has significant potential effects on soil carbon (Guo & Gifford 2002; Ogle *et al.* 2005; Ramankutty *et al.* 2007). If future demand for agricultural crops exceeds the yield of the traditional agricultural activities, agricultural intensification will become a necessity. This intensification could eventually require less land than currently to sustain the local population (DeFries & Rosenzweig 2010; Pelletier *et al.* 2012), thereby securing the remaining forest and its carbon stock. However, the choice of agricultural system will critically affect the carbon balance. Land management can, depending on the disturbance intensity, drastically change the amount of carbon stored in the soil, with tillage and fertilization affecting soil disturbance and carbon decomposition rates (Guo & Gifford 2002). The local integrated carbon balance of different agricultural systems therefore needs to be considered.

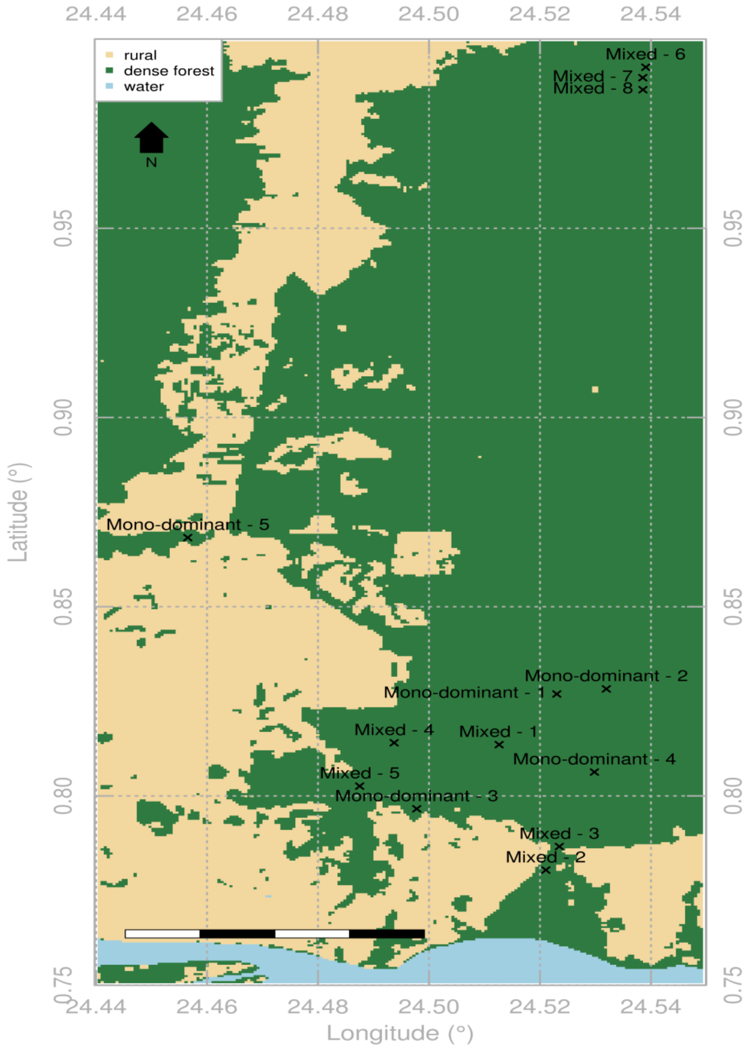
In the context of climate change mitigation policies (e.g. REDD) for tropical Africa, major challenges remain. Our results show that height-diameter regressions developed from data obtained from forest sites in the outer regions of the Congo Basin do not produce accurate aboveground carbon stock estimates for central areas of the basin. The current best carbon stock estimate for structurally intact closed canopy African tropical forest (Lewis *et al.* 2009) of 202 Mg C ha^{-1} is, therefore, probably an overestimate. There are significant consequences of the 24% overestimation of aboveground carbon stocks in Yangambi. With annual net deforestation and degradation rates in the Congo Basin estimated to be 0.17% and 0.09%, respectively, between 2000 and 2005 (Ernst *et al.* 2012), this biased carbon stock estimate could result in an overestimation of carbon loss. Nevertheless, confirmation of our results is needed through the establishment of inventory plots throughout the basin covering a larger area. Additionally, even though correcting for a bias in height estimations using site-specific models is shown to be important, it does not guarantee that the biomass estimations are correct. The use of pantropical biomass allometric equations (e.g. Chave *et al*. 2005) has been shown to produce large errors at multiple sites (e.g. Ebuy *et al*. 2011; Ngomanda *et al*. 2014) and may be biased for Africa due to fewer available data. Consequently, within this study, carbon stock estimates in this study are also prone to errors. The set-up of local biomass models could be an option to improve these estimations (Van Breugel *et al*. 2011), although the need for intensive sampling would be highly time and cost intensive.

Allometric equations developed specifically for Central Africa and pan-tropical models need to be validated and updated in order to improve the quality of regional and national carbon stock inventories. In addition, the spatial distribution, variability and response to future climate of soil carbon stocks are practically unknown (Ramankutty *et al*. 2007; Batjes 2008). We conclude that a spatially explicit understanding of both the aboveground carbon and the soil carbon stock remains crucial in developing an overall carbon budget for tropical African forests in order to support current and future climate policy measures.

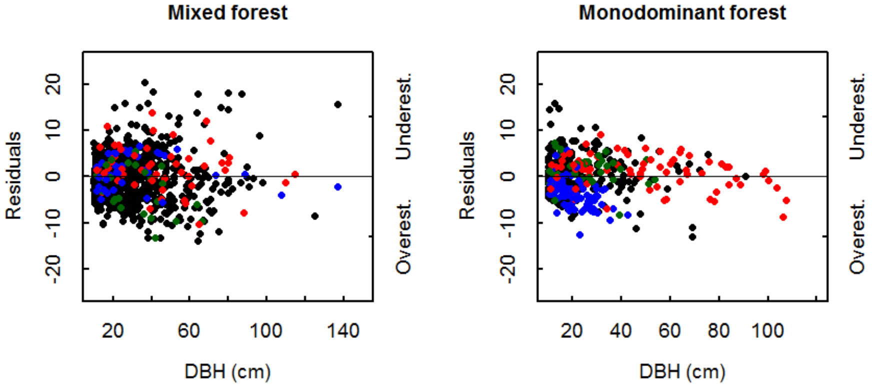
3.5 Supplementary Information



Supplementary Figure S3.1: Abundance of shade-tolerant and light-demanding individuals (Lebrun & Gilbert 1954) in each plot. For a large part of individuals the light tolerance is unknown. The abundance of light-demanding species compared to the abundance of shade-tolerant species is indicative for the disturbance (both natural and anthropogenic) in the plot. In young and old *Musanga* regrowth plots, the largest fraction of individuals are light-demanding species. This ratio becomes smaller for old mixed regrowth forest. In the mixed forest plots, shade-tolerant species represent the largest fraction. In monodominant forest plots, light-demanding species are almost absent.



Supplementary Figure S3.2: Plot distribution of mixed and monodominant forest plots in the Yangambi reserve. Green areas denote forested areas with a forest cover ≥ 50%, light brown areas denote areas with a forest cover < 50% and blue areas denote water bodies. Map data is based upon moderate resolution vegetation continuous field calibrated Landsat data with a spatial resolution of ~60m as described by Hansen *et al.* (2008) (http://globalmonitoring.sdstate.edu/projects/congo/). In the scale bar, one block equals 1.5 km.



Supplementary Figure S3.3: Residuals of optimized models for mixed and monodominant old-growth forest, with most abundant species in mixed forest *Scorodophloeus zenkeri* (red), *Petersianthus macrocarpus* (blue) and *Panda oleosa* (green), and in the monodominant forest *Gilbertiodendron dewevrei* (red), *Cavacoa quintasii* (blue) and *Scorodophloeus zenkeri* (green).

Supplementary Table S3.1: Summary soil properties per depth increment for each forest type. Soil organic carbon (SOC; Mg C ha^{-1}) and bulk density (BD; g cm^{-3}).

	Depth	**SOC**	**BD**	**% C**	**% N**	**Texture (% sand - silt - clay)**
Young *Musanga* regrowth	0-10	25.6 ± 1.9	1.27 ± 0.03	2.02 ± 0.19	0.14 ± 0.01	88 - 2 - 9
	10-20	11.8 ± 1.2	1.30 ± 0.00	0.90 ± 0.09	0.07 ± 0.01	87 - 3 - 10
	20-30	11.3 ± 1.7	1.30 ± 0.00	0.87 ± 0.13	0.06 ± 0.01	87 - 3 - 10
	30-50	11.7 ± 1.5	1.31 ± 0.00	0.45 ± 0.06	0.03 ± 0.01	85 - 2 - 13
	50-100	18.8 ± 0.4	1.32 ± 0.00	0.29 ± 0.01	0.02 ± 0.00	84 - 2 - 14
Old *Musanga* regrowth	0-10	24.9 ± 5.6	1.29 ± 0.03	1.93 ± 0.47	0.15 ± 0.04	83 - 2 - 16
	10-20	14.1 ± 2.9	1.35 ± 0.01	1.05 ± 0.22	0.08 ± 0.01	81 - 2 - 17
	20-30	15.2 ± 4.6	1.33 ± 0.01	1.15 ± 0.35	0.09 ± 0.03	82 - 2 - 16
	30-50	18.1 ± 4.9	1.41 ± 0.00	0.64 ± 0.18	0.05 ± 0.01	78 - 3 - 19
	50-100	28.3 ± 3.7	1.41 ± 0.00	0.40 ± 0.05	0.03 ± 0.01	78 - 2 - 20
Mixed	0-10	21.4 ± 6.5	1.29 ± 0.04	1.68 ± 0.57	0.13 ± 0.04	85 - 2 - 14
	10-20	16.1 ± 4.8	1.30 ± 0.01	1.24 ± 0.38	0.10 ± 0.03	85 - 2 - 13
	20-30	12.9 ± 2.8	1.31 ± 0.01	0.99 ± 0.22	0.08 ± 0.02	85 - 2 - 13
	30-50	15.7 ± 1.4	1.32 ± 0.01	0.60 ± 0.05	0.05 ± 0.01	84 - 3 - 14
	50-100	28.5 ± 3.1	1.37 ± 0.03	0.42 ± 0.05	0.03 ± 0.00	80 - 2 - 18
Mono-dominant	0-10	30.9 ± 4.4	1.21 ± 0.04	2.56 ± 0.44	0.18 ± 0.03	84 - 3 - 12
	10-20	19.1 ± 7.0	1.29 ± 0.04	1.50 ± 0.60	0.10 ± 0.04	85 - 3 - 13
	20-30	19.1 ± 5.9	1.31 ± 0.03	1.46 ± 0.45	0.10 ± 0.03	84 - 3 - 13
	30-50	22.4 ± 3.1	1.33 ± 0.04	0.84 ± 0.11	0.05 ± 0.01	83 - 3 - 14
	50-100	36.3 ± 6.7	1.35 ± 0.04	0.54 ± 0.11	0.03 ± 0.01	81 - 3 - 16

Supplementary Table S3.2: Summary plot characteristics: stem density (SD; ha^{-1}), basal area (BA; m^{2} ha^{-1}), mean wood density (WD; g cm^{-3}) weighted by basal area, aboveground carbon stock (AGC; Mg C ha-1), soil organic carbon stock (SOC; Mg C ha^{-1}) for depths up to 30 and 100 cm.

Site	Coordinates	SD	BA	WD	AGC	SOC 0-30 cm	SOC 0-100 cm
Young *Mus* regrowth-1	N 00°47'48.7" E 24°29'39.2"	350	5.39	0.37	6.7	48.3	80.1
Young *Mus* regrowth-2	N 00°47'34.8" E 24°29'51.1"	132	2.06	0.34	2.0	48.9	78.2
Young *Mus* regrowth-3	N 00°47'40.5" E 24°28'55.8"	364	6.65	0.44	10.3	29.2	64.6
Old *Mus* regrowth-1	N 00°47'20.4" E 24°31'01.5"	322	20.44	0.39	46.6	63.0	107.4
Old *Mus* regrowth-2	N 00°47'43.1" E 24°29'32.5"	447	16.63	0.32	27.8	61.4	118.1
Old *Mus* regrowth-3	N 00°47'36.9" E 24°29'26.0"	313	17.8	0.36	37.1	38.1	76.1
Old mixed regrowth-1	N 00°52'56.8" E 24°19'46.1"	384	19.48	0.56	81.8	-	-
Mixed-1	N 00°48'50.6" E 24°30'47.2"	563	34.81	0.64	168.0	49.1	91.1
Mixed-2	N 00°46'51.1" E 24°31'14.2"	403	35.25	0.61	174.6	44.3	87.7
Mixed-3	N 00°47'14.5" E 24°31'24.7"	367	30.69	0.6	150.3	42.3	85.7
Mixed-4	N 00°48'52.2" E 24°29'38.9"	432	33.01	0.64	168.6	66.0	114.3
Mixed-5	N 00°48'11.0" E 24°29'16.5"	329	25.2	0.62	124.2	50.3	94.1
Mixed-6	N 00°59'33.2" E 24°32'20.6"	490	32.63	0.67	203.8	-	-
Mixed-7	N 00°59'23.3" E 24°32'18.7"	598	31.47	0.61	146.1	-	-
Mixed-8	N 00°59'11.8" E 24°32'18.8"	556	29.2	0.64	148.2	-	-
Mono-dominant-1	N 00°49'38.7" E 24°31'21.2"	344	31.8	0.66	183.0	86.0	153.5
Mono-dominant-2	N 00°49'39.9" E 24°31'56.7"	436	32.06	0.67	173.6	73.6	137.7
Mono-dominant-3	N 00°47'51.1" E 24°29'52.6"	376	30.57	0.66	166.4	65.6	120.0
Mono-dominant-4	N 00°48'22.7" E 24°31'47.3"	374	27.69	0.66	145.6	47.1	96.3
Mono-dominant-5	N 00°52'04.1" E 24°27'25.2"	217	27.19	0.66	159.0	73.2	131.2

4

Regional variability in height-diameter relationships

Kearsley, E., Moonen, P., Hufkens, K., Doetterl, S., Lisingo, J., Toirambe, B., Baert, G., Steppe, K., Muys, B., Boeckx, P., Beeckman, H. & Verbeeck, H. (to be submitted)

Abstract

Quantification of variability in tree allometry and forest structure can improve our understanding of fundamental physiological trade-offs and improve the estimation of forest aboveground carbon storage. However, central African tropical forest remain underexplored in this regard. To improve our knowledge on how tree allometry varies across regional and local scales in a central region of the Congo Basin, we investigate height-diameter relationships at three old-growth forest sites. We show that the local height-diameter relationship differs from regional models used for this area, with a lower tree height found at the three sites, although a significant variability is also found between the sites.

4.1 Introduction

Reliable models determining the relationship between tree height and diameter in tropical forests are important to produce accurate estimates of tropical tree biomass (Feldpausch *et al.* 2012; Popkin 2015). It is unavoidable to use such models since the assessment of individual tree heights in tropical forest inventory plots is time consuming and thus costly and often only a limited number of trees is measured. Tree heights of the unmeasured trees are then estimated using either stand-specific or more generalized or region-wide equations. For tropical forests, recently a few generalized and region-wide equations have been developed (Lewis *et al*. 2009; Banin *et al.* 2012; Feldpausch *et al*. 2012). However, tree allometry can be highly variable, and the validity of using these models and the biases introduced by their use in different tropical forest regions needs to be quantified.

The structure of tropical rainforest in data-poor regions like the central Congo Basin still remains largely underexplored. The largest African continental study of aboveground biomass (AGB) and forest structure by Lewis *et al*. (2013) indicates significant intra-continental differences, although central Congo Basin is underrepresented in the study. In a previous study (*Chapter 3*), we identified significant differences in height-diameter relationships in this central region compared to the outer regions of the Congo Basin (Feldpausch *et al*. 2011; Banin *et a*l. 2012). The need for a better characterization of forest structure and tree architecture for this region is high, and further exploration regarding the variation of tree allometries is necessary (Wang *et al*. 2006; Feldpausch *et al*. 2011; Kempes *et al*. 2011; Banin *et al*. 2012). To improve our knowledge on how tree allometries vary across regional and local scales in this central region of the Congo Basin, we investigate height-diameter relationships for three old-growth forest sites. Two research questions were addressed (1) do generalized models for Central Africa provide a good fit for this region, or is a regional model necessary? (2) within this region, is allometry similar at different sites or do site-specific models need to be produced? We are specifically interested if the lower asymptotic tree height found at the Yangambi site (*Chapter 3*) is applicable for a larger area.

4.2 Methodology

Study area and data collection

This study is carried out at three intact tropical forest sites in the area of Kisangani, Democratic Republic of the Congo (DRC), namely at Yangambi, Yoko and Yambela (Figure 4.1). All sites are within approximately 100km distance from each other and a similar climate is assumed, as described in *Chapter 2*. The study area and data collection for the Yangambi site is described in detail in *Chapter 2*. The second site is located at the Yoko forest reserve (N00°17'; E25°18'). Five one hectare plots were inventoried for trees with DBH ≥ 10 cm and species are determined. Tree height was measured for all trees in twelve smaller plots of 0.25 hectare. The third site is located in Yambela (N00°21'; E24°49'). As this data was collected within a different project, inventory approaches were not uniform. In Yambela, a nested sampling was used, namely trees with DBH ≥ 30 cm are measured in twelve 0.25 ha plots, and smaller trees with DBH 10 - 30 cm are measured within 25x25 m subplots. Of all trees with DBH < 50cm, one in four have been measured for tree height. For all larger trees, half have been measured for tree height. Tree heights at all three sites were measured using a Nikon Laser Rangefinder Forestry Pro hypsometer. Height measurements at the three sites were made within the context of different projects, with differences in sampling protocols. A similar number of trees was however measured in different diameter classes, reducing the error introduced by sampling differences.

Basic forest structure variables for the three sites, namely plot specific basal area, stem density and weighted wood density, do have a high similarity among the three sites (Table 4.1).

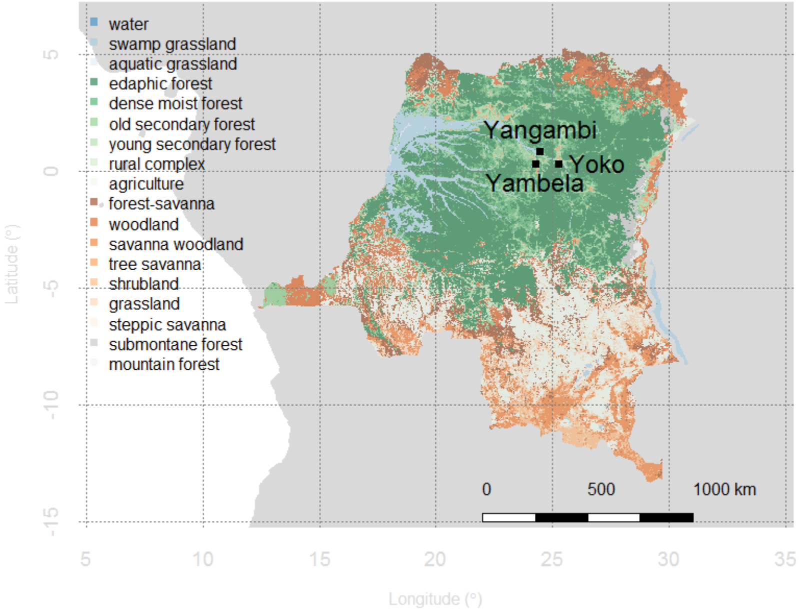


Figure 4.1: Location of the three study sites Yangambi, Yoko and Yambela on a land cover map of DRC (Verhegghen *et al*. 2012).

Table 4.1: Site properties. Plot averages and standard deviations are provided for the different sites. Plot-level mean wood density is weighted by basal area.

	Yangambi	**Yoko**	**Yambela**
Stand characteristics			
Stem density (ha^{-1})	419 ± 89	469 ± 35	467 ± 58
Basal area (m^{2} ha^{-1})	32 ± 3	34 ± 3	31 ± 5
Wood density (g cm^{-3})	0.63 ± 0.02	0.64 ± 0.02	0.63 ± 0.04
Coordinates			
Latitude	0.7995	0.2918	0.3493
Longitude	24.5077	25.3113	24.8217
Altitude (masl)	479 ± 13	471 ± 5	-
Plot size (ha)	1	0.25 - 1	0.25 (0.0625)
Number of plots	6	5	12

Height-diameter model development

The statistical analysis consisted of three main stages. First a selection is made of the best model function for this region. Secondly, the selected model is compared to generalized models for Central Africa. Finally, site-level differences are assessed by introducing site as random effect in a nonlinear mixed effects (NLME) version of the regional model.

Height-diameter model selection

To select the optimal height-diameter model for the study region, six commonly used function forms were compared (Supplementary Table S4.1). All models were fitted by nonlinear least-squares estimations (‘nls’ function in ‘nlme’ package in R software; Pinheiro *et al.* 2009) for the three study sites combined. The best model fit was selected by comparing Akaike Information Criterion (AIC) and the standard deviation of residuals, a measure of the variation explained by the model and residuals were examined to assess any model-specific biases (Supplementary Table S4.2 & Figures S4.1-3). The three parameter exponential function provided the best statistical fit, as demonstrated by the lowest AIC and RSE values (Table S4.2). Nonetheless, the difference between the best fit and worst was not large. Additionally, residual analysis did not reveal large differences between the studied function forms (Supplementary Figure S4.1).

A regional model

The three-parameter exponential equation was selected for further analysis:

$$H = a - be^{-cD} \qquad (1)$$

In this function, H is the individual tree height, D is the diameter at breast height, and a, b and c are the estimated curve parameters, which represent, respectively, the maximum asymptotic height, the difference between minimum and maximum height, and shape of the curve (Banin *et al*. 2012). This model is further referred to as the *regional model.*

Height-diameter models for Central Africa have recently been proposed by Feldpausch *et al*. (2012) and Banin *et al*. (2012). The validity of these models has however not been shown for this region in the central Congo Basin. Therefore, a comparison is made between these models and our regional model. Specifically, a residual analysis is performed comparing height estimations based on the generalized Central African models with measured height data for this region by RMSE and paired t-tests. This is done for the entire dataset, and for diameter classes of 10-20 cm, 20-40 cm and larger than 40 cm to assess biases in residuals across tree sizes.

NLME model

The three different sites used for setting up the regional model can have an important influence on the height-diameter relationship. Since trees within the same site are likely to be more similar in allometry than trees selected at random, related to stand density and site-specific characteristics, residuals are auto-correlated. However, nonlinear mixed effects (NLME) models can account for this dependence. The regional model is therefore also assessed by a NLME model, with ‘site” introduced as random effect (using ‘nlme’ function in ‘nlme’ package in R software; Pinheiro *et al.* 2009). Random effects were applied to all model parameters (a, b and c) to account for between-site variation (tested as described in Pinheiro & Bates 2000 Chapter 6), resulting in the NLME version of the 3-parameter exponential regional model:

$$H_{ij} = (a + \alpha_i) - (b + \beta_i)e^{-(c+\gamma_i)D_j} + \varepsilon_{ij} \tag{2}$$

with sites *i* and individuals *j*. The fixed effects a, b and c represent the mean values of the parameters in the population of individuals. The site deviations are represented by the random effects α_i, β_i and γ_i. The errors ε_{ij} are independently distributed as N(0, σ^2) and independent of the random effects. Parameters were estimated using the restricted maximum likelihood (REML) method. This allows for a comparison with the regional model by ANOVA to test the significance of including the random effects, as both models have the same fixed effects.

Next, a more detailed assessment is made of the between site differences in height-diameter allometry. The estimates of the random effects are used to predict heights at the three sites, and RMSE and paired t-tests are used to evaluate the predictions. This is again done at the three diameter classes.

4.3 Results

Tree height at the studied region could not be accurately estimated using the generalized Central African height-diameter relationships of Banin *et al.* (2012) and Feldpausch *et al.* (2012) (Figure 4.2). The residual analysis comparing measured and estimated tree heights showed that both generalized models produce an overestimation for tree heights in this region, for large trees and most small trees (Table 4.2; Figures 4.3a & 4.3b). Only for small trees in Yambela the general models estimate tree heights accurately (Table 4.2). The regional model (Table 4.3) performs significantly better in this area (Table 4.2; Figure 4.3c).

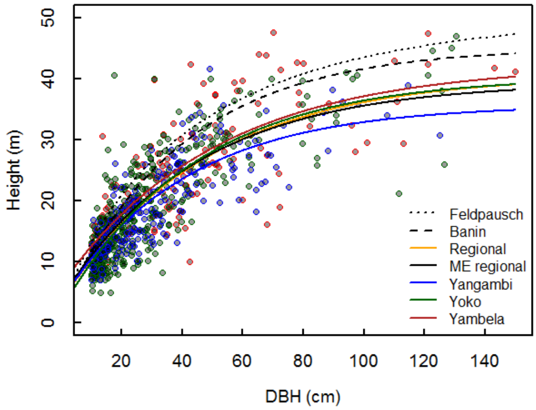


Figure 4.2: Height-diameter models for the studied region, namely the regional model (orange), the mixed effects regional model (full black line) with site-specific deviations for Yangambi (blue), Yoko (green) and Yambela (red). The generalized models for Central Africa by Feldpausch *et al*. (2012) (black dotted line) and Banin *et al*. (2012) (black dashed line) are indicated.

The regional model, however, does not necessarily produce accurate estimation for all sites separately. For both Yangambi and Yambela, the estimated heights were significantly different from the measured heights (Table 4.2). Introducing 'site' as a random effect in the mixed regional model proved to be a significant (p = 0.01) improvement of the model. This gives a first indication that site-specific differences in height-diameter relationships are important for this region.

The site-specific random deviations of the mixed effects model also show significant differences and produce significantly different height estimates when used across sites (Table 4.4). However, inspection of residuals at different diameter classes reveals that the differences are not equally large for all classes (Table 4.4). The heights in the smallest diameter class (10-20 cm) in Yangambi can be accurately estimated using the site-specific model of Yoko, although no longer for larger diameters. Conversely, tree height of trees up to 40cm DBH in Yoko can be correctly estimated using the mixed model for Yangambi. Trees in the largest diameter class in Yoko can be predicted by the model for Yambela. In Yambela, height estimations for the largest trees can be accurately made using the relationship for Yoko, while this is not the case for the smallest diameter class.

Table 4.2: The regional model and two generalized Central African models are used to estimate tree height in Yangambi, Yoko, Yambela and the combination of the three sites (All sites). Height estimations are compared over the entire diameter range (All trees), and for different diameter classes. RMSE between measured heights and estimated heights through different models is provided; p values of paired t-test are indicated: * p<0.05, ** p<0.01, *** p<0.001.

			General Central African model	
		Regional	**Feldpausch *et al.* (2012)**	**Banin *et al.* (2012)**
Measured data				
Yangambi	**All trees**	4.4 **	7.7 ***	6.6 ***
	10-20 cm	3.1	4.5 ***	3.5 ***
	20-40 cm	4.3 **	8.0 ***	6.6 ***
	> 40 cm	5.8 *	10.2 ***	9.1 ***
Yoko	**All trees**	4.6	6.7 ***	5.7 ***
	10-20 cm	3.8	5.5 ***	4.4 ***
	20-40 cm	5.6	8.0 ***	6.9 ***
	> 40 cm	5.2	7.7 ***	6.7 ***
Yambela	**All trees**	6.2 **	7.4 ***	6.7 ***
	10-20 cm	4.5 ***	3.8	3.7
	20-40 cm	5.6	7.3 ***	6.5 ***
	> 40 cm	7.4	9.2 ***	8.3 ***
All sites	**All trees**	4.9	7.1 ***	6.1 ***
	10-20 cm	3.7	5.1 ***	4.2 ***
	20-40 cm	5.2	7.9 ***	6.7 ***
	> 40 cm	6.2	8.9 ***	7.9 ***

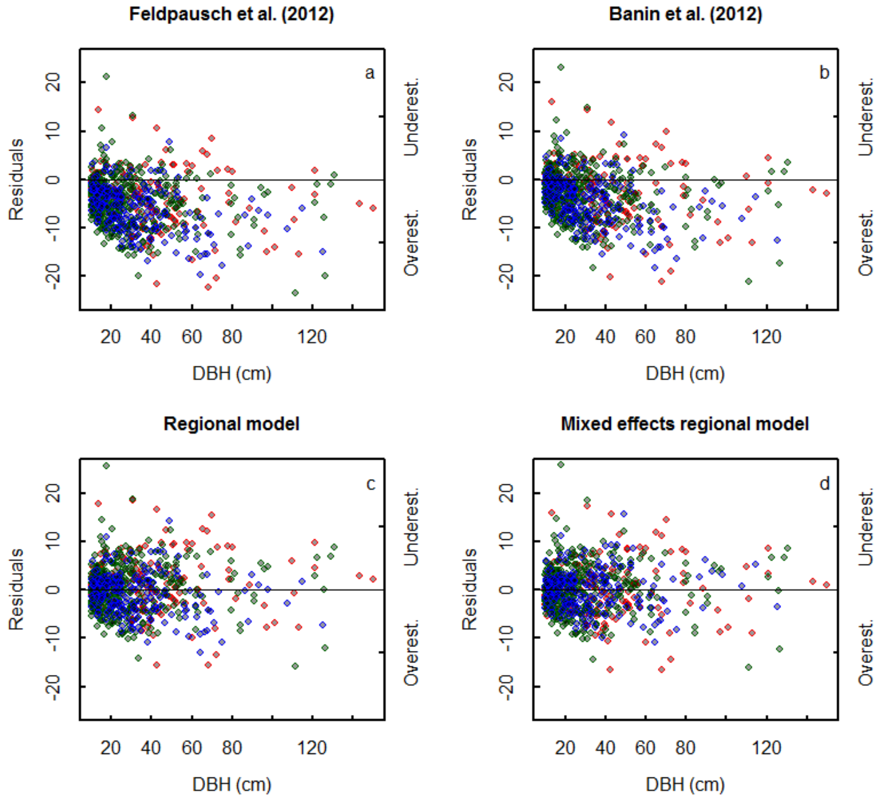


Figure 4.3: Residual analysis of height estimations of the three sites Yangambi (blue), Yoko (green) and Yambela (red) of the models by (a) Feldpausch *et al*. (2012); (b) Banin *et al*. (2012); (c) the regional model and (d) the regional mixed effects model with 'site' as random effect.

Table 4.3: Parameterization of the 3-parameter exponential model (H = a-b*exp(-c*D)) fitted by a nonlinear least-square estimation (NLS; regional model) and the nonlinear mixed effects (NLME) model with 'site' as random effect, with three sites Yangambi (Ygb), Yoko and Yambela (Yamb).

NLS	**Coeff**	**value**	**SE**	**t value**	**p value**				
	a	40.599	1.615	25.2	<0.001				
	b	37.181	1.247	29.8	<0.001				
	c	0.021	0.002	10.1	<0.001				
	RSE	4.916							
	AIC	4612							
NLME	**Fixed effect**					**Random effect**	**Site-specific coefficients**		
	Coeff	**value**	**SE**	**t value**	**p value**	**SD**	**Ygb**	**Yoko**	**Yamb**
	a	39.402	2.241	17.6	<0.001	2.958	35.674	40.315	42.218
	b	35.372	2.043	17.3	<0.001	2.893	32.039	38.090	35.989
	c	0.022	0.002	9.2	<0.001	0.002	0.0243	0.023	0.020
	RSE	4.818							
	AIC	4607							

Table 4.4: The site-specific estimates as random effects of the NLME model are used to estimate tree height in Yangambi, Yoko and Yambela. Height estimations are compared over the entire diameter range (All trees), and for different diameter classes. RMSE between measured heights and estimated heights through different models is provided; p values of paired t-test are indicated: * p<0.05, ** p<0.01, *** p<0.001.

		Site-specific random model deviations		
		Yangambi	**Yoko**	**Yambela**
Measured data				
Yangambi	**All trees**	4.2	4.5 **	4.8 ***
	10-20 cm	3.1	3.2 *	3.4 ***
	20-40 cm	4.2	4.3 **	4.9 ***
	> 40 cm	5.4	5.9 **	6.2 ***
Yoko	**All trees**	4.8	4.6	5.0 ***
	10-20 cm	3.8	3.7	4.4 ***
	20-40 cm	5.6	5.6	5.8 ***
	> 40 cm	5.9 ***	5.8	5.2
Yambela	**All trees**	6.5 ***	6.2 **	5.9
	10-20 cm	4.6 ***	4.7 ***	3.8
	20-40 cm	5.7 *	5.6	5.5
	> 40 cm	8.0 ***	7.3	7.3

4.4 Discussion

We investigate variability of height-diameter relationships at the regional and the site-level in a central study area in the Congo Basin. The first main finding is that the regional height-diameter relationship differs from generalized Central African models used for this area. Tree height in this region would be overestimated using these models by on average 6 to 7m, going up to an average of 9m for larger trees. Secondly, a high variability is found in height-diameter relationships at the site-level, indicating that even though a regional height-diameter model significantly improves height estimations, site-specific models can still improve its accuracy.

Lower tree height generally found in this region

We present a general height-diameter relationship for this region in the central Congo Basin based on measurements in three old-growth forest sites. A lower asymptotic tree height is found compared to the current general relationships by Feldpausch *et al*. (2012) and Banin *et al*. (2012). These generalized models for Central Africa systematically overestimate tree height in this region. Additionally, all site-specific random deviations from the mixed effects height-diameter model show a lower height-diameter relationship compared to the general Central African relationships, emphasizing the generality of the results. This confirms that the lower tree heights found earlier locally in Yangambi (*Chapter 3*) is probably applicable for a larger area in the central Congo Basin. The central Congo Basin region as defined by Feldpausch *et al*. (2012) is possibly too large for a uniform height-diameter relationship, bringing forward the need for better demarcation of regions with similar forest structure in tropical Africa. Banin *et al*. (2012) showed that tree allometry is altered by environmental conditions, forest structure and wood density. However, the mean environmental and forest structure variables of our study region do not differ from those in the central African region as indicated by Feldpausch *et al.* (2011), with similar mean annual precipitation, temperature and dry season length. Therefore, other factors driving this differentiation may be related to soil properties, the local available species pool or past natural and anthropogenic disturbances (Clark & Clark 2000; Malhi *et al*. 2006). Within this study, we are not able to identify the importance of each of the different drivers. Yet, this result emphasizes the poor knowledge on spatial distributions of forest structure in tropical Africa (Saatchi *et al*. 2011; Batjes 2008), resulting in large uncertainties for carbon storage (*Chapter 3*).

Significantly different height-diameter relationship at site-level

The use of site-specific height-diameter relationships at other sites showed to introduce significant deviations in the height estimation. This has important implications for carbon estimations in this region, and possibly in general for tropical forests, as site-specific height-diameter parameterizations seems necessary. This is not beneficial for additional fieldwork efforts, since height measurements are both time and cost intensive, and not always feasible. The regional model can therefore still be a good substitute compared to the Central African models, even at the site-level, since the bias of the estimates is significantly reduced. Accordingly, the site-specific models did produce accurate estimates for some diameter classes at different sites. A better understanding of the drivers behind these site-specific differences, and addressing these driving parameters in the regional model, could further improve the site-level height estimates.

Some hints about the driving factors of site-specific variation

The allometry of a tree has been shown to be affected by environmental factors including climate conditions and altitude (Wang *et al*. 2006; Feldpausch *et al*. 2011; Banin *et al*. 2012; Hulshof *et al*. 2015). Specifically, temperature and precipitation seasonality were identified as key drivers of height-diameter relationships across tropical forests (Feldpausch *et al*. 2011). Tree allometry also shows regional dependencies on forest structure through neighboring effects (Henry & Aarssen 1999; Antin *et al*. 2013), light environment (Poorter *et al*. 2003), soil nutrient and water availability (Heineman *et al*. 2011), soil characteristics regarding texture, mechanical stability and rooting depths (Heineman *et al*. 2011; Urban *et al.* 2013), the topography of the terrain (Antin *et al*. 2013) and natural and anthropogenic disturbances (Nogueira *et al*. 2008b).

In this Chapter, we are not able accurately pinpoint the main drivers for the differences in site-level height-diameter relationships, but we list here a few candidate drivers. A first important driver could be differences in soil characteristics. This is further developed in *Chapter 5* for Yoko and Yangambi. Unfortunately, at the moment no comparable soil characterization is made in Yambela.

Forest structure may also affect individual tree height-diameter allometry (Antin *et al*. 2013; Molto *et al*. 2014). For example, it has been shown that trees that are more widely spaced tended to have a greater diameter, but similar height, compared to those that were more closely packed (Hummel 2000). These differences may be associated with either the increased interference for light or the reduced wind stress in more densely packed stands (Henry & Aarssen 1999). Nevertheless, as all sites in this study are characterized by a similar plot-level stem density and basal area, interference in each stand induced through resource diminution by proximity of neighboring trees is similar and unlikely to cause the variation in allometry. However, more refined comparisons in forest structure could not be made due to the differences in inventory protocols. For example, detailed coordinates were not present at all sites, and different sizes of subplots did not allow for investigation of neighboring effects.

4.5 Conclusions

Best predictions of tree heights in this region can be made using site-specific height-diameter relationships. The regional model however is a good alternative compared to generalized height-diameter relationships for Central Africa, if site-specific measurements are lacking. In general, a better characterization of regional forest structural differences, particularly in the Congo Basin, is necessary despite the ongoing efforts made in this field (e.g. Lewis *et al*. 2013). This is especially true with regards to improving estimates and modeling of aboveground carbon stock and its spatial variability within tropical (African) forests (*Chapter 3*).

Supplementary Information

Table S4.1: Height-diameter function forms tested. H is height, D is diameter and a, b and c are constant coefficients to be estimated.

Equation name	**Function**	**Reference**
Power	$H = aD^b$	Huxley 1932; Enquist 2002
2-parameter exponential	$H = a(1-e^{-bD})$	Meyer 1940
3-parameter exponential	$H = a-be^{-cD}$	Pinheiro *et al*. 1994; Fang & Bailey 1998
Gompertz	$H = ae^{-be^\wedge(-cD)}$	Winsor 1932; Richards 1959
Logistic	$H = a/(1+be^{-cD})$	Winsor 1932; Richards 1959
Weibull	$H = a(1-e^{-bD^\wedge c})$	Yang *et al*. 1978; Bailey 1979

Table S4.2: Parameterization of the different models functions in Table S4.1 for the three sites combined (Yangambi, Yoko and Yambela).

Models	**a**	**b**	**c**	**RSE**	**AIC**
Power	3.481 (0.168)	0.518 (0.013)	na	5.012	4641
2-parameter exponential	36.997 (0.853)	0.029 (0.001)	na	4.960	4625
3-parameter exponential	40.599 (1.614)	37.181 (1.247)	0.021 (0.002)	4.916	4612
Gompertz	37.571 (1.053)	1.753 (0.056)	0.036 (0.002)	4.927	4615
Logistic	36.039 (0.843)	3.622 (0.184)	0.052 (0.003)	4.948	4622
Weibull	43.871 (3.279)	0.040 (0.003)	0.816 (0.048)	4.916	4612

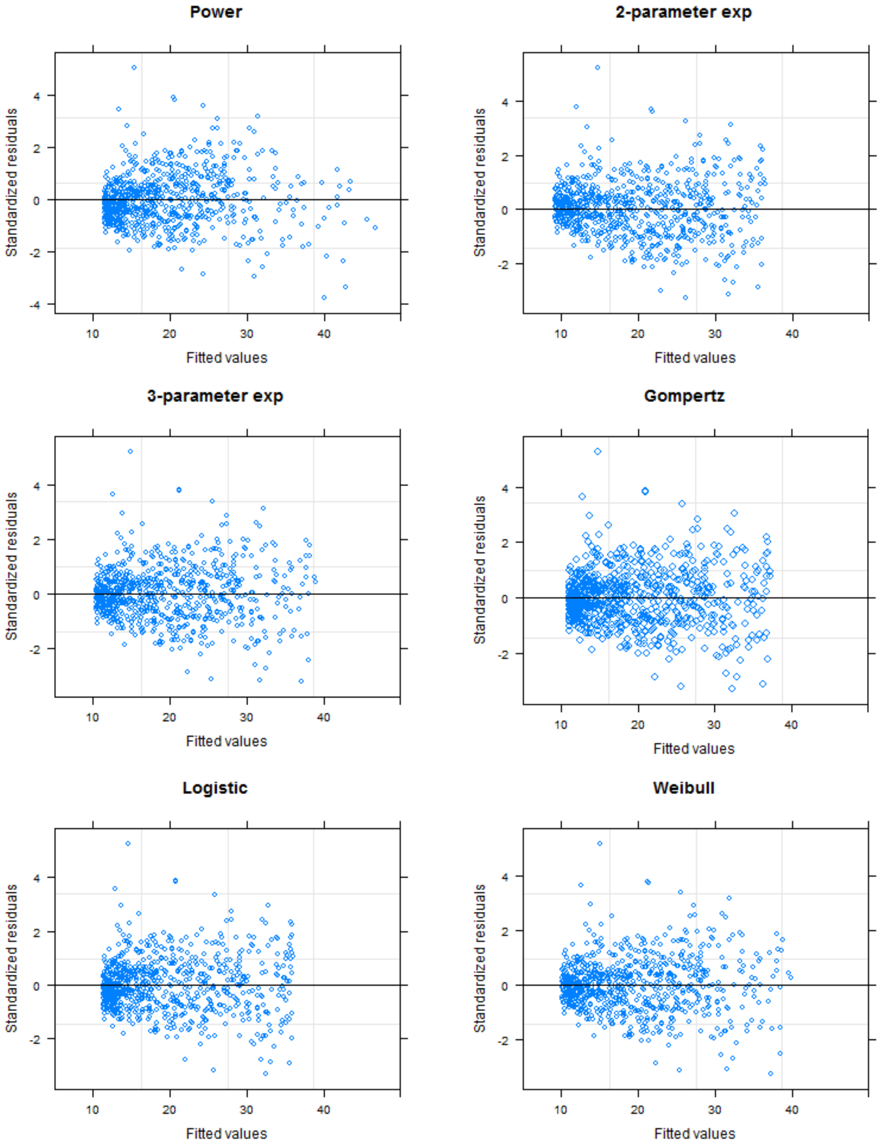


Figure S4.1: Residuals versus fitted height values of the models in Table S4.1 for the three sites combined (Yangambi, Yoko and Yambela) to investigate homogeneity.

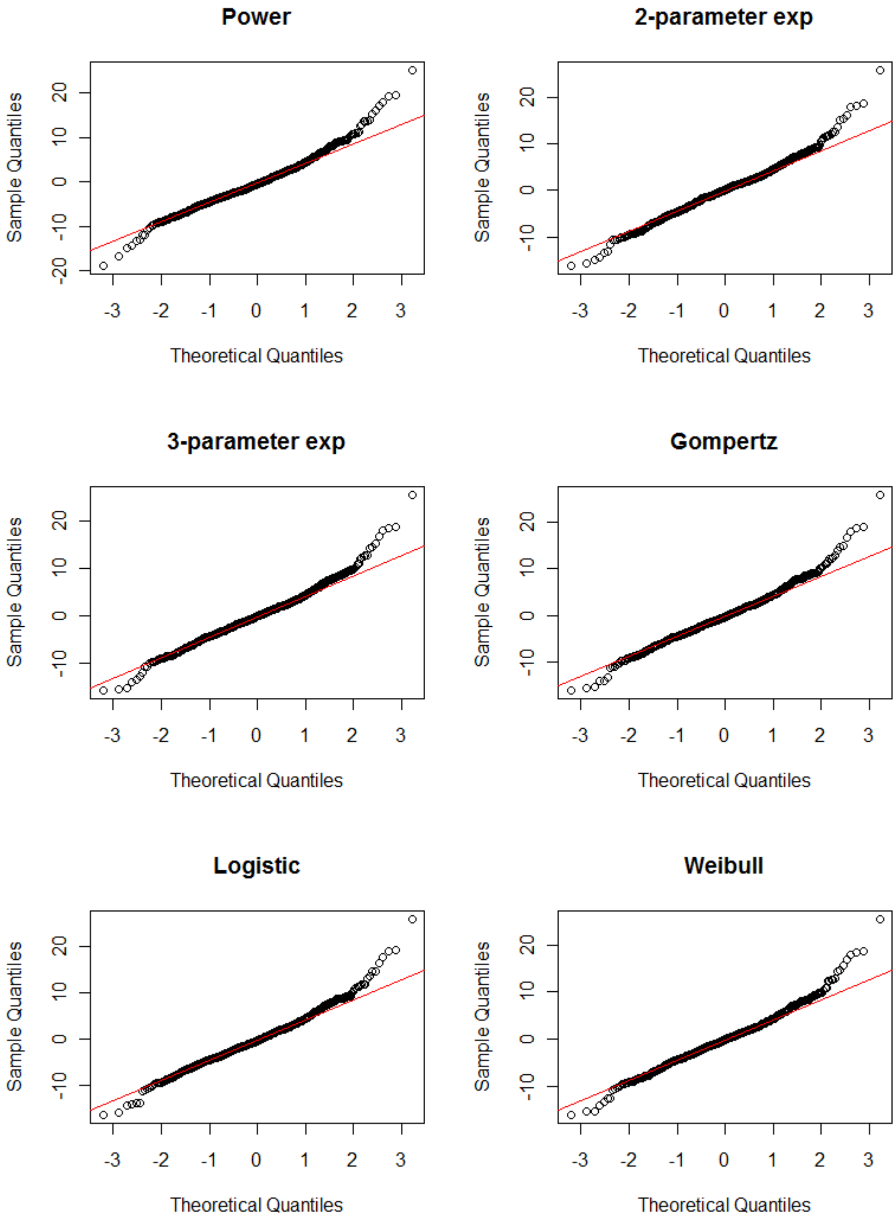


Figure S4.2: QQnorm plots of the models in Table S4.1 for the three sites combined (Yangambi, Yoko and Yambela) to investigate the assumption of normality.

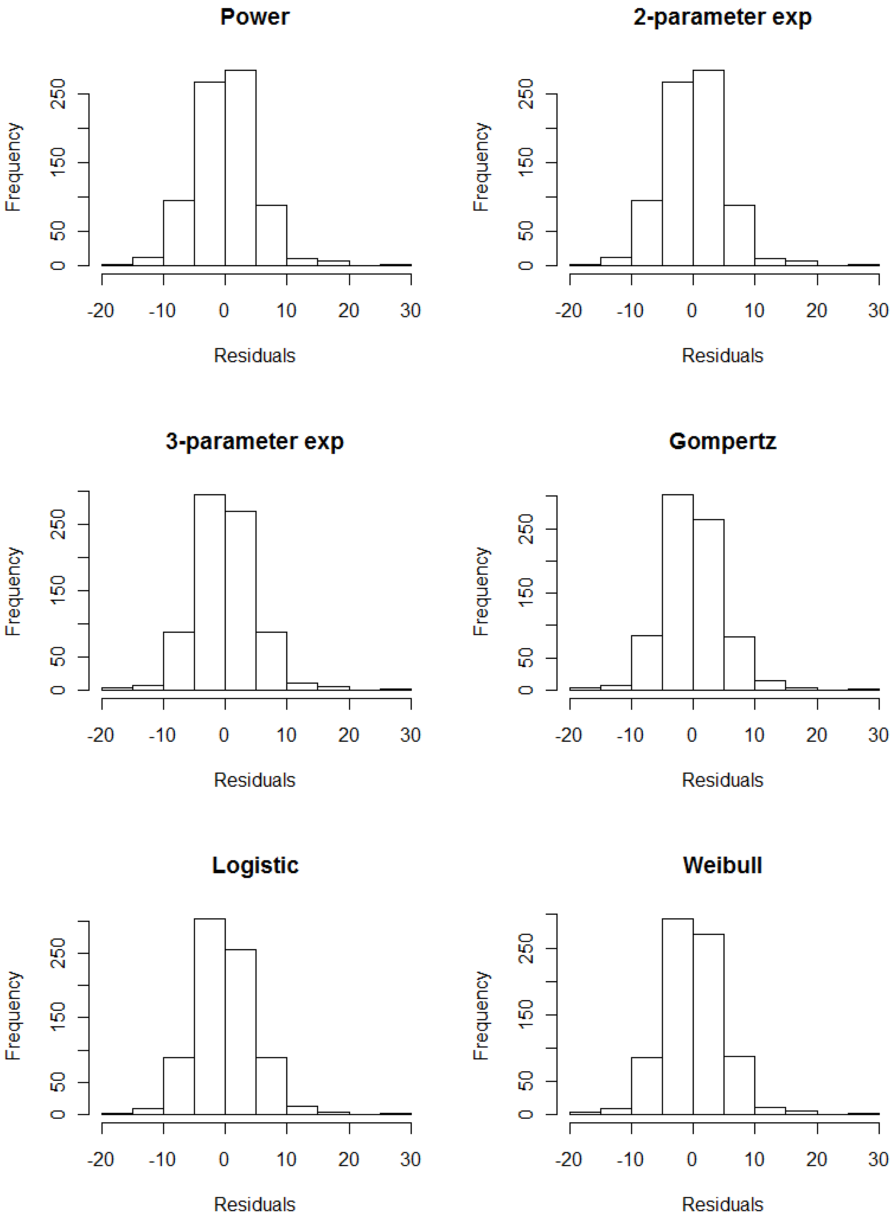


Figure S4.3: Histograms of the residuals of the models in Table S4.1 for the three sites combined (Yangambi, Yoko and Yambela) to test for normality.

5

Aboveground vs. belowground carbon stocks in African tropical lowland rainforest driven by nutrient availability

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Abstract

Tropical rainforests are among the largest terrestrial reservoirs for organic carbon. While the focus of estimating these stocks traditionally lies on the living aboveground biomass, belowground soil organic carbon (SOC) stocks have received little attention. Here we show, on the example of lowland rainforest in the Congo Basin, that despite similar vegetation, soil and climatic conditions, SOC stocks in an area with greater tree height/aboveground biomass were only half compared to an area with lower tree height/aboveground biomass. This suggests a substantial variability in the root:shoot carbon allocation strategy of two similar tropical tree communities for nutrient mining, especially potassium, and is reflected in changes of the SOC mass stored in fractions with differing functional interpretation. We discuss several current hypotheses on the underlying reasons and mechanisms for these findings and argue that adaptation of tree communities to nutrient limitation as well as nutrient limitation as a constraint on microbial activity offers some explanation. Our study highlights that a large and unaccounted variability in SOC stocks is to be expected in African tropical rainforests, introducing additional uncertainty in the response of tropical forest systems to climate change and its contribution to the current terrestrial carbon budget.

5.1 Introduction

The tropics are currently facing unseen changes due to population growth, continuous development of economic infrastructure and, ultimately, land use change through deforestation from natural tropical rainforest system to systems used for agriculture and forest plantations. At the same time, the tropics are a hot-spot of global warming, putting these vulnerable ecosystems under additional stress (Reyer *et al*. 2015; Phillips *et al*. 2009).

Forests are considered the most productive terrestrial ecosystems on earth, containing no less than 45% of the terrestrial carbon stock (Field *et al*. 2003), and have been increasingly recognized as a key player in global climate change mitigation. This holds especially for tropical forests, accounting for approximately 55% of this global stock in forests, with the Amazon basin and the Congo Basin being the largest two contiguous blocks (Pan *et al*. 2011). Research efforts from the last decade have answered the need for large-scale forest monitoring networks in the tropics (Malhi *et al*. 2002; Lewis *et al*. 2013), to gain insight in the spatial variability of the carbon stocks, and hence reduce the uncertainty in regional and global estimates and modeling efforts (Houghton 2005). However, most reports strongly focus on the above-ground carbon stocks, making rudimentary assumptions for the belowground stocks. There is still a large lack of knowledge on SOC stocks in tropical forest systems, their controls and the relationship of biomass allocation and SOC stocks (Malhi *et al*. 2009; Batjes 2008; Saiz *et al*. 2012 and references therein). Predictions of SOC stocks at different spatial scales are frequently based on few SOC depth profiles and additional information mainly regarding land use, soil texture and humidity, often deducted from DEM and soil maps with varying reliability (e.g. McKenzie and Ryan 1999; Mishra et al. 2010; Schwanghart & Jarmer 2011; Zhang et al. 2012). Although uncertainties are large and the soil compartment only compromises around 32% of the carbon stock in the total ecosystem in tropical forests (Pan *et al*. 2011), tropical evergreen forests are probably the biomes with the biggest total SOC storage worldwide (474 Pg C; Jobbágy & Jackson 2000).

The processes that control carbon sequestration in soils and plants of the tropics are likely underlying a different dynamic than those of boreal or temperate forests, as carbon cycling in the tropics is not constrained by climatic factors such as the availability of heat and water and, in addition, often takes place in a nutrient depleted environment due to the highly weathered state of soils (Ferralsols; IUSS Working Group WRB. 2014; Vitousek & Sanford 1986) after millions of years of soil weathering. Additionally, while it is well known that land use change and forest management can affect the SOC stocks in the tropics (Jandl *et al*. 2007; Don *et al*. 2011), much less is known of the effect of tree composition and edaphic gradients on soil carbon stocks, although tree species effects on soil carbon storage are considerable (Finzi *et al*. 1998; Schulp *et al*. 2008). A study for ten Amazonian forests plots reported that the ratio belowground to total NPP remains fairly invariant across a soil fertility gradient (Aragão *et al*. 2009).

In our study we investigate the aboveground vs. belowground carbon stocks in similar tropical lowland rainforest in the Congo Basin on two nearby locations and explore potential drivers behind differences in carbon allocation and retention. For this, we combine an assessment of the aboveground biomass, including species composition and growth characteristics with a depth explicit assessment of SOC stocks in these systems including soil geochemical variables related to soil fertility and an assessment of carbon stabilization in different SOC fractions.

5.2 Methods

Study area

This study was carried out biosphere reserves nearby Kisangani, Democratic Republic of the Congo (DRC). Two sites, ~100 km apart, within this region with similar climatic and topographic conditions as well as tree community structure have been selected. A first site is located in the UNESCO Man and Biosphere reserve in Yangambi and a second site is located in the Yoko reserve (*Chapter 2* and *4*). At both sites five one-hectare plots are inventoried in semi-deciduous mixed forest. A comparison and discussion of forest structure, species composition and light availability at the two sites is available in Supplementary Information.

Tree height and aboveground biomass estimation

Site-specific height-diameter regression models were developed for each forest type (*Chapter 4*). These models were further used to determine tree heights for aboveground carbon (AGC) stock estimation. Despite the differences in plot size between Yangambi and Yoko, roughly the same number of trees are height measured with a similar distribution over the different diameter sizes. The relation of Chave *et al*. (2005) for moist tropical forest including height and wood density was selected for AGC stock estimation, with biomass assumed to be 50% carbon. Site-specific wood density measurements were used for Yangambi (*Chapter 3*), and completed with genus level averages if species level data was not available. For species not determined in Yangambi, values from the Global Wood Density Database (Chave *et al*. 2009; Zanne *et al*. 2009) were used. For the remaining individuals for which no wood density was available, a wood density value was assigned through random sampling of wood density from other individuals within the same site.

Soil and litter sampling and analysis

On five plots per study site, ten soil cores have been taken following an S-curve covering edge and core of each plot and composed to three depth increments (0-30, 30-60, 60-90 cm) and oven-dried (50°C). Within these ten plots carbon stock and bulk density (soil only) have been measured. A more detailed analysis has been made at two plots per study site. Here, the complete litter layer was sampled from a randomly distributed 0.5 × 0.5 m square in triplicate to capture the variability in plant growth/litterfall in the area. Organic layers composed predominantly of litter at different stages of decomposition (L and F-horizons) and to a smaller extent of highly humified organic substances (H-Horizon), but have not been further differentiated for the analysis. After sampling, litter has been dried at 40°C and the dry weight has been taken. For both soil and litter the following additional variables have been measured in these plots:, soil texture, pH (soil only), potential cation exchange capacity (CEC_{pot}), base saturation, bioavailable P, NO_3 and NH_4 and SOC fractions.

Bulk density was determined on composites of 10 samples per plot using Kopecky cylinders. Soil texture was determined by means of the percentage of sand, silt and clay. Analyses were performed on air-dried soil fractions (<2 mm). The sand fraction (>63 μm) was separated by wet sieving; the silt and clay fractions were determined by the Köhn pipette method after dispersion with sodium hexametaphosphate (Pansu & Gautheyrou 2006).

Soil pH was determined potentiometrically in 25 ml 0.01 M $CaCl_2$ (1:2.5 soil:solution ratio) with a glass electrode using a portable multi-parameter Meter HI9828 (Hanna Instruments US Inc., USA). CEC_{pot} was determined by quantifying NH_4^+ exchanged with 2 M

KCl after saturating cation exchange sites with ammonium acetate buffered at pH 7.0 and measured with ICP-MS. Exchangeable Al was extracted by 1 M KCl solution and determined colorimetrically. The total percent base saturation (BS), defined as the relative availability of each cation for CEC_{pot}, was calculated in percent of CEC_{pot}.

Resin-extractable P was determined in the bulk soil using resin-impregnated membrane strips (Sharpley 2009) whereas P in litter was determined by dry ashing. NH_4^+ and NO_3^- were determined in a 1 M KCl extract (ratio 2:1) were measured from filtrates using a continuous flow analyzer (FIAstar 5000, Foss, Denmark) for both soil and litter.

To quantify the distribution of SOC fractions at both study sites, the soil samples were gently broken into smaller pieces by hand, sieved through an 8 mm sieve to get a homogenous substrate with the inherent aggregate structure remaining largely undisturbed (Six *et al.* 1998). A subsample of 100 g of this homogenized soil was then used in the SOC fractionation analysis. We used a method based on the conceptual SOC fraction model proposed by Six *et al.* (1998 & 2002) (Figure 5.1). The scheme consists of a series of physical fractionation techniques applied to isolate functional SOC fractions, differentiated by stabilization mechanisms (chemical, biochemical, and physical) which can also be associated with different turnover times and SOC stability (for an overview see e.g., Christensen 2001; Six *et al.* 2002; von Luetzow *et al.* 2006 & 2007). In a first step, SOC is fractionated into macroaggregate (>250 μm) (M), microaggregate (250 - 53 μm) (m), and free silt & clay (<53 μm) (s+c) fractions by slaking to define water-stable aggregates and no dispersion agent has been used. Then, the macroaggregate fraction gets further processed to derive more subcompartments (see Figure 5.1; Six *et al.* 2002), namely the coarse particulate organic matter (CPOM), microaggregates within macroaggregates (Mm) and silt and clay within macroaggregates (Ms+c). Soil mass and carbon concentrations for all aggregate fractions have been sand-corrected and we modified the original scheme by not separating the sample into a light and a heavy carbon fraction using density flotation, as the light fraction is typically very small at sites with low carbon content (e.g. John *et al.*2005; Don *et al.* 2009).

SOC concentration was measured in 1 g ground subsamples using a dry combustion analyzer (Variomax CN, Elementar GmbH, Hanau, Germany) with a measuring range of 0.2 - 400 mg C g^{-1} soil (absolute C in sample) and a reproducibility of < 0.5% (relative deviation). Recovery rates exceeding 97% and 91% were obtained for the soil mass and carbon mass, respectively, across all fractions. The isolated fractions were analyzed for total SOC using an elemental analyzer (ANCA-GSL PDZ Europa, Crewe, UK) coupled to an Isotope Ratios Mass Spectrometer (2020, SerCon, Crewe, UK). For each depth increment, carbon stocks (Mg C ha^{-1}) were determined as a product of bulk density (g cm^{-3}), carbon concentration (mg g^{-1}) and thickness of the increment layer (cm). For the litter, carbon stocks were determined as the product of the litter mass per area and the litter carbon concentration.

Statistics

Statistical tests for differences between the means of assessed soil variables between the two sites have been performed for the whole dataset and for top and subsoil samples separately using an ANOVA analysis with a post-hoc test to do multi-group comparisons (Bonferroni and Tamhane test; Bonferroni for normally distributed data, Tamhane for not-normal distributed data). Bonferroni corrections and Tamhane's T2 with SAS Enterprise 4.2 (SAS Institute Inc., Cary, NC, USA).

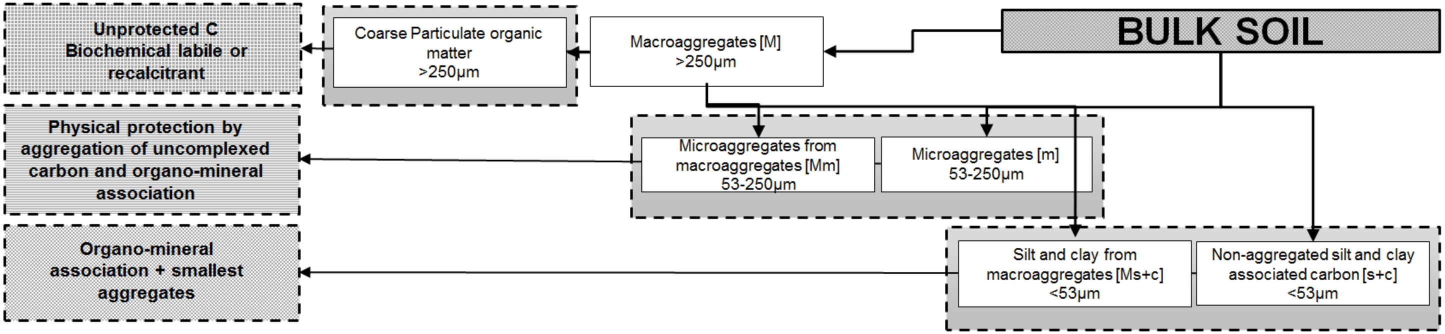


Figure 5.1: Applied fractionation scheme to derive SOC fractions and their functional interpretation in terms of present stabilization mechanisms.

5.3 Results

Forest structure and aboveground carbon storage

Both forests are highly similar in species composition, species diversity and aboveground forest structure concerning diameter distributions and light availability (see Supplementary Information), and no significant differences are found between stem density and basal area (Table 5.1). However, a significant difference is found in AGC storage, which is about 20% higher in Yoko (Table 5.1). Difference in AGC storage can be attributed to a difference in tree height where the maximal asymptotic height of the height-diameter model shows higher values in Yoko compared to Yangambi.

Physical and chemical soil variables

Soil texture at both study sites is similar and characterized by a predominantly sandy matrix (>80% sand content) (Table 5.2). Bulk density at Yoko and Yangambi were measured with an average of 1.2 g cm^{-3} and 1.5 g cm^{-3}, respectively. Typical for these type of tropical soils, pH values were low and highly acidic (4.0 - 4.6) accompanied with very low CEC_{pot} values (2.9 - 5.3 meq $100g^{-1}$). Exchangeable Al ranges between 15 - 52 ppm, decreasing with soil depth. Base saturation of CEC_{pot} did not exceed 30% and was generally lower in Yangambi than in Yoko and dominated by Ca (13 - 21%) (details not shown). While the concentration of the base cations Ca and Mg were similar between the study sites (7.4 - 137.5 ppm), K concentrations in the soil solution were more than doubled in Yoko (31.3 - 68.9 ppm) compared to Yangambi (14.9 - 34.2 ppm), and Na concentrations were about 50-70% higher in Yoko (12.0 – 13.3 ppm) compared to Yangambi (7.6 - 7.8 ppm). Nitrate-N (9.68 - 1.98 g kg^{-1}), Ammonia-N (9.54 - 1.95 g kg^{-1}) and bioavailable P (3.3 - 8.9 g kg^{-1}), decreased with soil depth but showed no significant difference ($p > 0.05$) in concentrations between both sites.

Table 5.1: Stand characteristics, including their standard deviations, aboveground carbon (AGC) and location of the two sites. Regression model ($H = a - b.e^{-cD}$): a, b and c are the optimized parameters for the individual equations per site, which represent, respectively, the maximum asymptotic height, the difference between minimum and maximum height, and shape of the curve (Banin *et al.* 2012). For each parameter, significance from t-test is provided between brackets comparing the two sites. Values within a row not sharing a common letter differ significantly ($p > 0.01$).

	Yangambi	Yoko
Stand characteristics		
Stem density (ha^{-1})	419 ± 89 (a)	469 ± 35 (a)
Basal area (m^2 ha^{-1})	32 ± 3 (a)	34 ± 3 (a)
AGC (Mg C ha^{-1})	**157 ± 21 (a)**	**189 ± 28 (b)**
H-D model ($H = a - b.e^{-cD}$)	a 36.358; b 31.659; c 0.022	a 42.502; b 39.147; c 0.020
Coordinates		
Latitude	0.7995	0.2918
Longitude	24.5077	25.3113
Altitude (m asl)	479 ± 13	471 ± 5
Plot size (ha)	1	0.25 - 1

Litter variables

While differences in litter mass (4.8 - 4.9 Mg ha^{-1}) and litter carbon stock (1.8 - 2.0 Mg C ha^{-1}) between both sites were insignificant, distinct differences in litter quality between both study sites have been found (Table 5.3). In general, concentrations of Ca, Mg and K cations in the CEC extract were between 18 and 58% lower in litter from Yoko compared to Yangambi and ranged between 1044 - 5143 ppm. In contrast, Na concentrations were two magnitudes lower (34 - 46 ppm) and differed only marginally between the two sites. While bioavailable P (0.80 - 0.84 g kg^{-1}) and Ammonia-N concentrations (0.68 - 0.63 g kg^{-1}) were similar for the litter of the different sites, Nitrate-N concentrations were about 86% higher at Yoko (1.98 g kg^{-1}) compared to Yangambi (1.06g kg^{-1}). However, this difference remains insignificant ($p > 0.05$) due to large variability between replicates at both sites. Carbon concentration in the litter from Yoko was significantly less (369 g kg^{-1}) than in the litter from Yangambi (410 g kg^{-1}) while CN ratios were similar (20.9 - 19.6).

SOC and Fractions

The highest carbon concentrations were found in the CPOM fraction, on average 2-3 times higher than in comparable mineral associated fractions for all measured depth increments. Despite the described similarity in forest composition, litter mass and soil properties, SOC stocks at Yoko (Table 5.4) (44.2 ± 4.0 Mg C ha^{-1}) were less than half of the stock of Yangambi (109.5 ± 21.4 Mg C ha^{-1}) and significantly different between depth increments and between the two study sites. These discrepancies are related to differences in carbon concentrations of the aggregate and CPOM fractions (Table 5.4) and the abundance of these fractions in the different soils and soil layers (Figure 5.2).

Soil fractionation (Figure 5.2) indicates that the non-aggregated silt and clay fraction (s+c) at both sites contributes to the respective total SOC mass in approximately the same amount (19 - 33% of total SOC mass) with an increasing contribution of non-aggregated silt and clay associated carbon in subsoils. Differences between sites are more pronounced for the aggregated fractions. The contribution of the free microaggregate associated carbon (m) to total SOC mass is higher, especially in subsoils, at Yoko (22 - 42% of total SOC mass) than at Yangambi (15 - 20 % of total SOC mass).

Between 25 – 51% of the total SOC mass were stored in macroaggregates (CPOM+Mm+Ms+c) at Yoko, with a relative decrease of about 82% with soil depth. At Yangambi, between 50 - 67% of the total SOC mass were stored in macroaggregates with a relative decrease of 69% with soil depth. The gross of these differences is related to significantly higher CPOM related carbon mass at Yangambi (12 - 28% of total SOC mass) compared to Yoko (2 - 11% of total SOC mass) and higher Mm values at Yangambi (25 - 28% of total SOC mass) compared to Yoko (13 - 30% of total SOC mass) while the contribution of Ms+C at Yangambi (11 - 14% of total SOC mass) compared to Yoko (10 - 13% of total SOC mass) was similar.

Table 5.2: Physical and chemical soil variables for Yoko and Yangambi (Ygb) at different depths, including standard deviations. Cation exchange capacity (CEC); Base saturation (BS); Bulk density (BD). No significant differences are found for most variables between the two sites, except for K in CEC, which is significantly higher in Yoko.

	Soil	**CEC**	**Base cations in CEC**									
	Depth	**BS**	**Ca**	**K**	**Mg**	**Na**	**CEC**	**exchang, Al**	**pH**	**Nitr-N**	**Amm-N**	**Bio-P**
		%	**ppm**	**ppm**	**ppm**	**ppm**	**meq 100g^{-1}**	**ppm**	**-**	**g kg^{-1}**	**g kg^{-1}**	**g kg^{-1}**
Yoko	0-30	29±2.4	137.5±0.7	68.9±13.0	12.9±1.3	12.0±1.4	3.5±0.1	52.3±25.7	4.0±0.2	9.68±0.51	8.56±0.48	7.62±2.94
	30-60	29±4.0	125.0±5.2	47.8±12.0	9.2±0.8	12.8±2.0	3.1±0.1	17.8±15.0	4.5±0.3	2.71±0.14	2.57±0.14	3.34±0.33
	60-90	30±1.4	120.5±6.4	31.3	8.1±0.2	13.3±1.4	2.9±0.4	14.5±6.5	4.6±0.2	3.52±0.18	1.95±0.10	3.33±0.54
Ygb	0-30	18±0.7	131.5±4.9	34.2±1.3	15.9±0.8	7.7±0.3	5.3±2.1	57.7±59.9	4.0±0.4	8.19±0.41	9.54±0.48	8.89±1.69
	30-60	20±1.7	126.0±5.7	18.1±6.4	9.4±1.2	7.5±0.5	4.0±1.3	45.1±28.8	4.2±0.3	4.56±0.22	4.91±0.25	5.91±2.70
	60-90	19±1.5	125.0±1.4	14.8±9.3	7.4±0.4	7.7±0.7	4.1±0.4	40.0±32.3	4.3±0.2	1.89±0.10	3.37±0.17	3.70±0.58

Table 5.2 continued

	Soil	**Texture (mass %)**			
	Depth	**Sand**	**Silt**	**Clay**	**BD**
		2000-63µm	**63-2 µm**	**<2µm**	**g cm^{-3}**
Yoko	0-30	83.2±4.1	3.7±0.6	13.1±3.5	1.19±0.08
	30-60	82.1±2.2	3.7±0.7	14.3±1.5	1.2±0.06
	60-90	80.1±2.2	5.7±1.4	14.3±0.8	1.23±0.03
Ygb	0-30	85.1±1.7	1.9±0.2	13.1±1.7	1.39±0.21
	30-60	83.5±2.8	2.6±0.6	13.9±3.5	1.53±0.15
	60-90	80.5±3.6	1.7±0.0	17.8±3.7	1.52±0.19

Table 5.3: Quantitative and qualitative litter variables for Yoko and Yangambi (Ygb), including standard deviations. Cation exchange capacity (CEC); Base saturation (BS).

	CEC	Base cations in CEC									
	BS %	Ca ppm	K ppm	Mg ppm	Na ppm	CEC meq 100g^{-1}	Nitr-N g kg^{-1}	Amm-N g kg^{-1}	Bio-P g kg^{-1}	Mass Mg ha^{-1}	C_{STOCK} Mg C ha^{-1}
Yoko	75.0±24.1	4217.8±1181	1720.9±645	1044.2±423	46.3±13	46.8±5.0	1.98±0.97	0.68±0.22	0.80±0.11	4.9±1.10	1.8±0.40
Ygb	81.9±23.6	5143.3±1630	2271.7±212	2448.3±1007	34.15±5	60.45±5.3	1.06±0.40	0.63±0.14	0.84±0.11	4.8±1.70	2.0±0. 70

Table 5.4: Carbon concentrations for litter, bulk soil and SOC fractions and the litter and soil C_{STOCK}, including standard deviations. Superscripted letters indicate ANOVA test results for significant differences ($p < 0.05$) of carbon concentrations and C_{STOCK} between sites and depths. Fractions and bulk soil have been tested separately for all variables. Same letters indicate no significant difference between depths and/or sites.

	C mg g^{-1}							SOC_{STOCK} Mg C ha^{-1}
	Bulk	Macro	Micro	s+c	CPOM	Mm	Ms+c	Bulk
Yoko								
Litter	369.0±81.5^{A}	-	-	-	-	-	-	1.8±0. 39^{A}
Soil depth								
0-30 cm	6.5±0.09^{a}	14.9±2.69^{a}	17.5±0.59^{a}	24.5±2.64^{a}	83. 6±5.25^{a}	28.8±1.16^{a}	31.3±2.64^{a}	23.1±1.9^{a}
30-60 cm	3.4±0.31^{b}	10.9±2.54^{b}	12.5±0.08^{b}	18.0±0.84^{b}	51.6±2.95^{b}	13.2±1.19^{b}	17.2±0.84^{b}	12.2±1.8^{b}
60-90 cm	2.4±0.02^{c}	4.1±0.42^{c}	9.9±0.02^{c}	14.9±0.07^{c}	36.3±8.32^{c}	10.3±1.35^{c}	14.9±0.07^{c}	8.90±0.3^{c}
Yangambi								
Litter	409.8±145.0^{A}	-	-	-	-	-	-	1.7±0.70^{A}
Soil depth								
0-30 cm	13.4±3.13^{d}	74.3±15.54^{d}	51.2±12.9^{d}	34.0±7.77^{d}	153.0±55.2^{d}	47.4±2.97^{d}	34.0±7.77^{d}	55.7±13.1^{d}
30-60 cm	6.7±0.38^{a}	32.7±0.67^{e}	21.5±2.89^{e}	25.7±0.71^{a}	77.4±29.76^{abe}	31.4±3.36^{e}	25.7±0.71^{e}	30.8±4.8^{e}
60-90 cm	5.0±0.13^{e}	27.5±1.53^{f}	14.9±0.37^{f}	18.0±1.53^{b}	64.7±3.43^{e}	21.4±0.90^{f}	18.0±1.53^{b}	23.0±3.5^{a}

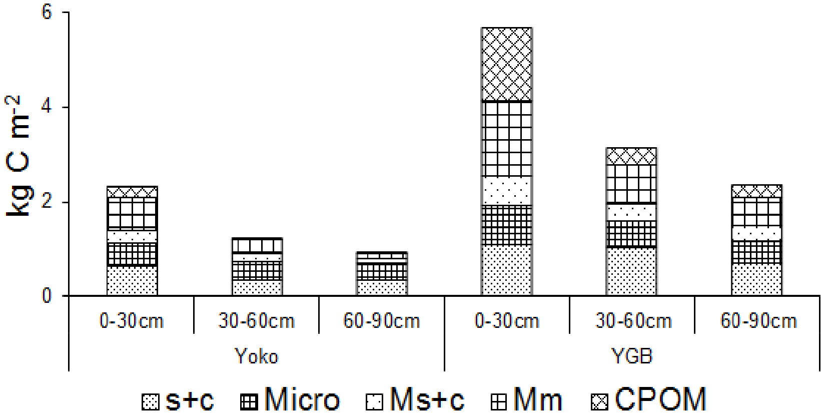


Figure 5.2: Relative contribution of isolated fractions to SOC stock per hectare for the specific depth layer.

5.4 Discussion

Importance of including SOC stocks in tropical systems

The results demonstrate significant differences in the trends of AGC (20% higher at Yoko compared to Yangambi) and soil organic carbon stocks (50% lower at Yoko compared to Yangambi) at these two sites with similar species composition and forest structure. While AGC represents 80% of the total measured carbon mass at Yoko, this value decreases to ca. 60% at Yangambi. Consequently, an assessment of aboveground living biomass alone would indicate Yoko as the higher carbon storing system (Table 5.5). However, including SOC stocks turns the calculation around showing that total measured carbon stocks (AGC, litter carbon mass and SOC stock combined) at Yoko (235 ± 32 Mg ha^{-1}) are lower than those at Yangambi (269 ± 43 Mg ha^{-1}). This has important implications when assessing the importance of the carbon storage capacity in tropical rainforest systems. Current monitoring projects such as the UN-REDD and REDD+ initiatives (www.un-redd.org) focus for central African forest on the carbon stock dynamics in the aboveground biomass. At this level, little attention is paid to SOC stocks in these systems. In the shown example, the combined assessment of SOC and AGC leads to a different conclusion regarding the carbon storage capacity compared to SOC and AGC assessments separately. To complete the assessment of total carbon in this system, both live belowground biomass and necromass should be included. Nevertheless, this will not change the outcome of the results presented here.

Table 5.5: Summary on average carbon stocks at both sites in different pools, and the combination of the measured pools (Total C), including standard deviations.

	C mass Mg ha $^{-1}$			
	Litter	**SOC**	**AGC**	**Total C**
Yoko	1.8±0.4	44.2±4.0	189±28	**234.8±32.4**
Yangambi	2.0±0.7	109.5±21.4	157±21	**268.5±43.1**

Reasons for SOC stock differences

As for the reasons governing these remarkable differences in two similar forest ecosystems, we argue that adaptation of tropical tree communities to nutrient limitation by altering the root:shoot allocation ratio of biomass and nutrient limitation as a constraint on microbial activity offers some explanation. First, the very low nutrient, and especially K levels at Yangambi might force plants to allocate a higher amount of biomass into (fine) roots for mining nutrients from this depleted soil. This is supported by observations of Wright *et al.* (2011) showing that K might be an overlooked element when it comes to assessing growth patterns of tropical forests and showed significantly reduced allocation of biomass to roots and increased height growth for lowland tropical forests after K addition. Our observations from two similar rainforest systems in the Congo Basin support this hypothesis as, here, SOC stocks were higher in the K depleted system (Yangambi; Table 5.2 & 5.5). The results further indicate that the similarity of soil texture and the amount of silt and clay associated carbon between both sites indicates that soil mineralogy, in terms of supporting the stabilization of carbon with minerals (Six *et al.* 2002; von Luetzow *et al.* 2006) does not play a significant role in explaining the observed differences in carbon stocks between Yangambi and Yoko (Table 5.2, 5.4 & Figure 5.2). On the contrary, the higher carbon input in soils at Yangambi are promoting the formation of macroaggregates, also at greater depths, while at Yoko macroaggregates decrease in importance at greater depth for SOC stocks (Figure 5.2). The higher (macro)aggregate associated carbon content at Yangambi is largely driven by coarse particular organic matter (CPOM) and microaggregate associated carbon (Mm). The formation of these two fractions is generally regarded to heavily rely on plant litter and root residues (Six *et al.* 2004; Kong & Six 2010; Six & Paustian 2013). Assuming the same mechanism to take place here, the high CPOM and Mm contribution to SOC stocks is an additional support for the latter hypothesis of increased allocation of biomass to roots in the nutrient (K) depleted system (Yangambi), consequently leading to higher SOC stocks. However, note that both sites are characterized by very poor soil fertility conditions, indicated by very low CEC content, base saturation of the CEC and soil texture (Table 5.2). Hence, in nutrient depleted soil systems, small changes in limiting factors for plant growth can have a large effect, not necessarily to be expected in more fertile soils.

Second, the strong influence of mycorrhiza types, microbial physiology and enzyme activity in connection with nutrient limitation on nutrient mining by different fungi and bacteria communities has been shown to be of great importance for the decomposition of organic matter (Averill *et al.* 2014; Schimel & Weintraub 2003; Allison *et al.* 2010; Fanin *et al.* 2011 & 2012; Nottingham *et al.* 2015). While the poor soil conditions (sandy texture, low pH, low CEC) at both sites are arguably factors of constraining microbial activity, it is unclear in how far this can be related to differences in SOC stocks. In our study, at Yangambi, where soil and litter CEC is higher than at Yoko, and nitrogen and phosphorus availability are similar, we observed higher SOC stocks at Yangambi compared to Yoko. This contradicts to some extent the latter described findings of other studies on nutrient limitation and microbial activity as higher CEC (more fertile soil conditions) should also lead to higher carbon decomposition by decomposers. However, as plants and decomposers stand in concurrence for nutrients, an extremely nutrient limited system, like the ones investigated here, might constrain microbial activity due to the limited availability of key nutrients, such as K. A successful nutrient mining tropical tree community might constrain the activity of decomposer communities even further, by supporting nutrient mining mycorrhiza communities and limit the access of decomposers to nutrients (Penton & Newman 2008; Averill *et al*. 2014), hence supporting the stabilization of SOC in soils. Arguably, we observe this at the K poor Yangambi site, where larger biomass allocation of plants to the soil, in consequence more concurrence for nutrients with decomposer communities, leads to higher SOC stocks vs. the more K rich Yoko site with lower SOC stocks. However, no data on microbial activity is available for our study sites so that a potential connection between SOC stocks and constraint microbial activity remains unverified.

In conclusion, in nutrient limited systems like the investigated tropical rainforest of this study, small changes in nutrient availability, especially K, seem to have large consequences on SOC stocks by governing the allocation of biomass by plants for mining nutrients from soil and litter (Wright *et al*. 2011; Wurzburger & Wright 2015), pumping carbon into different parts of the ecosystem with potentially fast (litter) or slower (SOC) turnover. A potential effect of nutrient limitation on constraining microbial activity and, in consequence, the decomposition of organic matter remains likely, but unverified.

In summary, our data shows differences of more than 100% in SOC stocks between two tropical forest systems with different average tree heights and aboveground biomass (low AGC stocks and smaller trees where SOC stocks are high), but very similar species composition, soil geochemistry and climate. This has important consequences for the assessment of total carbon stored in those systems leading to different conclusions regarding the carbon storage capacity of the whole system, i.e. above- and belowground carbon mass combined. Our observation derived from natural systems supports experimental studies on the effect of nutrient limitation, especially K and N, on SOC stocks and biomass allocation. The data indicates that small changes in nutrient availability can have large effects on the resulting biomass allocation in tropical lowland rainforest systems. However, the complex interplay of environmental factor governing the sequestration and release of carbon in plants and soils remains poorly understood. In consequence, as long as these large differences in SOC stocks cannot be adequately explained mechanistically, all modeling and estimates of the future response of the carbon storage of tropical forest ecosystems is subject to large uncertainties.

5.5 Supplementary Information

Forest structure and floristic composition

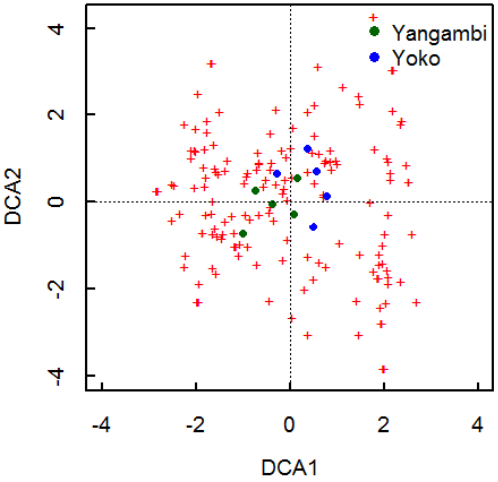
At each site within 5 plots of one hectare, the forest stands were characterized by computing plot specific basal area, stem density, wood density (basal area weighted) and biodiversity indices. The number of species found within one hectare represents the species richness. Species diversity indices were described using the Shannon-Weaver (Shannon & Weaver 1949) and Simpson (Simpson 1949) indices, and Pielou’s evenness (Pielou 1969). Evenness measures the similarity of the abundances of different species. The Shannon-Weaver index takes into account the evenness of the abundance of species, while Simpson’s index is less sensitive to the species richness but more sensitive to the most abundant species. All indices were calculated using the formulas provided in the package VEGAN 2.0 (Oksanen 2013) in R 2.13.1 (CRAN core-development team). The floristic composition of the plots was compared with a detrended correspondence analysis (DCA) (Hill & Gauch 1980), providing geometric representations of stands and species wherein stands of similar composition, or species of similar distribution are found near each other. The analysis was performed using the VEGAN package and was based on the abundance of species in each plot. Student-t tests were done on the plot scores of the first two axes, to evaluate whether species composition differed between Yoko and Yangambi.

Both sites show similar species richness, Shannon-Weaver and Pielou’s Evenness indices, although Simpson’s index is slightly higher in Yoko (Supplementary Table S5.1). Accordingly, the floristic comparison between plots at both sites as analysed using DCA did not show significant differences (Supplementary Figure S5.1). Both for first and second axis of the DCA, no significant difference ($p > 0.05$ and $p > 0.1$) is found between the plot scores of Yoko and Yangambi indicating a similar species composition.

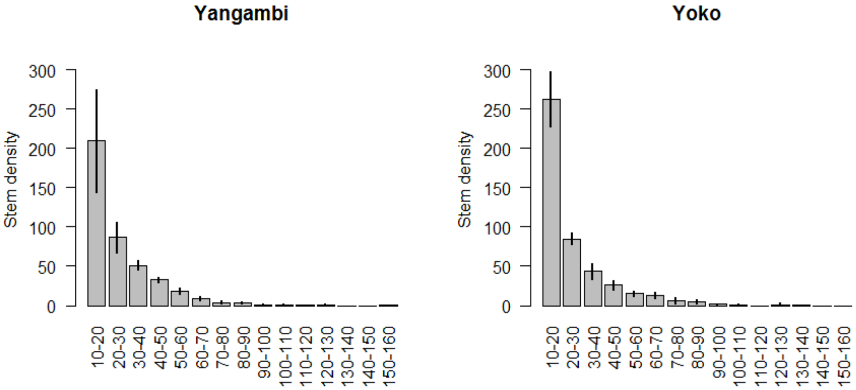
Stem density of the two sites is similar. Additionally, the number of individual plants in the different DBH size classes shows that both localities have the typical inverted J curve where abundance decreases with increasing diameter (Supplementary Figure S5.2).

Supplementary Table S5.1: Stand characteristic leaf area index (LAI) and species diversity indices for the two sites, including standard deviations. For each parameter, significance from t-test is provided between brackets comparing the two sites. Values within a row not sharing a common letter differ significantly ($p > 0.01$).

		Yangambi	**Yoko**
Stand characteristics			
	LAI	3.9 ± 0.7 (a)	4.1 ± 0.8 (a)
Species diversity			
	Species richness	76 ± 6 (a)	78 ± 7 (a)
	Pielou’s evenness	0.83 ± 0.03 (a)	0.85 ± 0.01 (a)
	Shannon index	3.6 ± 0.2 (a)	3.7 ± 0.1 (a)
	Simpson diversity	0.955 ± 0.007 (a)	0.962 ± 0.003 (b)



Supplementary Figure S5.1: Comparison of species composition at five one-hectare sites both in Yoko (blue) and Yangambi (green) using a detrended correspondence analysis (DCA). Red crosses represent the species.



Supplementary Figure S5.2: Distribution of individual trees in different diameter size classes. Bars represent mean of five hectares in both sites, with standard deviation indicated by line segments.

Leaf area index and light availability

In order to identify differences in light availability in the forests of Yangambi and Yoko, hemispherical images were collected to assess LAI. Hemispherical photographs were acquired in June 2010, at 1m above ground level using a Sigma 4.5mm f/2.8 EX DC HSM Circular Fisheye mounted on a Nikon D300 camera looking upward, level and oriented to magnetic north. Images were recorded with at a resolution of 12 MPixels, ‘fine’ image compression and an ISO 200 underexposing 3 stops. Understory present in the direct neighbourhood of the measurement location was cut down. Data was collected between 7:00 and 9:00 a.m. to avoid overexposure and to reduce sun reflections. At each site, images were acquired in a large grid of 9 hectare, using a gridded sampling scheme with measurement locations every 25 m. LAI was calculated using a histogram analysis based on entropy crossover method (Juárez *et al.* 2009).

Hemispherical photography based LAI assessment in Yoko and Yangambi old-growth forests revealed no difference. In Yoko, a similar LAI of 4.1 ± 0.8 is found compared with 3.9 ± 0.7 in Yangambi. Additionally, the absolute range of LAI was similar at both sites ranging between 2.6 - 7.4 in Yoko and between 2.8 - 6.9 in Yangambi. The large variability does indicate a variable canopy structure at both sites. Light availability at these two sites is thus similar, although differences in vertical forest structure and occurrence of natural disturbance can induce strong local differences in light availability. Accordingly, a similar abundance of light-demanding and shade-tolerant species is present at Yoko and Yangambi.

PART II

The diversity-side of the story

6

Refinement of classical plant functional types of tropical tree species through resource use variation

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Abstract

Species classification is an important tool to reduce the high species diversity of tropical forests, while at the same time retaining key information for ecosystem functioning. This study is a preliminary investigation to combine individual trees from a site-specific inventory into plant functional types, which can be used to simulate forest productivity via an ecosystem model. Therefore, a site-specific classification is made incorporating intra-specific species variability and local abundances. We investigated this classification using traits reflecting widely used knowledge-based classifications regarding light requirement and adult stature combined with functional traits reflecting the leaf economic spectrum (LES). Our main finding is that the primary axis of variation follows the knowledge-based classification, while a secondary and orthogonal variation is introduced by the functional leaf traits. We therefore propose a fine-tuning of the knowledge-based classifications with a subdivision based on leaf traits, wood density and potential tree height. The second important finding is that due to the large intra-species variability present, the subdivision of classes representing the LES are not species-specific. This indicates that individuals of the same species growing in a different local environment show variable traits. Forest growth modelling could benefit from distinguishing between these individuals and optimizing the parameterization of the derived classes.

6.1 Introduction

The high species diversity in tropical ecosystems foster the need for classification of species in order to simplify the representation of these complex systems. Classification of species into functional groups that have similar functions in the ecosystem is a useful tool to reduce the high diversity while retaining key information concerning ecosystem functioning (Díaz & Cabido 1997; Baker *et al*. 2003; Mcgill *et al*. 2006). Such classifications allow us to better understand the origin and the functioning of species-rich ecosystems (Gitay *et al*. 1999), or to model the dynamics of such ecosystems (Köhler *et al*. 2000; Picard *et al*. 2009 & 2012; Fyllas *et al*. 2012). At the same time, numerous different motivations to classify species, each with different criteria for their classification, have produced a diversity of functional classifications (Köhler *et al*. 2000; Picard and Franc 2003). Additionally, many techniques have been used for classification, either expert knowledge-based or data-driven (Gitay *et al*. 1999; Gourlet-Fleury *et al*. 2005; Souza *et al*. 2014), aiding in the diversity of the different classifications suggested.

Within this study, tropical forest growth modelling is the motivation to classify species. The underlying goal is the simulate forest succession using the Ecosystems Demography model (ED2; Moorcroft *et al*. 2001; Medvigy *et al*. 2009), although the subsequent simulation is not finalized for this dissertation. In this model, tropical tree species are classified as early, mid, or late successional tree types based on their wood density (Moorcroft *et al*. 2001). With this model, simulations of inventory-based forest plots can be made, with individual trees grouped according to plant functional type, plant size and disturbance history, which are simulated together as a single cohort. Even though realistic simulations have been performed for Neotropical forest inventories, preliminary results were not realistic for African tropical forests of this study. A better means for classification, specifically for this forest, is sought, while retaining the link with the early, mid, and late successional classification. Commonly used classifications related to ecological strategies are therefore selected as a starting point.

Ecological strategies are key in most classifications and either form the basis for a priori classification based on expert knowledge or a posteriori identification of data-driven classes. Several studies agree on the importance of classifying species according to their light requirements for regeneration and their adult stature (Hawthorne 1995; Turner 2001; Gourlet-Fleury *et al*. 2005; Poorter *et al*. 2006; Valladares & Niinemets 2008), with a consensus on the existence of four main ecological strategies, namely short-lived pioneer, long-lived pioneer, partial shade-tolerant and shade-tolerant species (Poorter *et al*. 2006). Even though this knowledge-based classification can be perceived as subjective, numerous studies show the relevance and value of it. Accordingly, several studies show that adult stature and light requirement capture a large portion of the variation in functional traits found among tropical tree species (Loehle 2000; Turner 2001; Poorter *et al*. 2006), although the functional and the demographic trade-offs is not always so obvious (Poorter & Bongers, 2006; Delcamp *et al*., 2009; Wright *et al*., 2010). This variation has however shown high correspondence with leaf trait variation found along the 'leaf economic spectrum' (LES) (Wright *et al*. 2004). This spectrum namely represents a continuum of carbon and nutrient investment strategies at the leaf level (Reich *et al*. 1997), which is essentially a fast – slow continuum of resource acquisition and stress tolerance (Grime 1977; Reich 2014). Species at the fast end of the spectrum are characterized by a short leaf lifespan, high specific leaf area (SLA) and high nutrient concentrations. These species generally also show small and numerous wind- or animal-dispersed seeds (Baraloto et al. 2005; Moles & Westoby 2006), high recruitment rates, higher gas exchange rates and growth rates (Domingues *et al*. 2010) but lower survival rates under stress conditions (Poorter & Bongers 2006). These functional characteristics are typically related to pioneer and light-demanding species, characterized by an efficient use of readily available resources (Grime & Pierce 2012). Conversely, species on the other side of the spectrum follow a more conservative resource use strategy, with a lower SLA and nutrient concentrations generally characteristic for shade-tolerant/late-successional species. In a forest environment, this strategy gradient is also expected to develop vertically, with vertical light partitioning related to canopy distribution and thus the potential tree size of a species (Poorter *et al*. 2006). Taller trees can potentially harvest more light during their lifetime compared with shorter ones (Poorter *et al*. 2005) and reduce light availability of smaller trees in their direct neighborhood (Poorter *et al*. 2008). Though, small trees are generally more shade-tolerant and have higher survival rates under low light availability (Poorter 2007). The combination of vertical and horizontal light gradient of these classes provides an important link with the cohort structure of the ED2 model for which light limitation is an important factor.

Few studies however combine these functional leaf traits with traits related to light requirement and adult stature in data-driven classification techniques. Within our study, we identify functional groups using data-driven hierarchical clustering of tropical tree species of the central Congo Basin. We collected trait data from 123 species in 15 plots of one hectare covering pristine and intervened forests resulting in a unique dataset for the central Congo Basin. We aim to propose a classification of tropical trees specific for this study site, which can represent main plant functional types for this forest and can be used to realistically simulate forest growth (in a later stage of the study). Specifically, we aim to better identify plant functional types by combining functional traits related to resource use and traits representing the knowledge-based classifications, to aid in an overall better characterization of this tropical forest site and its succession.

6.2 Methods

Study area

This study was carried out in the UNESCO Man and Biosphere reserve in Yangambi, of which details can be found in *Chapter 2*. This study focuses on 15 plots installed in young *Musanga* (n = 2; age since disturbance ± 7 years), old *Musanga* regrowth forest (n = 3; age since disturbance ± 20 years), old-growth mixed forest (n = 5) and old-growth monodominant forest of *Gilbertiodendron dewevrei* (De Wild.) J. Leonard (n = 5). Within all plots, all trees with a DBH larger or equal to 10 cm have been included and identified to species level.

Trait collection and analysis

Leaf samples and wood samples from the stem were collected for all species covering a cumulative 95% basal area of each plot, i.e. species were ranked from highest to lowest basal area with species included in the selection until the cut-off of 95% basal area was reached. If multiples of the same species were present in a plot, two individuals were selected for sample collection within each pre-assigned diameter class of 10-20, 20-30, 30-50 and >50 cm DBH, when possible. A total of 995 individuals were sampled, covering 123 species, 79 genera, 33 families. *Scorodophloeus zenkeri* Harms, *Musanga cecropioides* R. Br. ex Tedlie, *Gilbertiodendron dewevrei* (De Wild.) J. Léonard, *Macaranga spinosa* Müll. Arg., *Petersianthus macrocarpus* (P. Beauv.) Liben, *Garcinia punctata* Oliv. and *Carapa procera* DC. are some of the most abundant species in the collected dataset. All samples were collected between March and May 2012. All leaves are measured for specific leaf area (SLA), leaf dry matter content (LDMC), carbon content (LCC), nitrogen content (LNC), carbon isotope composition ($\delta^{13}C$), nitrogen isotope composition ($\delta^{15}N$) and additionally the carbon to nitrogen ratio (C:N) was derived. The leaf phosphorus content (LPC), the derived nitrogen to phosphorus ratio (N:P) and the oxygen isotope composition ($\delta^{18}O$) were measured on a subset of individuals covering 88 species. For the wood traits, wood density (WD) was measured for all individuals collected covering the total 123 species.

A selection of functional traits is made, focusing on traits with clear roles for determining how species acquire resources, grow, reproduce (Westoby *et al*. 2002; Westoby & Wright 2006), which can be directly used or translated to parameters in the ED2 model. Morphological, anatomical and chemical leaf traits have been shown to affect important functions in forest ecosystems, as they describe nutrient status, growth and longevity (e.g. Wright *et al*. 2004). Additionally, wood traits have been shown to provide independent and orthogonal information compared to leaf traits (Baraloto *et al*. 2010b). We therefore focus on a variety of leaf and wood traits covering numerous potential processes of the individual tree. Specific leaf area (SLA) and wood density (WD) have been selected because numerous studies have shown their importance for different ecosystem processes (Lavorel & Garnier 2002; Chave *et al*. 2009). SLA influences primary production, carbon and nutrient cycling and litter decomposition (Díaz *et al*. 2004; Poorter *et al*. 2009), and WD is an important trait characterizing biogeochemical ecosystem processes such as carbon sequestration and turnover rates (Chave *et al*. 2009). The leaf carbon content (LCC) is considered for representing the carbon economy of the leaf. Other selected leaf traits are included in this study to reflect nutrient status and nutrient cycling strategy of trees, namely leaf nitrogen content (LNC), leaf phosphorus content (LPC) and the isotopic composition of nitrogen ($\delta^{15}N$). Nutrient availability has a strong effect on photosynthetic carbon gain, as both phosphorus and nitrogen availability constrain leaf photosynthetic capacity (Domingues *et al*. 2010). Phosphorus is generally considered as the most limiting nutrient for productivity in tropical forests, but nitrogen losses during land use change might change the balance in nutrient cycles, causing shifts in N:P ratios with lower values during secondary forest succession (Davidson *et al*. 2007). $\delta^{15}N$ reflects the nature of the N cycle in ecosystems, with high values indicating greater N availability and a more open N cycle (Pardo *et al*. 2006). The isotopic composition of carbon ($\delta^{13}C$) is included as a proxy of the intrinsic water use efficiency (WUE), which is the ratio of photosynthetic carbon fixation to stomatal conductance (Farquhar *et al*. 1989; Dawson *et al*. 2002). The oxygen isotopic composition of leaves ($\delta^{18}O$) is also included as it provides a time-integrated measure of stomatal conductance when other sources of variation (mainly source water $\delta^{18}O$) are minimized (Barbour 2007; Farquhar *et al*. 2007; Hasselquist *et al*. 2010). The simultaneous measurements of $\delta^{13}C$ and $\delta^{18}O$ in leaf material can help separate independent effects of carbon fixation and stomatal conductance on WUE (Grams *et al*. 2007; Hasselquist *et al.* 2010).

From each individual tree, 10 leaves were sampled at various tree heights, which were fully expanded and no signs of pathogens or herbivory. Fresh mass of the leaf samples was measured as a composite sample, and high-resolution images were taken to determine leaf area while leaves were flattened between transparent Plexiglas. Leaf surface is determined by analyzing these images using ImageJ software (from the US National Institutes of Health; http:// www.nih.gov/). Leaves were subsequently dried at 60°C for 72h, or until no more mass change occurred, and dry mass was determined. Leaf dry matter content (LDMC, leaf dry mass divided by fresh mass) and SLA (leaf area divided by dry mass) were determined. Next, chemical analysis of the leaves was performed at the Isotope Bioscience Laboratory (Ghent University, Belgium). Composite leaf samples were ground to fine powder using a ball mill (ZM200, Retsch, Germany). Mass based LCC and LNC, and $\delta^{13}C$ and $\delta^{15}N$ were determined using an elemental analyzer (ANCA-SL, SerCon, Crewe, UK) coupled to an isotope ratio mass spectrometer (20-20, SerCon, Crewe, UK) (EA-IRMS). Isotope ratios were expressed in delta notation relative to Vienna Pee Dee Belemnite (VPDB) standard for $\delta^{13}C$ and atmospheric air for $\delta^{15}N$. LPC and $\delta^{18}O$ were determined on a subset of samples, with priority to species with more replicates. Samples were retained if more than 3 individuals from a species was measured within a forest type, of which 3-5 individuals were randomly selected for analysis. In total 446 individuals covering 88 species were measured for LPC and $\delta^{18}O$. For LPC determination samples were prepared using the Chapman and Pratt (1961) procedure with some slight modifications and measured using the auto analyzer method, No.G-103-93 Rev.2 (Multitest MT7/MT8). $\delta^{18}O$ are analysed using a high temperature furnace interfaced with an EA-IRMS (20-20, SerCon, Crewe, UK). $\delta^{18}O$ is expressed relative to the Vienna Standard Mean Ocean Water (VSMOW2) standard.

Wood samples with an average size of 5x5x5 cm^3 are taken under the bark. The volume of the fresh sample was taken using the water displacement method. Samples were subsequently dried in an oven at 60°C until completely dry and dry mass was measured. WD could then be determined as the ratio of oven dry mass divided and fresh volume.

Knowledge-based classification

We focus on two traits for the knowledge-based classification, namely light requirement and adult stature. Light requirement is based on the classification of Lebrun & Gilbert (1954) who performed their research in the same Yangambi reserve. Their classification included light-demanding, shade-tolerant and ombrophile classes. Additional information is retrieved from Hawthorne (1995) providing traits of species from Ghanaian forests, from which classifications matched between species found in both studies. Non-pioneer light-demanding (NPLD) species from Hawthorne (1995) were not as distinctly classifiable between light-demanding and shade-tolerant classes from Lebrun & Gilbert (1954), so a forth classification of NPLD is added.

Two classes are selected representing adult stature through their location of adult trees within the canopy in the old-growth forests, namely understory and canopy (Tailfer 1989; Hawthorne 1995; Prota database http://www.prota4u.org). Species exclusively present in the open canopy of the young regrowth forest are analyzed as a separate class. Additionally, species specific maximal tree height and maximal diameter are determined as a proxy for potential size. We used the 95% range as maximal value to eliminate possible outliers. These measurements are based on a larger inventory in the Yangambi reserve (*Chapter 2*).

The relationship between the two knowledge-based classifications can be found in Supplementary Table S6.1.

Statistical analysis

The clustering analysis is performed using leaf traits reflecting resource use, and WD and maximum height reflecting light requirement and potential tree size. As resource use related traits SLA, LNC, LPC, LCC, $\delta^{13}C$ and $\delta^{18}O$ are selected because of their relationship with water and carbon cycling. Other leaf traits are removed from this analysis due to their high correlation with these traits (pairwise correlations are summarized in Supplementary Table S6.2). Since missing values are present within some traits (LPC, $\delta^{18}O$), values from within the same species are first assigned to all individuals not measured. Herein trait variability is taken into account, with a random selection of a value between minimal and maximal species-specific values. Subsequently, remaining missing values (7.4% of LPC and $\delta^{18}O$ values) are assigned through Expectation-Maximization (Nelson *et al.* 1996; Stanimirova *et al.* 2007). The Shapiro-Wilk test was preliminarily used to test for normality. The leaf traits SLA, LNC and LPC presented a right skewed distribution and were log transformed prior to analysis. Subsequently all traits are scaled to a mean of zero with unity standard deviation. Next a principal component analysis (PCA) is performed of which axes with an eigenvalue higher than one were retained for clustering. Hierarchical clustering was performed using the Ward method after Euclidian distance assessment to explore if distinct functional groups could be determined based on the similarity of observed traits. Clustering was performed using the ‘pvclust’ function in the ‘pvclust’ package in R software (Suzuki & Shimodaira 2011), with significant clusters ($p < 0.01$) identified through 1000 bootstrap resamplings.

Both the PCA and the clustering analysis are performed on the individual observations in order to account for within species variability, mainly of highly occurring species in this forest site, which are more numerously represented in the dataset. The mean of each trait within each hierarchical cluster was compared using an ANCOVA analysis, followed by Tukey’s HSD test to test for differences in the means. The same analysis is performed on the classical classifications of light strategy and location within the canopy. All analyses were performed with the R statistical platform (R Development Core Team 2010).

6.3 Results

Knowledge-based classifications

All knowledge-based classifications show trait distinctions within the classes indicating differences in ecological strategies (Table 6.1). Light requirement classification showed the most difference along all traits, with the largest distinction found for light-demanding species. This class has a significantly lower WD, higher LPC, lower N:P combined with less negative $\delta^{13}C$ values compared to ombrophiles and shade-tolerant species. Shade-tolerant species have higher LNC, lower C:N and higher N:P compared to ombrophile and light-demanding species. The ombrophiles do show the lowest SLA with a high $\delta^{18}O$. The NPLD classification showed no apparent distinction with the other classes.

The location within the canopy also presented differences among multiple traits (Table 6.1). Evidently, differences in maximal tree height and diameter are found between the understory and the canopy layer. The canopy of the young regrowth forest is also lower compared to the old-growth forest. Comparing layers within the old-growth forest, the canopy layer has higher values of LNC, with low C:N and high N:P. Differences are also found for $\delta^{18}O$ with higher values in the understory. Trees from the canopy layer of the young regrowth distinguish themselves with low N:P values, less negative values of $\delta^{13}C$ and low LDMC.

Table 6.1: Mean trait values of classical classification groups, namely light-demanding (LD), non-pioneer light-demanding (NPLD), ombrophile (O), shade-tolerant (ST), species in the canopy layer of old-growth forest (C-OG), species from the understory in the old-growth forest (US-OG) and species from the canopy layer of the young regrowth forest (C-YRG). The number of species (n species) and number of individuals (n individuals) in each class is indicated. Traits investigated include wood density (WD), maximal tree height (HeightMax), maximal diameter at breast height (DBHmax), leaf nitrogen content (LNC), leaf carbon content (LCC), carbon to nitrogen ratio (C:N), leaf phosphorus content (LPC), nitrogen to phosphorus ratio (N:P), stable carbon isotope composition (δ^{13}C), stable nitrogen isotope composition (δ^{15}N), stable oxygen isotope composition (δ^{18}O), specific leaf area (SLA). Mean location on the principal component (PC) axes are indicated. In all cases ANCOVAs were significant for the overall difference between the four groups. Different letters denote significance difference ($p < 0.001$) in the mean trait value based on a Tukey HSD post hoc test. In bold important differentiation between different classes are shown.

	Light requirement				**Adult stature**		
	LD	**NPLD**	**O**	**ST**	**C-OG**	**US-OG**	**C-YRG**
WD (g cm^{-3})	**0.4 ± 0.1 a**	0.6 ± 0.1 b	0.6 ± 0.1 b	0.6 ± 0.1 b	0.63 ± 0.12 a	0.63 ± 0.13 a	0.37 ± 0.06 b
HeightMax (m)	22 ± 8 a	31 ± 7 bc	28 ± 6 b	33 ± 8 c	**33 ± 7 a**	**23 ± 5 b**	**17 ± 4 c**
DBHmax (cm)	60 ± 28 a	81 ± 25 bc	68 ± 37 ac	84 ± 25 b	**91 ± 26 a**	**51 ± 17 b**	**43 ± 18 b**
LNC (mg g^{-1})	28 ± 8 a	29 ± 5 ab	29 ± 9 a	**34 ± 9 b**	**32 ± 9 a**	28 ± 7 b	27 ± 8 b
LCC (mg g^{-1})	443 ± 21 a	457 ± 64 a	454 ± 37 a	456 ± 49 a	456 ± 40 a	454 ± 40 ab	443 ± 21 b
C:N (g g^{-1})	17 ± 5 a	16 ± 3 ab	17 ± 5 a	**15 ± 4 b**	**16 ± 5 a**	17 ± 4 b	18 ± 5 b
LPC (mg g^{-1})	**0.7 ± 0.3 a**	0.7 ± 0.3 ab	0.6 ± 0.3 b	0.5 ± 0.2 b	0.6 ± 0.3 a	0.6 ± 0.3 a	0.7 ± 0.3 a
N:P (g g^{-1})	**45 ± 18 a**	48 ± 17 ab	56 ± 20 b	**76 ± 39 c**	**66 ± 32 a**	57 ± 23 b	**46 ± 15 c**
δ^{13}C (‰)	**-31 ± 2 a**	-32 ± 2 ab	-33 ± 2 b	-33 ± 2 b	-33 ± 2 a	-33 ± 2 a	**-31 ± 2 b**
δ^{15}N (‰)	6.5 ± 2.2 a	6.3 ± 2.2 a	7.3 ± 2.3 a	7.3 ± 2.1 a	7 ± 2 a	7 ± 2 a	7 ± 3 a
δ^{18}O (‰)	21 ± 4 a	21 ± 6 ab	23 ± 3 b	20 ± 4 a	21 ± 4 a	**23 ± 4 b**	21 ± 4 a
LDMC (g g^{-1})	**0.33 ± 0.10 a**	0.36 ± 0.07 ab	0.39 ± 0.09 b	0.36 ± 0.10 ab	0.38 ± 0.09 a	0.37 ± 0.09 a	**0.31 ± 0.10 b**
SLA (m^2 kg^{-1})	17 ± 8 a	17 ± 4 ab	**13 ± 4 b**	18 ± 6 a	17 ± 7 a	15 ± 5 a	16 ± 8 a
PC1	-1.4 ± 1.3 a	0.1 ± 0.9 bc	0.3 ± 0.7 b	0.8 ± 1.3 c	0.8 ± 1.1 a	0.1 ± 0.8 b	-2.0 ± 0.6 c
PC2	-0.3 ± 1.3 a	-0.5 ± 1.2 a	0.3 ± 1.4 b	-0.5 ± 1.2 a	-0.3 ± 1.4 a	0.3 ± 1.3 b	-0.1 ± 1.3 ab
PC3	-0.1 ± 0.8 a	0.2 ± 1.5 a	0.0 ± 1.0 a	0.2 ± 1.2 a	0.2 ± 1.1 a	-0.2 ± 1.1 b	0.0 ± 0.8 ab
n individuals	235	37	195	170	379	284	189
n species	22	7	20	19	46	35	13

PCA and hierarchical clustering

Principal components analysis revealed that the primary axis of trait differentiation among our individuals reflects covariation in traits related to light strategy and potential tree size (Supplementary Table S6.3; Supplementary Figure S6.2). Specifically, the first PC axis (explaining 23.2% of variation) reflects wood density and maximal tree height ($r > 0.5$), in addition to $\delta^{13}C$ ($r > 0.4$). The secondary axis (21.9% of variation) reflects leaf chemistry and size, with high loadings of LNC and SLA ($r > 0.5$), in addition to LPC ($r > 0.4$). The third axis (14.3% of variation) mainly reflects the carbon content ($r > 0.8$). Seven clusters were identified using hierarchical clustering of the three principal component axis (Figure 6.1A, Table 6.2). Based on the clusters we defined plant functional types (Table 6.3, Supplementary Table S6.4). A high overlap is found with light requirement and adult stature classifications (Figure 6.1B & C; Supplementary Table S6.5), with a significant dependency found between the groups (Chi^2; $p < 0.001$). The first two clusters show a high occupancy of light-demanding species from the canopy of the young regrowth forest (Supplementary Table S6.5), although they differentiate along the LES, namely in SLA and nutrient contents, therefore named 'fast light-demanding individuals' and 'slow light-demanding individuals'. They are separated along both the second and third PC axes, with the fast light-demanding individuals having a significantly higher LNC, $\delta^{15}N$ and LPC, but a similar N:P combined with a significantly higher SLA. These individuals also have a significantly lower LCC and C:N. The next two classes show most similarities with understory species and ombrophile species. Their main difference is along the third PC axis with significantly different LCC, LNC and $\delta^{15}N$ values, although a similar C:N. These classes are therefore referred to as 'low/high nitrogen understory ombrophile individuals'. LPC values are similar between the two clusters. The low nitrogen group also has a significantly higher WD, indicating they are also found on the slower end of the LES. The next cluster brings together 'shade-tolerant canopy individuals' which distinguishes itself by containing the tallest species with the largest maximal diameter. This group shows the highest N:P compared to all other clusters and one of the highest SLA. Within the last two clusters, the similarities with knowledge-based classifications is less profound, with both canopy and understory present, and shade-tolerant and ombrophile species. Their main distinction is found along the secondary PC axis. These two clusters are therefore further referred to as 'slow or fast shade-bearing individuals', with the fast group having significantly higher LNC and LPC values and larger SLA and lower LDMC. The slow group does show a higher WD.

Some species proved to be non-exclusive to specific clusters (Supplementary Table S6.4). For example *Macaranga monandra* and *M. spinosa* occur both as fast and slow light-demanding individuals. More notable, the low N understory ombrophile individuals only contain few individuals from the species *Cavacoa quintasii*, *Drypetes* sp., *Erythrophleum suaveolens* and *Garcinia punctata*, although all these species are not exclusive within this cluster.

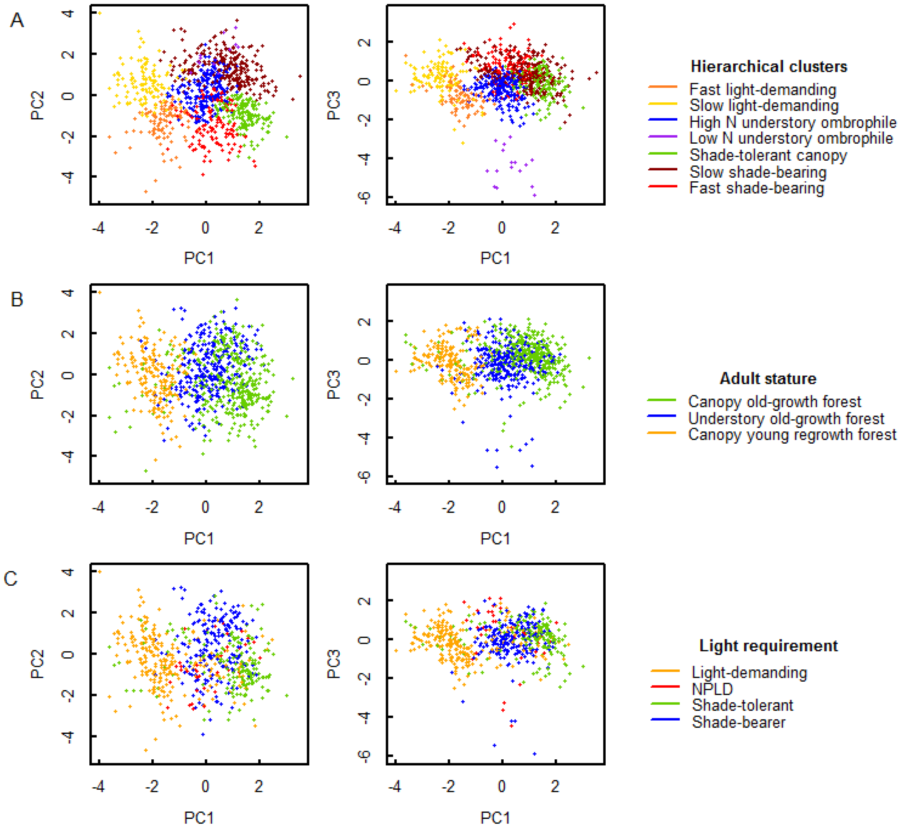


Figure 6.1: Principal component ordination. Colors show (A) hierarchical clusters based functional traits: specific leaf area (SLA), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf carbon content (LCC), carbon isotope composition ($\delta^{13}C$), oxygen isotope composition ($\delta^{18}O$), wood density (WD) and maximal tree height, (B) adult stature and (C) light requirement.

Table 6.2: Mean trait values of hierarchical clustering groups. The number of species (n species) and number of individuals (n individuals) in each class is indicated. Traits investigated include wood density (WD), maximal tree height (HeightMax), maximal diameter at breast height (DBHmax), leaf nitrogen content (LNC), leaf carbon content (LCC), carbon to nitrogen ratio (C:N), leaf phosphorus content (LPC), nitrogen to phosphorus ratio (N:P), stable carbon isotope composition (δ^{13}C), stable nitrogen isotope composition (δ^{15}N), stable oxygen isotope composition (δ^{18}O), specific leaf area (SLA). However, only WD, HeightMax, LNC, LCC, LPC, δ^{13}C, δ^{18}O and SLA are used in defining the clusters. Mean location on the principal component (PC) axes are indicated. Different letters denote significance difference ($p < 0.001$) in the mean trait value based on a Tukey HSD post hoc test. In bold important differentiation between clusters are shown.

	Fast light-demanding individuals	**Slow light-demanding individuals**	**High N understory ombrophile individuals**	**Low N understory ombrophile individuals**	**Shade-tolerant canopy individuals**	**Slow shade-bearing individuals**	**Fast shade-bearing individuals**
WD (g cm^{-3})	0.39 ± 0.09 a	0.35 ± 0.08 a	**0.59 ± 0.13 b**	**0.73 ± 0.05 c**	0.67 ± 0.06 c	**0.68 ± 0.11 c**	**0.60 ± 0.08 b**
HeightMax (m)	18 ± 5 a	18 ± 4 a	24 ± 5 b	26 ± 5 bcd	35 ± 6 e	28 ± 7 c	31 ± 6 d
DBHmax (cm)	47 ± 23 a	48 ± 23 a	53 ± 22 a	60 ± 28 abc	86 ± 26 b	71 ± 35 c	80 ± 23 bc
LNC (mg g^{-1})	**33 ± 7 a**	**24 ± 5 bc**	**28 ± 5 d**	**17 ± 3 b**	37 ± 6 a	**24 ± 5 c**	**37 ± 9 a**
LCC (mg g^{-1})	430 ± 16 a	446 ± 23 b	**448 ± 24 b**	**276 ± 32 c**	451 ± 22 b	468 ± 21 d	474 ± 53 d
C:N (g g^{-1})	13 ± 3 a	20 ± 5 b	16 ± 3 c	17 ± 3 abc	13 ± 3 a	20 ± 4 b	14 ± 3 a
LPC (mg g^{-1})	**0.9 ± 0.4 a**	**0.6 ± 0.2 bc**	0.6 ± 0.2 b	0.5 ± 0.1 bc	0.5 ± 0.2 bc	**0.4 ± 0.1 c**	**0.8 ± 0.3 a**
N:P (g g^{-1})	43 ± 12 a	42 ± 14 a	**53 ± 20 a**	**38 ± 9 a**	78 ± 33 b	**68 ± 30 b**	**56 ± 28 a**
δ^{13}C (‰)	**-32 ± 2 a**	**-30 ± 1 b**	-33 ± 2 c	-34 ± 2 c	-33 ± 2 c	-33 ± 2 c	-32 ± 2 a
δ^{15}N (‰)	**8 ± 2 a**	**6 ± 2 b**	7 ± 2 a	5 ± 2 b	8 ± 2 a	6 ± 2 ab	8 ± 2 a
δ^{18}O (‰)	20 ± 3 ab	22 ± 4 acd	24 ± 3 e	25 ± 2 de	21 ± 3 a	23 ± 3 ce	19 ± 4 b
LDMC (g g^{-1})	**0.25 ± 0.07 a**	**0.37 ± 0.09 b**	0.37 ± 0.08 b	0.36 ± 0.06 bc	0.35 ± 0.08 b	**0.44 ± 0.08 c**	**0.34 ± 0.08 b**
SLA (m^2 kg^{-1})	**21 ± 8 a**	**11 ± 3 b**	15 ± 4 c	15 ± 2 bc	20 ± 7 a	**12 ± 3 b**	**18 ± 7 a**
PC1	-1.7 ± 0.6 a	-2.3 ± 0.6 b	0.0 ± 0.5 c	0.3 ± 0.6 cd	1.4 ± 0.5 e	0.8 ± 1.0 d	0.3 ± 0.6 c
PC2	-1.4 ± 0.8 a	0.6 ± 0.9 b	0.3 ± 0.8 b	1.8 ± 0.7 c	-0.9 ± 0.6 d	1.3 ± 0.7 c	-1.4 ± 1.0 a
PC3	-0.7 ± 0.6 a	0.2 ± 0.8 bc	-0.4 ± 0.6 ad	-4.4 ± 0.9 e	-0.1 ± 0.7 cd	0.4 ± 0.7 b	0.8 ± 1.2 f
n individuals	101	188	208	16	161	244	133
n species	25	24	56	5	40	52	38

Table 6.3: New plant functional types through refinement of the knowledge-based classification based on light requirement and adult stature. The subdivision is made by a clustering analysis of leaf traits, wood density and potential tree height. The distinction of each subdivision along the fast - slow continuum of resource acquisition and stress tolerance as described in the LES (Grime 1977; Wright *et al*. 2004; Reich 2014) is indicated, as are the main characteristics and key species.

Cluster	**Knowledge-based classification**	**Sub-classification**	**Characteristics**	**Key species**
1	Light-demanding species	Fast light-demanding individuals	High SLA and nutrient contents, low stature, low WD	*Ricinodendron heudelotii*, *Tetrorchidium didymostemon*, *Vernonia conferta*
2		Slow light-demanding individuals	Low SLA and nutrient contents, low stature, low WD	*Musanga cecropioides, Musanga smithii* and *Macaranga zenkeri*
3	Understory ombrophile	High N understory ombrophile individuals	High LNC, high N:P	*Anonidium mannii*, *Cavacoa quintasii*, *Cola griseiflora*, *Isolona thonneri*, *Panda oleosa* and *Pycnanthus angolensis*
4		Low N understory ombrophile individuals	Low LCC and LNC	-
5	Shade-tolerant canopy individuals		Tallest trees, high LNC, high N:P, high SLA	*Combretum lokele*, *Cynometra hankei*, *Drypetes gossweileri*, *Greenwayodendron suaveolens*, *Scorodophloeus zenkeri* and *Staudtia kamerunensis*
6	Shade-tolerant and ombrophile	Slow shade-bearing individuals	Lower SLA and nutrient contents, higher WD	*Carapa procera*, *Cleistanthus mildbraedii*, *Dialium pachyphyllum*, *Garcinia punctata*, *Gilbertiodendron dewevrei*, *Synsepalum subcordatum* and *Tridesmostemon claessensii*
7		Fast shade-bearing individuals	Higher SLA and nutrient contents, lower WD	*Petersianthus macrocarpus*, *Prioria balsamifera*, *Trichilia gilgiana*, *Trichilia monadelpha* and *Turraeanthus africanus*

6.4 Discussion

We investigated the classification of species using traits reflecting knowledge-based classifications regarding light requirement and adult stature combined with functional traits reflecting the leaf economic spectrum (LES). Our main finding is that the primary axis of variation follows the knowledge-based classification, while a secondary and orthogonal variation is introduced by the functional leaf traits. We therefore propose a fine-tuning of the knowledge-based classifications with a subdivision based on leaf traits, wood density and potential tree height. We discuss possible sources of differentiation between these groups that are generally unified in knowledge-based classifications. A second finding is the presence of some species within multiple groups, indicating intraspecific variability of species regarding resource use related functional traits.

The knowledge-based classifications show trait differentiations related to their ecological strategies, although the expected fast – slow continuum of resource acquisition and stress tolerance as described in the LES (Grime 1977; Wright *et al*. 2004; Reich 2014) is not strictly followed. Light-demanding species are expected at the fast end of this continuum having high SLA and nutrient contents (Grime & Pierce 2012). Nevertheless, only higher values of LPC for light-demanding species are found compared to the shade-tolerant species, while LNC is lower. Additionally, SLA of the light-demanding species is not distinguishable from that of the shade-tolerant species. Ombrophiles do have a lower SLA compared to the shade-tolerant species indicating they are on the slower end of the continuum. Canopy species within the old-growth forest do show higher LNC and SLA compared to the understory species indicating a faster growth and resource acquisition but lower stress tolerance. The knowledge-based classifications thus show some diversification in traits, although the lack of distinct traits differentiations indicates they do not suffice to distinguish between their functions within this forest, specifically for classification based on light requirement.

Through hierarchical clustering of species based on their traits related to this light requirement and potential tree size (Westoby 1998; Poorter *et al*. 2006; Souza *et al*. 2014) combined with resource use related leaf traits, a more detailed distinction within the knowledge-based classification is presented. Most of the variation within our studied species is captured by wood density and maximal tree height (PC1), indicating a strong link with knowledge-based classifications based on light requirement and potential tree size. The identified groups broadly corresponds to the scheme presented by Poorter *et al*. (2006), namely short-lived pioneers (fast light-demanding individuals), long-lived pioneers (slow light-demanding individuals), shade-tolerant species which are small statured (high and low nitrogen understory ombrophile individuals) and partial-shade-tolerant species with a large adult stature (Shade-tolerant canopy individuals). The slow and fast shade-bearing individuals both have low light requirement but no clear distinction is made along the potential tree size axis disabling the link with the classification of Poorter *et al*. (2006).

The second axis of variation (PC2) relates to the leaf traits, indicating an orthogonal relation between the leaf traits and the light requirement/tree height axis, and creates a subdivision of the knowledge-based functional groups. Pioneers show a subdivision with high SLA and nutrient content, on the one hand, and low SLA and nutrient contents on the other but similar stoichiometry of N and P. This first group shows most similarities with general trait descriptions of early-pioneer species (Grime & Pierce 2012). The leaf traits from this second group suggest an adaptation with higher investment in leaf economics with higher lifespan. The understory ombrophiles show a subdivision based on WD, LNC, N:P and LCC although similar C:N. These results suggest that the location of pioneers and late successional species along the LES (Grime 1977; Reich 2014) is not as straightforward. Multiple drivers could cause differences in resource acquisition traits within the knowledge-based functional groups, including species-specific mycorrhizal associations, differences in nutrient requirements, rooting depths, opportunities through vegetation dynamics, or differences in the a priori defined light requirement specifically during adult stages. Environmental differences are minimal since all trees were sampled within a small measurements area with similar climate and soil characteristics (*Chapter 2*).

Differentiation of ecological strategies within the a priori defined light requirement classes could indicate the necessity for subdividing these groups. For example, the slow and fast shade-bearing clusters are both shade-tolerant but possibly deal differently with light limitation (Craine *et al*. 2012). Limited light resources could induce the need for increased leaf area for higher light capture. Fast shade-bearing individuals shows traits related with this strategy with a higher SLA and nutrient contents increasing total photosynthesis. This group also shows a lower WD and marginally higher maximal tree height indicating larger growth rates and greater possibilities to reach the canopy first. Fast shade-bearing individuals most likely benefit more from additional light during later stages of its life. Slow shade-bearing individuals however shows an alternative strategy showing thicker leaves with longer life span minimizing losses due to foliage turnover, herbivory and mechanical damage (Pauw *et al*. 2004; Hanley *et al*. 2007; Kitajima & Poorter 2010), and by possibly having low respiration rates (Baltzer & Thomas 2007). An additional benefit would be the increased production of shade for competitive purposes (Anten 2005). This difference in strategies regarding light limitation within similar light requirement classes suggests the need for refinement of these classes (Valladares & Niinemets 2008). Specifically light requirement shifts during ontogeny can aid in defining functional groups that can better explain functional diversity and ecosystem functioning.

Strategies in nutrient uptake, nutrient residence time and differentiation in nutrient requirement show potential for explaining differences in leaf traits within the knowledge-based classes, with significant differences found in leaf nutrients and N:P stoichiometry. Foremost, all groups experience P rather than N limitation as indicated by the leaf N:P varying between 38 and 78. This range is much higher than the threshold of 16 above which biomass production is presumed to be P limited (Koerselman & Meuleman 1996; Aerts & Chapin 2000; Hättenschwiler *et al*. 2011). Accordingly, low soil available P concentration of approximately 8.5 mg available P kg^{-1} of soil indicates P-deficient conditions which can limit tree growth and net primary productivity as shown in other tropical forest regions (Quesada *et al*. 2010). Identifying causes of variations of leaf N:P and nutrient concentrations of individual trees growing in the same environment is a challenge and requires partitioning of physiological and external controls. A first important aspect is that, notwithstanding the suggested P limitation at our site, species level differences in nutrient requirements and a difference of perceived nutrient limitation are possible (Townsend *et al*. 2007). This is highlighted by the large variability found in LNC and LPC within the site. Similar results in other areas with P limitation suggest that different physiological strategies and responses to nutrient limitation within different species are present, possibly related to the degree of mycorrhizal association of the different species, and that the extent of limitation may vary among species within a single site (Townsend *et al.* 2007; Hättenschwiler *et al.* 2008). Accordingly, Davidson *et al.* (2004) showed highly variable leaf nutrient responses across species to N-P fertilization in a secondary forest located on P limited soils in the eastern Amazon. Variability in the degree of P limitation among species could indicate that different species exhibit distinct P use strategies, including P resorption efficiencies (Hättenschwiler *et al.* 2008). Nevertheless, P resorption is not commonly considered as a major nutrient flux (Aerts 1996).

Important physiological strategies of species are their nitrogen fixing abilities and/or interactions with mycorrhiza. For example, species level differences in leaf nutrients in a West African forest were associated with ectomycorrhizal abundance (Chuyong *et al*. 2000), a characteristic that is common although highly variable in tropical forests (Malloch *et al*. 1980). Also within our study, at least a fraction of the N uptake of the trees is from biological N_2 fixation or provided by mycorrhiza, as indicated by the leaf $\delta^{15}N$ values for all species which are all lower than the $\delta^{15}N$ values (7.0 to 9.6 ‰, data not shown) observed in the top soil (0-10 cm) in all plots. A ^{15}N depletion within some clusters could suggest important associations with (arbuscular) mycorrhizal fungi (Amundson *et al*. 2003; Craine *et al*. 2009). Additionally, some species could have N_2-fixing symbioses and could be expected to have at least high leaf N concentrations (McKey 1994; Batterman *et al.* 2013). Unfortunately, the N_2 fixation capacity of the studied species and their symbiosis with mycorrhiza are hardly documented in literature. Species from the Fabaceae family (excluding the subfamily Caesalpinioideae) might be associated with N_2-fixing bacteria, although no significant differences are found with other species within this study (data not shown). This could be due to the temporal variability in N_2 fixing capacity of Fabaceae, with a down-regulated symbioses in latter stages of the succession. Accordingly, species from the Fabaceae are not uniformly found within clusters with high LNC. This could suggest that N_2 fixation contributes little to a functional explanation of the reported range in leaf nutrients. This conclusion was also made by Hättenschwiler *et al.* (2008), although other studies within the Amazonian forest did find significantly higher leaf N contents in legumes versus other families analyzed (e.g. Martinelli *et al*. 2000).

The differences in N:P between the clusters, regardless of the driving factors, affect the physiology of the tree. For example, N:P ratio has been shown to correlate positively with WUE (Cernusak *et al.* 2010). Cernusak *et al.* (2010) suggested that this relationship results from the correlations between plant N concentrations and WUE, and between plant transpiration and the transport of P to root surfaces by mass flow. However, this relationship is not evident between the clusters as N:P, LNC and LPC of the clusters do not correlate well with $\delta^{13}C$, as a proxy for WUE.

Several species are not uniquely constrained to a single cluster. It could be argued that discrete functional groups are ambivalent with the continuity of the trait distributions (Wright *et al.* 2003). Even though we distinguished clusters related to the knowledge-based classifications, the spread of some species within multiple clusters suggest that the continuous physiological and morphological traits do not show natural discontinuities. However, the large variance in leaf traits among knowledge-based functional groups in a homogeneous environment at the small local scale reported here, suggest different adaptive responses to nutrient limitation. Inclusion of this variation, and specifically the tolerance of species to low nutrient availability, in the classification of species will allow us to better understand ecosystem processes in species rich tropical forests.

6.5 Conclusion

We conclude that with functional classes based on light requirement and adult stature, a large degree of variation of wood density, potential tree height and leaf traits related to resource acquisition is found. The subdivision of the knowledge-based classifications will augment the strength of the classifications for simulating forest dynamics at this specific site. The fine-tuning of knowledge-based classification could provide a useful approach for more realistically representing the highly diverse tropical tree species and inform plant functional types of models.

Supplementary Table S6.1: Cross tabulation between the two knowledge-based classifications, namely light requirement and adult stature (Canopy old-growth forest (C-OG), understory old-growth forest (US-OG) and canopy regrowth forest (C-RG)). Chi^2 test reveals dependency between the two classification.

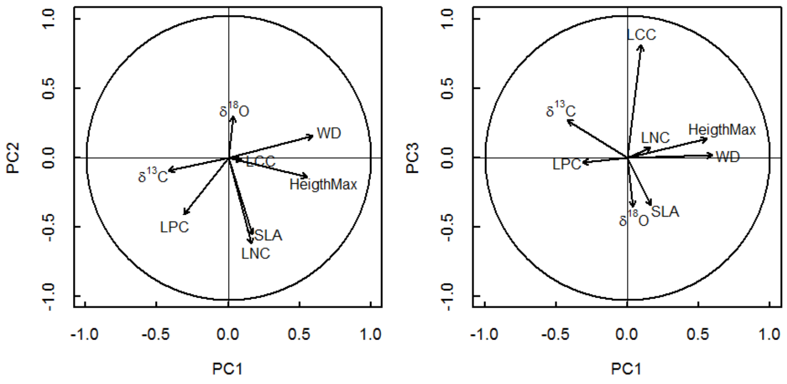
	Light-demanding	**NPLD**	**Ombrophile**	**Shade-tolerant**
C-OG	68	15	70	128
US-OG	161	0	0	8
US-RG	6	22	90	22

Supplementary Table S6.2: Spearman correlation coefficients between all leaf and wood traits, namely wood density (WD), leaf nitrogen content (LNC), leaf carbon content (LCC), leaf phosphorus content (LPC), carbon to nitrogen ratio (C:N), nitrogen to phosphorus ratio (N:P), carbon isotope composition (δ^{13}C), nitrogen isotope composition (δ^{15}N), oxygen isotope composition (δ^{18}O), leaf dry matter content (LDMC) and specific leaf area (SLA). P-values are indicated: * p<0.05, ** p<0.01,*** p<0.001.

	LNC	**LCC**	**LPC**	**C:N**	**N:P**	**δ^{13}C**	**δ^{15}N**	**δ^{18}O**	**LDMC**	**SLA**
WD	-0.088**	0.171***	-0.290***	0.100**	0.235***	-0.295***	-0.065*	0.127***	**0.398*****	-0.077*
LNC	1	-0.076*	**0.303*****	**-0.956*****	0.382***	-0.043	**0.491*****	-0.180***	**-0.358*****	**0.490*****
LCC		1	-0.088	0.305***	0.092	-0.094*	-0.051	-0.041	0.255***	-0.258***
LPC			1	**-0.297*****	**-0.775*****	**0.361*****	0.203***	**-0.118***	**-0.386*****	0.195***
C:N				1	-0.336***	0.044	**-0.476*****	0.121*	**0.393*****	**-0.523*****
N:P					1	-0.221***	0.094	-0.009	0.171***	0.072
δ^{13}C						1	0.066*	**-0.047**	-0.187***	-0.071*
δ^{15}N							1	-0.085*	**-0.324*****	0.178***
δ^{18}O								1	0.133***	-0.112***
LDMC									1	**-0.625*****
SLA										1

Supplementary Table S6.3: Principal component analysis including leaf nitrogen content (LNC), leaf carbon content (LCC), leaf phosphorus content (LPC), carbon isotope composition (δ^{13}C), oxygen isotope composition (δ^{18}O), specific leaf area (SLA), wood density (WD) and species-specific maximal tree height (HeigthMax). Only principal components with eigenvalues more than one are shown. The highest correlations (> 0.5) are indicated in bold.

	PC1	**PC2**	**PC3**
LNC	0.163	**-0.622**	0.068
LCC	0.094	-0.016	**0.812**
LPC	-0.314	-0.407	-0.033
δ^{13}C	-0.421	-0.095	0.270
δ^{18}O	0.037	0.299	-0.354
SLA	0.166	**-0.553**	-0.344
WD	**0.594**	0.156	0.016
HeigthMax	**0.555**	-0.138	0.137
Standard deviation	1.362	1.324	1.071
Proportion of variance	0.232	0.219	0.143
Cumulative proportion	0.232	0.451	0.594



Supplementary Figure S6.1: Correlation circle of the principal component analysis presenting the contribution of the different variables to the principal components. Leaf nitrogen content (LNC), leaf carbon content (LCC), leaf phosphorus content (LPC), carbon isotope composition (δ^{13}C), oxygen isotope composition (δ^{18}O), specific leaf area (SLA), wood density (WD) and species-specific maximal tree height (HeigthMax).

Supplementary Table S6.4: Number of individuals from each species within the defined clusters (Cl). Cl1: Fast light-demanding individuals; Cl2: Slow light-demanding individuals; Cl3: High N understory ombrophile individuals; Cl4: Low N understory ombrophile individuals; Cl5: Shade-tolerant canopy individuals; Cl6: Slow shade-bearing individuals; Cl7: Fast shade-bearing individuals. Key species of each cluster indicated in bold.

Species	**Cl 1**	**Cl 2**	**Cl 3**	**Cl 4**	**Cl 5**	**Cl 6**	**Cl 7**	**All**
Allanblackia floribunda	0	0	1	0	0	0	0	1
Alstonia boonei	0	0	0	0	0	0	1	1
Anonidium mannii	1	0	**16**	0	0	0	2	19
Aphanocalyx cynometroides	0	0	0	0	0	2	0	2
Baikiaea insignis	0	1	0	0	0	1	1	3
Balanites wilsoniana	1	0	0	0	0	0	0	1
Bellucia grossularioides	0	1	0	0	0	**14**	0	15
Blighia welwitschii	0	0	1	0	1	3	1	6
Canarium schweinfurthii	0	1	0	0	0	0	0	1
Carapa procera	0	0	5	0	0	**15**	0	20
Cavacoa quintasii	0	0	**12**	3	0	1	0	16
Cecropia concolor	1	2	0	0	0	0	0	3
Celtis mildbraedii	0	0	0	0	4	2	0	6
Celtis tessmannii	0	0	2	0	5	4	0	11
Chrysophyllum africanum	0	0	2	0	0	**6**	1	9
Chrysophyllum lacourtianum	0	0	0	0	3	1	4	8
Chrysophyllum sp.	2	1	0	0	0	0	0	3
Cleistanthus mildbraedii	0	0	4	0	1	**12**	3	20
Coelocaryon preussii	0	1	**9**	0	0	**5**	0	15
Cola griseiflora	0	0	**10**	0	0	1	1	12
Cola lateritia	0	0	3	0	0	2	0	5
Cola sp.	1	0	0	0	0	0	0	1
Combretum lokele	0	0	0	0	**11**	0	0	11
Craterispermum sp.	0	0	**5**	0	0	0	0	5
Cynometra hankei	0	0	0	0	**4**	0	0	4
Dacryodes edulis	0	0	1	0	0	0	0	1
Dacryodes osika	0	0	2	0	0	0	0	2
Dialium corbisieri	0	0	0	0	1	0	1	2
Dialium excelsum	0	0	0	0	2	0	0	2
Dialium pachyphyllum	0	0	2	0	3	**11**	3	19
Dialium pentandrum	0	0	0	0	0	2	0	2
Dialium sp.	0	0	**4**	0	0	**5**	0	9
Diospyros boala	0	0	0	0	0	**4**	0	4
Diospyros crassiflora	0	0	1	0	2	4	0	7
Diospyros sp.	0	0	2	0	1	5	0	8
Drypetes gossweileri	0	0	1	0	**10**	0	0	11
Drypetes louisii	0	0	0	0	0	1	0	1
Drypetes sp.	0	0	4	4	3	10	0	21
Drypetes sp.1	0	0	3	1	0	0	0	4
Entandrophragma candollei	0	1	1	0	0	0	0	2
Entandrophragma utile	0	0	1	0	0	0	0	1

Supplementary Table S6.4 continued

Species	**Cl 1**	**Cl 2**	**Cl 3**	**Cl 4**	**Cl 5**	**Cl 6**	**Cl 7**	**All**
Erythrophleum suaveolens	0	0	2	3	0	3	0	8
Garcinia punctata Oliv.	0	0	2	5	0	**18**	0	25
Garcinia smeathmannii	0	0	0	0	0	2	0	2
Garcinia sp.	0	0	1	0	0	0	0	1
Gilbertiodendron dewevrei	0	0	1	0	1	**30**	0	32
Gilletiodendron mildbraedii	0	1	1	0	0	2	0	4
Greenwayodendron suaveolens	0	0	0	0	6	1	0	7
Grossera multinervis	0	0	0	0	0	0	2	2
Guarea cedrata	0	0	0	0	0	0	3	3
Guarea thompsonii	0	0	4	0	0	0	8	12
Hannoa klaineana	0	0	1	0	0	0	0	1
Harungana madagascariensis	1	1	0	0	0	0	0	2
Homalium longistylum	0	0	1	0	0	0	0	1
Irvingia gabonensis	0	0	0	0	0	1	0	1
Irvingia grandifolia	0	0	0	0	1	2	1	4
Isolona thonneri	0	0	**10**	0	0	1	0	11
Julbernardia seretii	0	0	1	0	0	0	0	1
Macaranga monandra	**8**	**9**	4	0	0	0	0	21
Macaranga spinosa	**12**	**14**	1	0	0	0	0	27
Macaranga zenkeri	0	**9**	0	0	0	0	0	9
Maesopsis eminii	4	0	1	0	0	0	1	6
Margaritaria discoidea	3	0	0	0	0	0	0	3
Microdesmis sp.	0	0	0	0	1	0	2	3
Microdesmis yafungana	0	0	2	0	1	0	2	5
Millettia drastica	0	0	2	0	0	0	0	2
Monodora angolensis	2	0	0	0	0	0	0	2
Monodora myristica	0	0	1	0	0	0	0	1
Musanga cecropioides	6	**35**	0	0	0	0	0	41
Musanga smithii	1	**22**	0	0	0	0	0	23
Ongokea gore	0	0	0	0	2	4	2	8
Pancovia harmsiana	0	0	**9**	0	0	1	0	10
Pancovia laurentii	0	0	**7**	0	0	2	0	9
Panda oleosa	0	0	**10**	0	3	0	2	15
Parkia bicolor	1	3	0	0	0	0	0	4
Pausinystalia lane-poolei	0	1	0	0	0	0	0	1
Pentaclethra macrophylla	0	0	0	0	3	2	0	5
Persea americana	0	0	**5**	0	0	0	0	5
Petersianthus macrocarpus	0	0	3	0	**11**	1	**12**	27
Piptadeniastrum africanum	0	0	0	0	1	1	0	2
Polyalthia suaveolens	0	0	1	0	**5**	0	1	7
Prioria balsamifera	0	0	0	0	1	0	**5**	6
Prioria oxyphylla	0	0	0	0	3	4	0	7

Supplementary Table S6.4 continued

Species	**Cl 1**	**Cl 2**	**Cl 3**	**Cl 4**	**Cl 5**	**Cl 6**	**Cl 7**	**All**
Prioria sp.	0	0	0	0	0	0	1	1
Pterocarpus soyauxii	0	0	0	0	3	3	0	6
Pycnanthus angolensis	1	1	**9**	0	0	1	0	12
Quassia undulata	2	4	1	0	0	4	0	11
Ricinodendron heudelotii	**8**	2	0	0	0	0	0	10
Rinorea oblongifolia	2	2	0	0	0	0	0	4
Rinorea sp.	1	1	0	0	0	0	0	2
Scorodophloeus zenkeri	0	0	0	0	**31**	1	**13**	45
sp.2	0	0	1	0	1	2	0	4
Spathodea campanulata	1	0	0	0	0	0	0	1
Staudtia kamerunensis	0	0	0	0	**13**	2	5	20
Strombosia grandifolia	0	0	7	0	4	0	3	14
Strombosia pustulata	0	0	0	0	2	0	2	4
Strombosiopsis tetrandra	0	0	0	0	1	0	5	6
Symphonia globulifera	0	0	0	0	0	1	0	1
Synsepalum subcordatum	0	0	0	0	1	**8**	1	10
Tabernaemontana crassa	**8**	0	0	0	0	0	0	8
Tessmannia africana	0	0	0	0	5	6	1	12
Tetrapleura tetraptera	0	0	1	0	0	0	0	1
Tetrorchidium didymostemon	**16**	2	0	0	0	0	0	18
Trichilia gilgiana	0	0	0	0	0	0	**5**	5
Trichilia monadelpha	0	1	0	0	1	1	**11**	14
Trichilia prieuriana	0	0	0	0	2	0	2	4
Trichilia sp.	0	0	2	0	0	0	3	5
Tridesmostemon claessensii	0	0	2	0	0	**10**	0	12
Tridesmostemon omphalocarpoides	0	0	2	0	0	6	0	8
Trilepisium madagascariense	0	0	0	0	2	3	1	6
Turraeanthus africanus	0	0	0	0	0	0	**7**	7
Vepris louisii	0	0	1	0	0	0	0	1
Vernonia conferta	**11**	0	0	0	0	0	0	11
Vitex congolensis	0	2	0	0	0	0	0	2
Vitex sp.	2	0	0	0	0	0	0	2
Vitex welwitschii	5	0	2	0	0	0	1	8

Supplementary Table S6.5: 3-way cross tabulation of the 7 identified classes and their relation to light requirement classes and adult stature classes (Canopy old-growth forest (C-OG), understory old-growth forest (US-OG) and canopy regrowth forest (C-RG)).

		Light-demanding	**NPLD**	**Ombrophile**	**Shade-tolerant**
Fast light-demanding individuals	**C-OG**	9	0	0	3
	US-OG	1	2	3	0
	US-RG	**62**	0	0	8
Slow light-demanding individuals	**C-OG**	4	0	1	7
	US-OG	0	1	2	2
	US-RG	**92**	0	0	0
High N understory ombrophile individuals	**C-OG**	16	2	5	5
	US-OG	1	1	**45**	3
	US-RG	6	0	0	0
Low N understory ombrophile individuals	**C-OG**	0	3	0	0
	US-OG	0	0	0	0
	US-RG	0	0	0	0
Shade-tolerant canopy individuals	**C-OG**	15	2	10	**74**
	US-OG	2	1	11	3
	US-RG	0	0	0	0
Slow shade-bearing individuals	**C-OG**	10	7	**32**	**24**
	US-OG	0	1	**21**	11
	US-RG	0	0	0	0
Fast shade-bearing individuals	**C-OG**	14	1	**22**	**25**
	US-OG	2	16	8	3
	US-RG	1	0	0	0

7

Influence of non-persistent and persistent monodominance on functional diversity and functional community structure in central African tropical forests

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Abstract

Monodominant forests are frequently found in African tropical rainforests, generally characterized by a low diversity in tree species. However, functional diversity and functional structure of these forests remains poorly understood. In this study we investigated the functional diversity and functional community structure of persistent and non-persistent monodominant forests compared to the adjacent mixed forest, using 15 functional leaf and wood traits covering 95% of the species found over 16 one-hectare plots. We identified similar differences in functional diversity in both monodominant forest types compared to the adjacent mixed forest, with lower functional richness and higher functional divergence in the monodominant forests. In the persistent monodominant forest, shifts in community-level means are identified for nutrient contents, water use efficiency traits and specific leaf area. These shifts are driven by environmental filtering, possibly enforced by presence of the monodominant species by altering probabilities of traits suitable for this environment. In the non-persistent monodominant forest, differences in community-level means have also been identified, with its successional stage after deforestation the main driver of this difference. Shifts in N-P limitation have been identified for this young monodominant regrowth forest, in combination with shifts in resource acquisition and stress tolerance strategies. The non-persistent monodominant species itself does not show signs of influence on other species in this community.

7.1 Introduction

Lowland tropical rainforests are complex systems with a high diversity of species. Nevertheless, not all tropical communities are equally diverse. African tropical rainforests are less diverse in terms of tree species then Amazonian and SE-Asian rainforests (Parmentier *et al.* 2007; Slik *et al.* 2015). Additionally, forests with a lower tree species diversity are frequently found in South-East Asia and the Neotropics, but are most common in Central Africa (Hart 1985; Connell & Lowman 1989; Torti *et al.* 2001; Peh *et al.* 2011a). An important type of forest with a reduced number of species is the monodominant forest dominated by a single canopy species. Such monodominance has been defined as ≥ 60% of canopy level trees belonging to the same species (Hart 1985; Connell & Lowman 1989; Peh *et al.* 2011b), although higher percentages of abundance is regularly attained in these systems (Connell & Lowman 1989). Two main types of monodominant forest can be defined namely non-persistent and persistent dominance (Peh 2009).

Non-persistent dominance, by definition, does not have the ability to regenerate under its own canopy, and thus lasts for only one or at most a few generations (Connell & Lowman 1989; Peh 2009). This short-term dominance is usually related to secondary forest succession (Hart *et al.* 1989) that occurs following anthropogenic clearance or large-scale natural disturbance such as windstorms. Several non-persistent monodominant floodplain forests can be found in the Neotropics, for example dominated by pioneer species *Ceropia* sp. or *Salix humboldtiana* Willd. (Parolin *et al.* 2002), or in Africa by *Mitragyna stipulosa* DC. Kuntze (Hughes & Hughes 1992). An important monodominant species that occurs after forest clearance in tropical Africa is *Musanga cecropioides* R.Br. ex Tedlie (Coombe & Hadfield 1962). Forest conversion in tropical Africa is substantial and mainly driven by shifting cultivation, resulting in large areas of secondary forest. Depending on the definition of different forest types, secondary forest area is estimated to be between 28% (Pan *et al.* 2011) and 65% (FAO 2011) of the total forest area of tropical Africa or the Congo Basin, respectively.

Among the persistent monodominant old-growth forests, multiple types of monodominance and their drivers can be found, including water-logged forest such as mangroves and swamp forests, low-nutrient forests such as Amazonian caatinga and heath forests in Southeast Asia. Another type of persistent monodominant forest grows in similar environmental conditions as their adjacent high-diversity forests apparently not caused by major edaphic differences or recent disturbance. They are found in a variety of substrates ranging from low to high nutrient status. The best-studied of these monodominant forest is dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Leonard from which naturally occurring monodominant patches are commonly found across Central Africa alongside forests with high species diversity (Hart 1985; Peh *et al.* 2011a; Viennois *et al.* 2013; Fayolle *et al.* 2014a). The presence of an environmental filter for establishment of its monodominance is not always evident. For example, Peh *et al.* (2011a) did not find evidence for differences in soil characteristics between this monodominant forest and the adjacent mixed forest, similar to findings of Hart (1985) and Conway (1992), while Torti *et al.* (2001) did report a lower availability of nitrogen in the monodominant forest.

The total species richness and biodiversity of both the non-persistent and persistent monodominant forest has been the topic of many studies (e.g. Makana 1999; Anbarashan & Parthasarathy 2013; Bu *et al.* 2014). The non-persistent forest type generally has lower species richness compared to the adjacent mixed forest. Yet, the species richness of persistent monodominance compared to the adjacent mixed forest is variable. Both similar (Hart *et al.* 1989; Connell & Lowman 1989) and lower species richness (Peh *et al.* 2009; Djuikouo *et al.* 2010) in the persistent monodominant forest has been documented. Nevertheless, low species diversity does not necessarily indicate an equivalently low functional diverse system. Non-dominant species could fill functional niches in the system, and both dominant and non-dominant species could have a wide functional range. Assessment of functional diversity, defined as the value, range and distribution of functional traits in a given ecosystem (Diaz *et al.* 2007), could provide more insight. Functional diversity has been shown to be a good indicator for ecosystem resource dynamics, stability and productivity (Tilman 2000; Díaz & Cabido 2001; Cardinale *et al.* 2006; Díaz *et al.* 2007), and is now widely used to describe ecosystem functioning (e.g. Grime 1998; Tilman 2001; Lohbeck *et al.* 2012).

Within this study we investigate functional diversity and functional community structure in 17 one-hectare plots of monodominant and mixed forests in a central region of the Congo Basin, in DRC. A unique dataset of 15 leaf and wood traits (described in *Chapter 6*) covering 95% (basal area weighted) of all species present in the plots is used. Plant traits are scaled up from individuals to community level trait distributions as a means to investigate ecosystem functioning and community assembly trough environmental filtering (e.g. Laughin *et al.* 2011; Fayolle *et al.* 2012; Fortunel *et al.* 2014). In this study, we investigate if the presence of a monodominant species affects the functional diversity of its community, irrespective of the type of monodominance and how the monodominance is attained. It is hypothesized that a monodominant forest holds a lower functional diversity than a mixed forest, either due to the environmental filtering which causes the monodominance and/or due to the presence of the dominant species itself. In this respect a comparison is made between the functional niche space filled by the monodominant species and other species in the community. It is hypothesized that the dominant species, related to its high abundance, holds a specific functional niche space in the community, and co-regulates – combined with other environmental filters – which other species with a specific functional set-up are present in this forest. However, this ‘co-regulation’ is only expected in the persistent monodominance and not in the non-persistent monodominance, as the longevity of their persistence suggests. The following specific research questions are investigated to address these hypotheses: (1) is lower species diversity reflected in a lower functional diversity, and which aspects of diversity are affected? (2) which community level traits differ between high and low species diverse systems? (3) how does the dominant species influence community distributions of traits? (4) does the monodominant species act as an environmental filter for the establishment of other species?

7.2 Methods

Study area

This study is carried out in Yangambi (DRC), described in *Chapter 2*, focusing on the following plots:. This chapter focusses on the following plots: young *Musanga* regrowth forest (n = 3; age since disturbance ± 7 years), old *Musanga* regrowth forest (n = 3; age since disturbance ± 20 years), old-growth mixed forest (n = 5), and old-growth monodominant forest (n = 5). As both young and old *Musanga* regrowth forests are dominated by *Musanga cecropioides* R.Br. ex Tedlie, they together represent the non-persistent monodominant forest.

The old-growth monodominant forest dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Leonard represents the persistent monodominant forest. Within all plots, all trees with a DBH larger or equal to 10 cm have been measured and identified to species level. Details of each forest type can be found in Table 7.1.

Species diversity

A comparison is made of the tree species diversity in the mixed forest and the persistent and non-persistent monodominant forests. Therefore, diversity indices species richness, Pielou’s evenness (Pielou 1969), Shannon-Weaver (Shannon & Weaver 1949) and Simpson (Simpson 1949) indices are calculated on a plot level (1 ha). The number of species found within one hectare represents the species richness. Evenness measures the similarity of the abundances of different species. The Shannon-Weaver index takes into account the evenness of the abundance of species, while Simpson’s index is less sensitive to the species richness but more sensitive to the most abundant species. All indices were calculated using the formulas provided in the package VEGAN 2.0 (Oksanen 2010) in R 2.13.1 (CRAN core-development team).

Even though plot sizes are the same, species richness still depends on the amount of individuals included in the analysis. Rarefaction curves are therefore investigated as a means to compare species richness independently from sample size. Rarefied species richness is assessed using the ‘rarefy’ function in the same VEGAN package.

Sampling and trait analysis

Leaf samples and wood samples from the stem were collected on all species within a cumulative 95% basal area of each plot. Sample repetitions within species were collected, namely two individuals in each plot were selected within each pre-assigned diameter class of 10-20, 20-30, 30-50 and >50 cm DBH, if present. A total of 995 individuals were sampled, covering 123 species. All samples were collected between March and May 2012 and we measured 11 traits related to leaf and wood morphology and functioning. Another 4 wood traits are determined on xylarium specimens from the Yangambi forest of the Royal Museum for Central Africa (RMCA), covering 82 species (Table 7.2).

Details on sample analysis for trait determination can be found in *Chapter 6*, namely for SLA, LDMC, LCC, LNC, LPC, $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$ and WD. Additional wood traits are measured on already prepared sections of slides from the xylarium of the RMCA. Species were selected which match the species selected at the inventory sites, and 3 slides were used for measurements. VDm was measured on a minimum of 30 vessels in both horizontal and vertical directions and an average VDm is determined for each sample. All vessels are counted within a known area to determine VD. Ray width is determined by counting the cells along the horizontal axis of each ray on the radial section, and both RWMin and RWMax are determined. All measurements on permanent slides are done using the software Analysis.

Table 7.1: Stand characteristics and species diversity for each forest type. Species abundance and wood density are basal area weighted. Full species names: *Musanga cecropioides, Albizia adianthifolia, Vernonia conferta, Macaranga spinosa, Bellucia grossularioides, Macaranga monandra, Petersianthus macrocarpus, Scorodophloeus zenkeri, Panda oleosa, Anonidium mannii, Staudtia kamerunensis, Gilbertiodendron dewevrei, Cavacoa quintasii, Cleistanthus mildbraedii* and *Dialium pachyphyllum.*

	Non-persistent monodominance			**Persistent monodominance**
Site characteristics	**Young *Musanga* regrowth**	**Old *Musanga* regrowth**	**Old-growth mixed**	**Old-growth monodominant**
Stand characteristics				
Plots of 1 ha	3	3	5	5
Stem density (ha^{-1})	279 ± 127	360 ± 76	419 ± 89	349 ± 81
Basal area (m^{2} ha^{-1})	4.6 ± 2.4	18.3 ± 2.0	32.4 ± 3.5	29.7 ± 2.6
Wood density (g cm^{-3})	0.38 ± 0.05	0.36 ± 0.03	0.62 ± 0.02	0.657 ± 0.001
Species diversity				
Species	*M. cecropioides* (55.9%)	*M. cecropioides* (62.7%)	*S. zenkeri* (16.1%)	*G. dewevrei* (65.1%)
(5 most abundant, %)	*V. conferta* (9.6%)	*M. monandra* (8.7%)	*P. macrocarpus* (6.8%)	*C. quintasii* (6.0%)
	M. spinosa (6.8%)	*M. spinosa* (6.3%)	*P. oleosa* (5.6%)	*S. zenkeri* (5.5%)
	B. grossularioides (5.5%)	*P. macrocarpus* (3.1%)	*A. mannii* (4.7%)	*C. mildbraedii* (2.7%)
	A. adianthifolia (4.6%)	*S. zenkeri* (2.4%)	*S. kamerunensis* (3.0%)	*D. pachyphyllum* (1.5%)
Species richness	29.3 ± 9.5	36 ± 9.6	81.8 ± 5.1	54.4 ± 12.9
Pielou’s evenness	0.64 ± 0.08	0.58 ± 0.03	0.84 ± 0.03	0.73 ± 0.03
Shannon index	2.1 ± 0.5	2.1 ± 0.2	3.7 ± 0.1	2.9 ± 0.2
Simpson diversity	0.76 ± 0.10	0.75 ± 0.05	0.96 ± 0.01	0.89 ± 0.02

Table 7.2: List of all plant functional traits including the used abbreviations and units. General strategy correlations are provided. (Adapted from Baraloto *et al*. 2010b; Fortunel *et al*. 2014).

Trait	Abbreviation	Unit	Strategy correlations
Specific leaf area	SLA	m^2 kg^{-1}	Resource capture and defense
Leaf dry matter content	LDMC	g g^{-1}	Resource capture and defense
Foliar carbon content	LCC	mg g^{-1}	Resource capture and defense
Foliar nitrogen content	LNC	mg g^{-1}	Resource capture
Foliar phosphorus content	LPC	mg g^{-1}	Resource capture
Foliar C:N ratio	C:N	g g^{-1}	Resource capture and defense
Foliar N:P ratio	N:P	g g^{-1}	Resource capture
Foliar ^{13}C composition	δ^{13}C	‰	Resource capture
Foliar ^{15}N composition	δ^{15}N	‰	Resource capture
Foliar ^{18}O composition	δ^{18}O	‰	Resource capture
Wood density	WD	g cm^{-3}	Transport, structure and defense
Vessel density	VD	μm^{-2}	Transport, structure and defense
Vessel diameter	VDm	µm	Transport, structure and defense
Minimum ray width	RWMin	cells	Transport, structure and defense?
Maximum ray width	RWMax	cells	Transport, structure and defense?

Statistical analysis

Univariate statistics of trait distributions is performed for all plots. Community weighted means (CWM) are investigated which account for intraspecific trait variability and abundance of species. Specifically, these CWM are based on plot level distributions of each trait which are generated by including species specific trait variations. The entire range of trait values for each species is assumed as equally likely values. Outliers are removed to prevent overly skewed species trait distributions. Next, a species specific uniform distribution between the minimum and maximum value is set up and a random value from within this distribution is assigned to all individuals from the same species that have not been measured. CWM are subsequently calculated on these communities with generated species-specific trait values for each individual.

To investigate the effect of monodominance on the community trait composition, more detailed species groups are investigated within each type of monodominant forest. In the non-persistent monodominant forest, the trait space of the dominant species *Musanga cecropioides* is compared to the trait space of all other early successional species found within the community and to those species which are not classified as early successional species. These non-early successional species are present from ingrowth of the adjacent old-growth forest or from remnants of the old-growth forest before the forest degradation. In the persistent monodominant forest a distinction is made between species that are also found in the adjacent mixed forest and species unique for the monodominant forest. The same distinction is made within the mixed forest, namely shared and unique species for this community, allowing us to investigate the influence of the presence of the dominant species *Gilbertiodendron dewevrei* for species establishment in this monodominant forest. This species distinction between the mixed and persistent monodominant forest is tested using detrended correspondence analysis weighted using species basal areas (Supplementary Figure S7.1).

Multivariate statistical analysis is performed here since the ecology of species inherently relates to a combination of traits. Multivariate functional diversity indices are calculated for each plot. Functional diversity consists of different dimensions, and according to Mason *et al*. (2005) and Villéger *et al*. (2008), at least three different indices are needed to capture these different dimensions, namely functional richness, functional evenness and functional divergence. Functional richness is defined as the amount of niche space filled by species in the community, thus describing trait dissimilarity. Functional richness is measured for each plot as the convex hull volume encompassing all traits. Functional evenness is the evenness of abundance distribution in filled niche space. Functional divergence is the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community. Since a monodominant tree community could have a large influence on the distribution of trait values, we include another measure of divergence, namely functional dispersion (Laliberté & Legendre 2010). Functional dispersion is the mean distance in multidimensional trait space of individual species to the centroid of all species, while functional divergence quantifies how species diverge in their distances from the center of gravity in the functional space (Villéger *et al.* 2008; Laliberté & Legendre 2010). Both functional divergence and functional dispersion are calculated relative to the centroid per plot. All indices are calculated using the R package FD (Laliberté *et al*. 2014).

7.3 Results

Diversity indices

Species and trait diversity of persistent and non-persistent monodominant forest has been compared with an adjacent mixed forest. Lower species diversity is found both in the persistent and non-persistent monodominant forest compared to the mixed forest, with a lower overall species richness, species evenness index and Simpson’s index (Table 7.1, Figure 7.1). Both types of monodominant forest have a significantly lower functional richness compared to the mixed forest (Non-persistent monodominance $p < 0.01$, Figure 7.2; Persistent monodominance $p < 0.01$, Figure 7.3). Additionally, functional divergence and dispersion indicate a similar relationship for both monodominant forest types with the mixed forest (Figure 7.2 & 7.3). In the non-persistent monodominant forest, both functional divergence and dispersion show significantly higher values compared to the mixed forest ($p < 0.01$; Figure 7.2). In the persistent monodominant forest, functional dispersion is also significantly higher, although the difference is not significant for functional divergence (Figure 7.3). Functional evenness is similar for both types of monodominant forest and the mixed forest.

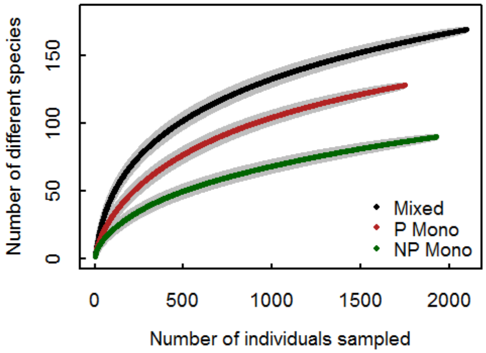


Figure 7.1: Species richness of the mixed forest (Mixed, black), the persistent monodominant (P Mono) forest of *Gilbertiodendron dewevrei* (red) and the non-persistent monodominant (NP Mono) forest of *Musanga cecropioides* (green) presented by rarefaction curves. Standard errors are presented by the grey backgrounds.

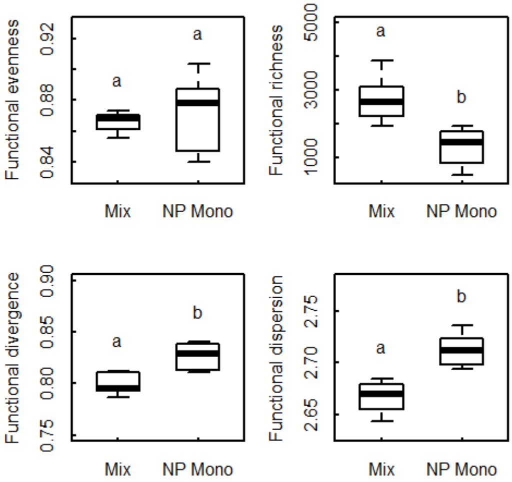


Figure 7.2: Comparison of functional diversity measures of the non-persistent monodominant forest (NP Mono) and the adjacent mixed forest (Mix). Young and old *Musanga* regrowth forest make up the non-persistent monodominant forest. Functional diversity measures are calculated on a plot level and represented per forest type. Letters indicate if there is a significant difference ($p < 0.01$) between the forest types.

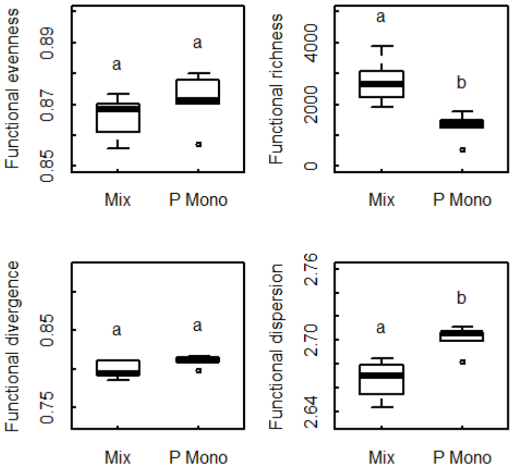


Figure 7.3: Comparison of functional diversity measures of the persistent monodominant forest (P Mono) and the adjacent mixed forest (Mix). Functional diversity measures are calculated on a plot level and represented per forest type. Letters indicate if there is a significant difference ($p < 0.01$) between the forest types.

Functional community structure and influence of the monodominant species

For most traits a significant difference is found between their distributions in mixed or monodominant forests. The non-persistent monodominant forest shows differences from the adjacent mixed forest on the community level (indicated as ‘All’ in Figure 7.4) with significant differences in mean values of nutrient status, namely lower values of LNC but higher LPC, lower WD and VD, but larger VDm, smaller SLA and LCC, and higher values $\delta^{13}C$ in the leaves (Figure 7.4). Community level differences are also found between the persistent monodominant forest and the adjacent mixed forest (Figure 7.5). Within the persistent monodominant forest we found lower nutrient contents, thicker leaves (low SLA and high LDMC), higher WD combined with lower VD and higher VDm, and lower values for $\delta^{13}C$ combined with lower $\delta^{18}O$ values. The functional structure of these communities can be highly influences by the presence of the monodominant species since they make up a large part of the community basal area, namely 60% and 65.1% for *Musanga cecropioides* and *Gilbertiodendron dewevrei* respectively (Table 7.1).

Within the non-persistent monodominant forest a detailed comparison between the community level traits, the traits of *Musanga cecropioides* and other early successional species provides more insight into the influence of this monodominance (Figure 7.4). Mean trait values of *Musanga cecropioides* show high similarity for the community level traits, although not for all, and larger differences are found between the other species and the community level means for these traits. The traits of other early successional species in this forest do not always differ from the mixed forest, for example for SLA, LNC, $\delta^{15}N$ and xylem traits. Nevertheless, WD of both *Musanga* and early successional species remains lower compared to the mixed forest. The higher LPC of the non-persistent forest community is also not solely due to the high values of *Musanga*, but is also found for the early successional species. A difference between other early successional species and the mixed forest is also apparent for the $\delta^{13}C$ which is higher in the non-persistent monodominant forest. *Musanga* also shows a lower $\delta^{18}O$, but this is not different for the other early successional species.

Average *Gilbertiodendron dewevrei* traits are generally not similar to the community-level mean and a stronger difference between *Gilbertiodendron dewevrei* and other species in the community is found. *Gilbertiodendron dewevrei* has a unique niche for most traits. WD is similar to other species in the community but the VDm is significantly higher and VD significantly lower. Additionally RWMin and RWMax of *Gilbertiodendron dewevrei* is significantly lower than for other species indicating the unique niche of *Gilbertiodendron* considering wood traits. The leaf nutrients of *Gilbertiodendron* are significantly lower with low LNC, LPC, and a high C:N. Leaf investment traits also differ significantly with a lower SLA and a higher LDMC, although LCC is similar to the other species. Comparing species within the monodominant tree community that are unique for the persistent monodominant forest with species that are also present in the mixed forest gives an indication of what type of traits are important for species establishment in this monodominant forest. LNC of the unique species is significantly lower ($p < 0.001$) than for the shared species, and *Gilbertiodendron* has even significantly lower values of LNC ($p < 0.001$). Additionally the N:P ratio of the unique species is significantly lower ($p < 0.001$) than the shared species with values similar to *Gilbertiodendron*. All wood traits except for WD differ significantly ($p < 0.05$) between the unique and shared species in the monodominant forest. VD is higher while VDm is smaller. Both RWMin and RWMax are smaller for the unique species, which more closely resembles the ray width size of *Gilbertiodendron dewevrei*. In addition to the presence of unique species, the influence of the presence of *Gilbertiodendron* is also visible on the entire tree community level. Both the unique and the shared species show significant shifts of mean trait values compared to the mixed forest. LNC is significantly lower for unique and shared species in the monodominant forest ($p < 0.001$; $p < 0.01$) and the C:N ratio is generally higher ($p < 0.05$) with a maximum for *Gilbertiodendron dewevrei*. LPC of the shared species is lower in the monodominant forest. LDMC of *G. dewevrei* is significantly higher than the other species. Nevertheless, the other species have a significantly higher LDMC compared to the mixed forest and thus important for the community mean. SLA remains lower in the monodominant tree community, both for *Gilbertiodendron dewevrei* and the other species. WUE trait $\delta^{18}O$ is higher for all species groups in the monodominant forest (unique $p < 0.001$; shared $p < 0.01$) while $\delta^{13}C$ is only significantly lower ($p < 0.01$) for the unique species compared to the mixed forest. Species unique for the mixed forest - not present in the monodominant forest - only showed a difference for WD, $\delta^{13}C$ and $\delta^{18}O$ compared to species also present in the monodominant forest. Within the mixed forest, WD was marginally lower ($p = 0.1$) for unique species, $\delta^{13}C$ was higher ($p < 0.01$) and $\delta^{18}O$ was lower ($p < 0.05$). All other traits were similar between unique and shared species in the mixed forest.

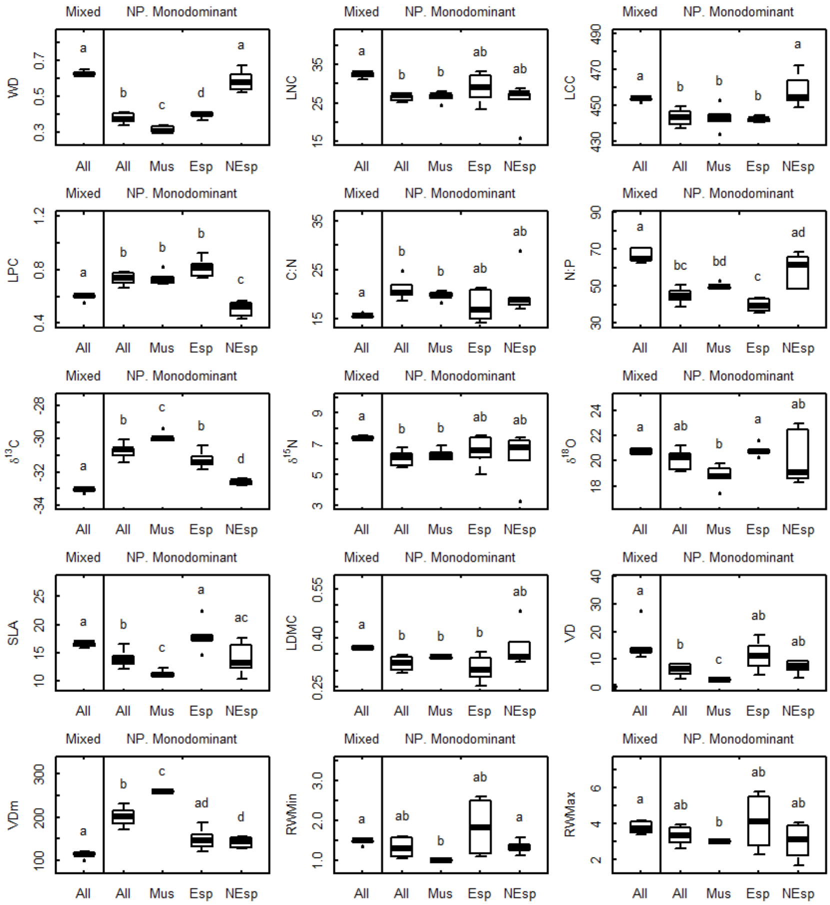


Figure 7.4: The mean of each single trait distribution is compared between species groups within the non-persistent (NP) monodominant forest and the mixed forest. Within the monodominant forest, the dominant species *Musanga cecropioides* (Mus) is compared to the trait space of all other early successional species (Esp) found within the non-persistent monodominant forest and to those species which are not classified as early successional species (NEsp). For each forest type, the community mean is also indicated (All). Both the young and old *Musanga* regrowth forests are included in the non-persistent monodominant forest. Letters indicate if there is a significant difference ($p < 0.01$) between the forest types.

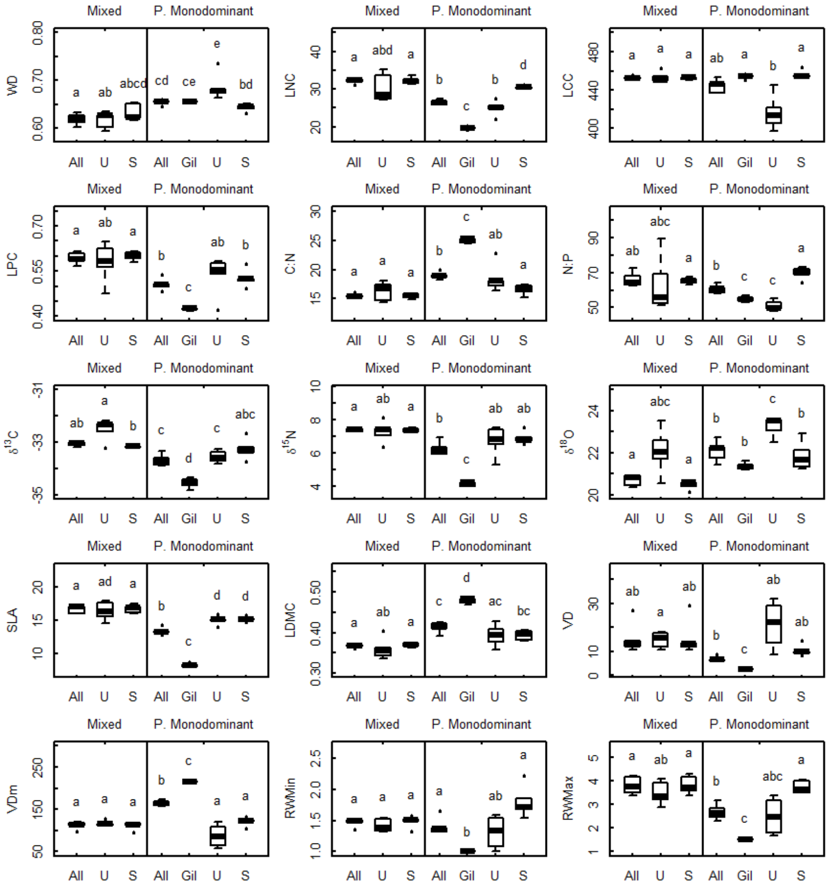


Figure 7.5: The mean of each single trait distribution is compared between species groups within the persistent (P) monodominant forest and the mixed forest. Within the monodominant forest, the dominant species *Gilbertiodendron dewevrei* (Gil) is compared to the trait space of all species unique for this forest (U for unique) and the species also present in the mixed forest (S for shared). Within the mixed forest, the species unique for the mixed forest (U) and the species also present in the monodominant forest are shown (S). For each forest type, the community mean is also indicated (All). Letters indicate if there is a significant difference ($p < 0.01$) between all species groups.

7.4 Discussion

Functional diversity and functional community structure of high and low species diverse systems provide more insight into ecosystem processes. In this study we investigated the functional community structure and functional diversity of persistent and non-persistent monodominant forests compared with an adjacent mixed forest. Additionally we assess the influence of the monodominant species on the functional diversity of the tropical tree community and its effect on individual trait shifts.

Systems with lower species diversity show low functional richness but high divergence due to monodominance

Both monodominant forest types show similar differences in diversity measures compared to the mixed forest. Functional richness was lower for both monodominant forest types indicating a higher amount of functional niche space filled in the mixed forest (Mason *et al.* 2005; Villéger *et al.* 2008), and thus higher trait dissimilarity within mixed forests. The mixed forest also had a higher species richness (both at plot scale and rarified) and Simpson diversity index, indicating that higher species richness increases the functional niche space. Additionally, the smaller functional niche space in the monodominant forests indicates the presence of environmental filtering (Mason *et al.* 2005; Villéger *et al.* 2008), possibly caused by the monodominant species and discussed further on. Within the niche space possible in the presence of the environmental filter, the monodominant forest and mixed forest show a similar niche differentiation since a similar functional evenness is found (Villéger *et al.* 2008; Paine *et al.* 2011). Functional divergence is slightly different in the two types of monodominance. The high functional divergence and dispersion of the non-persistent monodominant forest compared to the old-growth mixed forest indicates the large influence of the monodominant species *Musanga cecropioides*, with its niche occurring at the extremities of the community trait range. The same is true for the persistent monodominant forest, although this forest only shows a marginal difference in functional divergence with the mixed forest. A more similar distribution is present due to the high species diversity in both forests, while *Gilbertiodendron dewevrei* occupying a niche at the extremities of the functional range causes the divergence. The difference between species diversity within the *Gilbertiodendron* forest and the adjacent mixed forest is not always evident. Within some areas in Africa a similar species diversity between the two forest types has been recorded (Makana *et al.* 2004b), while lower diversity in the *Gilbertiodendron* forest is also possible (Hart *et al.* 1989; Read *et al.* 2000; Peh *et al.* 2009) as found in this study.

Regardless of the non-persistent monodominance in the regrowth forest, how functional diversity changes along successions in tropical forests is far from clear. For example, both decreasing (Fukami *et al.* 2005; Böhnke *et al.* 2014) and increasing functional richness (Mason *et al.* 2011) along successional gradients have been observed. Environmental filtering caused by disturbance can be expected during forest succession after deforestation, possibly increasing functional similarity and decreasing functional richness during the young stages. However, the importance of maximizing differences in traits in order to avoid competitive exclusion during regeneration is not well characterized (although see Lasky *et al.* 2014). An increasing functional divergence along the forest succession would indicate that competitive exclusion becomes more important in later stages of the succession. This is thus not found within this study, although the higher functional divergence in the *Musanga* forest could be caused by the monodominant character of the succession.

Mechanisms for persistent monodominance

As is already indicated by the relatively high functional divergence of the monodominant tree community, *Gilbertiodendron dewevrei* contains trait combinations located at the extremities of the community trait space, which could possibly benefit its establishment as a monodominant species. The monodominance of *Gilbertiodendron dewevrei* has been attributed to its life-history traits such as ectomycorrhizal associations increasing nutrient supply, being shade tolerant, possessing a closed canopy, producing large seeds and creating a deep litter layer that decomposes slowly (Connell & Lowman 1989; Peh *et al*. 2009 & 2011b). Peh *et al*. (2011b) presented a framework linking different mechanisms for monodominance and showed multiple routes through which monodominance can be conceived. Our data supports the mechanism of slow decomposition rate leading to low nutrient availability (Mechanism 3 in Peh *et al*. 2011b), inferred from the low SLA, high LDMC and high C:N ratio of *Gilbertiodendron dewevrei*, indicating thick, toughly decomposable leaves leading to low nutrient turnover rates (see also McGuire *et al*. 2010; Peh *et al*. 2012), also confirmed by the thick litter layer dominated by *Gilbertiodendron* leaves as observed in this forest. Monodominant species also show a high nutrient use efficiency with low nutrient availability in the soil (Vitousek 1982; Brookshire & Thomas 2013), possibly combined with ectomycorrhizal associations (Mechanism 4 in Peh *et al.* 2011b). Leaf nutrient content and $\delta^{15}N$ also suggest an altered nutrient availability, which could be due to the altered nutrient status of the litter layer (see Vitousek *et al*. 2004), although soil properties between the monodominant and the adjacent mixed forest are similar (*Chapter 3*). Nevertheless, all other mechanisms for monodominance presented by Peh *et al*. (2011b) are not tested with our data. However, within this study we present traits not previously discussed by Peh *et al*. (2011b), which can increase our understanding of the mechanisms for monodominance of *Gilbertiodendron dewevrei*. *Gilbertiodendron dewevrei* showed significantly different trait values for 12 out of 15 traits compared to all other species in the community, showing the distinctiveness of the niche taken in by *G. dewevrei*. One new aspect is related to the water use and water transport of this species. *Gilbertiodendron dewevrei* possesses xylem traits that are not general for a late successional tropical species, namely high VDm combined with low VD indicating a low safety margin against xylem cavitation. The values of VD and VDm of *Gilbertiodendron* even closely resemble those of the fast growing early successional species in the young regrowth forest. Additionally, *Gilbertiodendron* shows a low WUE as deducted from the $\delta^{13}C$, combined with a high stomatal conductance as deducted from the low leaf $\delta^{18}O$ (Farquhar *et al*. 1989). The high stomatal conductance suggests little need for water loss regulation for *Gilbertiodendron* in this environment, and the vessel size and low WUE indicate a reduced drought resistance of *Gilbertiodendron*. These combined xylem and WUE traits could indicate a beneficial adaptation to the moist soils as these forests are located near forest rivers in this study area. Accordingly, monodominant *Gilbertiodendron* forests have been shown to occur mostly along forest streams, although they have been found on a variety of soil types (Fayolle *et al*. 2014a). A second aspect could be related to differentiation in relative contribution of water sources, possibly related to rooting depths. Naturally occurring $\delta^{18}O$ soil profiles can provide information regarding water use depths of different species, with soil water near the surface generally most enriched in $\delta^{18}O$ (Gazis & Feng 2004). The low leaf $\delta^{18}O$ of *Gilbertiodendron* could possibly indicate that this species uses deeper water sources and has deeper rooting depths, although more research is needed to confirm this hypothesis.

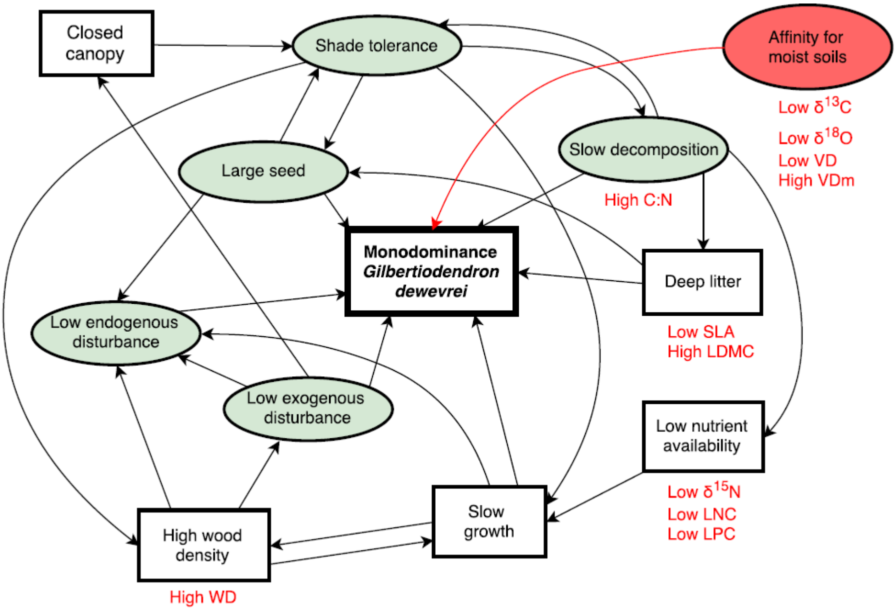


Figure 7.6: Model of possible mechanisms (grey boxes) and their consequences (white boxes) leading to persistent monodominance of *Gilbertiodendron dewevrei* as presented by Peh *et al.* (2011b). Arrows show that one factor beneficially alters the environment to favour another in the direction of the arrow. In red text the traits measured in this study that provide supporting data for this model are indicated. In the red box the additional possible mechanism of affinity for moist soils as hypothesized in this study is shown. Details on the shown model can be found in Peh *et al.* (2011b).

Dominance of *Gilbertiodendron dewevrei* acts as environmental filter for other species

In the conceptual framework of Peh *et al.* (2011b), it is hypothesized that the existence of some traits of the monodominant species alters the probability of the same and other traits in this environment. Some of these connections act as positive feedbacks increasing the probability of further modifications favoring specific traits and enhancing the monodominance (Peh *et al.* 2011b; Brookshire & Thomas 2013). For example, deep litter layers from *Gilbertiodendron dewevrei*'s slow decomposing thick leaves favor large-seeded species which tend to be more shade tolerant, in turn advantageous under the dense canopy (Kitajima 2002; Peh *et al.* 2011b). This positive feedback leads to a greater probability of monodominance being achieved. However, the traits associated with monodominance and the positive feedbacks enhancing monodominance by altering probabilities of traits (Peh *et al.* 2011b) could also have consequences for the establishment of other non-dominant species and their associated traits. This concept is supported within this study, as overall community differences – for the different species groups – have been found between the monodominant and the mixed forest. Both dominant and non-dominant species shift nutrient contents, WUE traits and SLA away from the mean of the mixed forest in the same direction indicating environmental filtering. The shift in nutrient contents of all species within this tropical tree community could be due to a difference of resource availability as a consequence of the long-term dominance of *Gilbertiodendron dewevrei* (Peh *et al*. 2011b; Brookshire & Thomas 2013). The combined trait set of *Gilbertiodendron* with slow growth rates (deducted from its dense wood and thus high construction cost; Enquist *et al*. 1999), slow-decomposing litter and high nutrient use efficiency with low nutrient availability in the soil could have implications on the nutrient cycling, with nitrogen in particular (Menge 2011; Brookshire & Thomas 2013). This is because the rate of detritus mineralization and plant nitrogen use efficiency governs nitrogen limited plant growth (Menge 2011; Brookshire & Thomas 2013). Even though tropical forest systems are generally not nitrogen limited (Brookshire *et al*. 2012), it has been shown that individual trees can influence local nitrogen cycling and retention in soils (e.g. Binkley & Giardina 1998). Especially in this case of high dominance, the balance of nitrogen inputs and losses could be affected at the ecosystem level (Vitousek & Walker 1989), with internal nitrogen turnover possibly restrained (Torti *et al*. 2001; Peh *et al*. 2011a). This would mean that nitrogen bio-availability would be lower compared to the adjacent mixed forest. Accordingly, the ecosystem nitrogen cycle in the monodominant forest is possibly different from the adjacent mixed forest, indicated by lower leaf δ^{15}N in the monodominant forest suggesting lower nitrogen availability and a less open nitrogen cycle (Högberg 1997; Pardo *et al*. 2006). The establishment of specific species in the monodominant forest thus appears to be affected by an altered nitrogen cycle, resulting in a different community structure in terms of species and functional traits.

The species established in the monodominant forest also show a lower mean SLA compared to the species in the mixed forest. These leaves with low SLA, high tissue density (see LDMC) and low nutrient concentrations (both nitrogen and phosphorus) generally have lower photosynthetic rates but a long life span (Reich *et al*. 1998; Wright & Westoby 2002). The longer leaf life span could have advantages for the species under the closed canopy of *Gilbertiodendron*, susceptible to the limited nitrogen availability, with an increased return of investment. Additionally, these leaves are more effectively defended against herbivores and pathogens (Hanley *et al*. 2007) and thus have higher survival rates (Poorter *et al*. 2003).

WUE related traits also show potential for explaining differences in establishment probabilities. As discussed earlier, *Gilbertiodendron dewevrei* showed a low WUE most likely caused by a high stomatal conductance, which is possibly beneficial for the moist soil conditions in these forests. We found that species in the mixed forest that have a high WUE (high δ^{13}C) combined with a reduced stomatal conductance (high δ^{18}O; Farquhar *et al*. 1989) did not establish in the monodominant forest. Species with a low WUE that keep their stomata open, thus reducing their stomatal resistance, could have a higher resource use efficiency for other limiting resources (e.g. light) enabling them to compete, or keep up, with the monodominant species. Further research is needed to confirm this hypothesis, since the isotopic compositions can only provide indications thereof.

Other studies also discussed the importance of life-history traits for the establishment of species from the mixed forest in the monodominant forest (Makana 1999; Poorter *et al*.

2003; Peh *et al.* 2009 & 2014). For example, it has been proposed that shorter, shade-tolerant species are more adapted for establishment in the monodominant stand (Makana *et al.* 2004b), or that slender species that have faster height growth rates will more easily gain access to light (Poorter *et al.* 2003; Poorter *et al.* 2005), although these hypotheses were not supported by Peh *et al.* (2009). Peh *et al.* (2009) showed that species establishment in the monodominant forest was mostly influenced by their relative abundance in the mixed forest, their light requirement for seedling establishment and their WD. Their result that species with a higher WD had a greater probability of establishment in the monodominant forest, is supported by our data. The mean WD of species in the mixed forest that were not found in the monodominant forest was significantly lower than the WD of all non-dominant species in the monodominant forest. These species containing a high WD, generally linked with slow-growing shade-tolerant species, are very similar to *G. dewevrei* and probably occupy a similar niche as the monodominant species. Having a high WD might also have the additional benefit of reduced chance of physical damage caused by falling debris under the dense canopy of *Gilbertiodendron* (Peh *et al.* 2009), where frequencies of falling branches might be higher compared to the mixed forest.

Shifts in traits means in the non-persistent monodominant forest related to its successional stage

The community traits composition changes significantly over the course of the succession due to changes in forest structure i.e. light environment, resource availability and forest composition, indicating the presence of strong environmental filtering (e.g. Kraft *et al.* 2008; Réjou-Méchain *et al.* 2014). A large difference is found in the nutrient status of the non-persistent monodominant regrowth forest compared to the mixed old-growth forest. Low LNC is found in these young forest while a higher LPC is present. These regrowth forests experience greater N-limitation, which gradually recovers along the succession and the dominance of P-limitation typical of mature lowland tropical forests re-emerges, also indicated by the increasing N:P ratio. This shift in N-P limitation confirms the results of Davidson *et al.* (2007) from a Neotropical forest succession. Accordingly, Réjou-Méchain *et al.* (2014) reported higher N-fixing capacities in the earlier stages of the succession, related to this greater N-limitation, irrespective of soil type.

The decrease in C:N values with on-going succession indicates an increase in leaf decomposability, also related to the increase in SLA. A similar pattern of increasing SLA along succession has been found (Mason *et al.* 2011). Contrary, Kröber *et al.* (2012) showed that SLA, together with nutrient content, decreased with succession following the leaf economics spectrum (Wright *et al.* 2004). Although the general relationship found in this study indicates an increase of SLA along the succession, this is mainly driven by the monodominance of *Musanga cecropioides* having a significantly lower SLA than all other early successional species. These species thus more closely follow the leaf economic spectrum, even though their SLA does not differ from the mean found in the mixed forest.

Non-persistent monodominance gained through opportune trait combinations within degraded forest

Strong environmental filtering has been shown along the succession in this study. Contrary to the persistent monodominance, the non-persistent monodominance does not cause an environmental filter, but its high presence is due to specific trait combinations opportune within this regrowth forest (Lohbeck *et al*. 2014). The most important traits are those that allow for massive establishment, namely tolerance to full sunlight, desiccation resistance, fast growth rate, favorable seed dispersal mechanism, certain mycorrhizal associations and an ability to modify soil chemistry (Connell & Lowman 1989; Peh *et al*. 2009). However, these traits do not allow for regeneration underneath its own canopy causing the non-persistence of this dominance (Connell & Lowman 1989). In this study *Musanga cecropioides* distinguishes itself from other early successional species in the community in this regard. The N:P ratio for *Musanga* is larger compared to other early successional species, indicating a lower nitrogen limitation and thus possibly mycorrhizal associations (Onguene & Kuyper 2001). Additionally, its WD is even lower than for the other early successional species, including higher sapwood conductivity but also a higher risk for xylem cavitation due to large VDm (Santiago *et al*. 2004; Baraloto *et al*. 2010b). This less dense wood requires less construction costs (Enquist *et al*. 1999) and faster growth rates can be attained. *Musanga cecropioides* also distinguishes itself for WUE traits. The low δ^{18}O indicates a high stomatal conductance. In order to achieve a high WUE, inferred from the high δ^{13}C, a significantly higher photosynthetic capacity is expected.

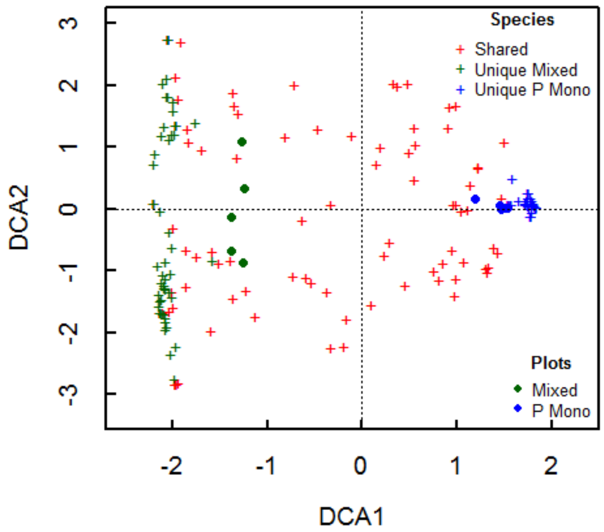
7.5 Conclusion

In summary, both non-persistent and persistent monodominant forest types show differences in functional diversity and functional structure of the community compared to the adjacent mixed forest. In both types of monodominant forest, functional richness is smaller indicating that a smaller amount of functional niche space is filled, related to the lower species diversity and the presence of an environmental filter. This indicates the validity of the first hypothesis. Additionally in both monodominant forests, a high functional divergence shows the presence of the dominant species at the extremities of the niche space, already suggesting that the first part of the second hypothesis holds, namely that the dominant species hold a specific functional niche space in the community.

In the persistent monodominant forest, shifts in traits of the entire tropical tree community suggests the presence of an environmental filter possibly enforced by the monodominance. The high abundance of *Gilbertiodendron dewevrei* can influence the environment by altering probabilities of traits suitable for this environment, thereby influencing the establishment of non-dominant species. Accordingly, community-level traits shifts, away from the mean of the mixed forest, have been identified for nutrient contents, WUE traits and SLA. The dominance of *Gilbertiodendron* thus possibly co-regulates the occurrence of other species in the community, as proposed in the second hypothesis.

In the non-persistent monodominant forest, community-level trait shifts have also been identified, with its successional stage after deforestation the main driver of this difference. Shifts in N-P limitation along the successional stage has been identified, in combination with shift in resource acquisition and stress tolerance strategies. The non-persistent monodominance of *Musanga cecropioides* itself does not show signs of influence on other species in this tropical tree community, as suggested in the second hypothesis.

7.6 Supplementary Information



Supplementary Figure S7.1: Detrended correspondence analysis for 10 plots in mixed and persistent monodominant (P Mono) forest, with species weighted by their basal area. Species are colored according to the classification used in Figure 7.5.

8

Functional diversity in resource-acquisition is supported by rare tree species in central African forest

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Abstract

We examined the relationship between the rarity of tree species and their contribution to functional diversity at a central location in the tropical rainforest of the Congo Basin. Our main finding is that within mixed and monodominant forest ecosystem, rare species support the trait combinations with the highest functional distinctiveness. Rare species however cover the entire range of low and high functional distinctiveness, contributing both unique and redundant functions. Common species only show a low contribution to functional diversity but are crucial for aboveground carbon storage. We argue that within carbon sequestration initiatives, inclusion of both functional diversity and biodiversity conservation is imperative not only for conservation purposes but also to sustain the stability of the ecosystem.

8.1 Introduction

Tropical forests are characterized by a high biodiversity, genetic diversification (Hubbell & Foster 1983) and often highly specific species interactions (Loreau *et al.* 2001; Lang & Benbow 2013). The dominance structure of ecological communities, considered as the oldest and most universal law in ecology (McGill *et al.* 2007), shows that the species present are not evenly distributed (Whittaker 1965; Magurran & Henderson 2003) with a large number of species showing a low abundance (Gaston *et al.* 1994). Identifying processes underlying the maintenance of species diversity, co-existence and species community assembly, including the relative abundances of species within the tropical tree community, is a central question in community ecology (Vellend 2010) and a wide variety of theoretical models have been proposed (reviewed in Vellend 2010). Recent studies (e.g. Kraft *et al.* 2008; Cornwell & Ackerly 2010; Maire *et al.* 2012) emphasize the importance of two processes for addressing these questions, namely habitat filtering (Keddy 1992b) and niche differentiation (MacArthur & Levins 1967). Habitat filtering imposes ecological filters related to the abiotic environment, i.e. environmental conditions, resource availability and disturbance, selecting for species suitable for this habitat (Keddy 1992b). Habitat filtering therefore leads to a convergence of trait values and for species to be functionally similar within the community (Cornwell & Ackerly 2009; de Bello *et al.* 2009). This similarity however can decrease relative fitness differences, and the presence of species with trait dissimilarity could favor species coexistence by avoiding competitive exclusion (MacArthur & Levins 1967). This is the basis for niche differentiation which limits coexistence of similar plants and encourage the complementarity of resource use (Silvertown 2004). These two processes are expected to have a different relative importance for common and rare species, with common species dominating through habitat filtering and rare species being favored by niche differentiation (Maire *et al.* 2012). The resulting species composition will determine the functional diversity, defined as the value, distribution and range of species traits (Tilman 2001; Petchey & Gaston 2006; Díaz *et al.* 2007) within the ecosystem.

Nevertheless, the relative contribution and importance of changes in biodiversity and functional diversity of mainly low abundant, rare, species on ecosystem functioning remains disputed. The biomass ratio hypothesis (Grime 1998) argues that common species drive ecosystem functions related to carbon and nutrient cycling due to their high abundance (Loreau *et al.* 2001; Gaston 2010). Additionally, recent studies have shown that the abundance of trees in tropical forests is skewed towards a small number of hyperdominant species accounting for a high amount of carbon storage within the community (ter Steege *et al.* 2013; Fauset *et al.* 2015). Yet, measurements of ecosystem processes may not be sensitive enough to assess the effects of uncommon species (Lyons & Schwartz 2001; Smith & Knapp 2003; Gaston & Fuller 2008; Gaston 2010). Consequently, the impact of rare species loss on ecosystem functioning has been questioned (Grime 1998; Bracken & Low 2012) despite the fact that unique or complementary trait combinations have shown to influence functional diversity and support ecosystem processes and functioning (Smith & Knapp 2003; Lyons *et al.* 2005; Mouillot *et al.* 2011; Richardson *et al.* 2012; Mouillot *et al.* 2013; Jain *et al.* 2014) and could invariably affect the biogeochemical properties of an ecosystem (Naeem *et al.* 2012). For example, it has been suggested that biodiversity loss of rare species in highly diverse tropical forests has the potential to shift the balance between carbon gains and losses (Díaz *et al.* 2009), affecting long-term carbon storage. As such, rare species have shown the potential to support important traits adding to the functional diversity within the community (Cardinale *et al*. 2006).

The question whether distinct trait combinations and ecological functions are mainly supported by rare or common species remains unanswered for central African tropical humid forest ecosystems. Additionally, the importance of habitat filtering and niche differentiation in tropical forest ecosystems is rarely tested. African humid tropical forests differ significantly from Neotropical forests regarding their lower species diversity (Parmentier *et al*. 2007) and presence of wide-spread monodominant forests (Hart 1990), possibly changing the influence of rare species on ecosystem functioning. Although some rare species are characterized by distinct trait combinations in Neotropical forests (Mouillot *et al*. 2013), no such relationships are available for central African tropical rainforest.

Here we examined the relationship between the rarity of tree species and their contribution to functional diversity at a central location in the tropical rainforest of the Congo Basin. This study focusses on resource-acquisition traits as they can reflect inter-specific competition for resources, addressing niche differentiation. Our results show that within both mixed and monodominant forests, species with a distinct set of traits within the ecosystem are mainly rare, while common species only show low distinctiveness but are crucial contributors for carbon storage. Additionally, rare species cover the entire range of low and high functional distinctiveness, thus contributing both unique and redundant functions.

8.2 Methods

Study area and traits

We examined the influence of rare species on the functional diversity of tropical communities at the UNESCO Man and Biosphere reserve in Yangambi, DRC, of which the details can be found in *Chapter 2*. This study focuses on 10 plots installed in old-growth mixed forest (n = 5) and old-growth monodominant forest of *Gilbertiodendron dewevrei* (De Wild.) J. Léonard (n = 5). Within all plots, all trees with a DBH larger or equal to 10 cm have been measured and identified to species level. Leaf samples and wood samples from the stem were collected for those species covering a cumulative 95% basal area of each plot. Repeated samples within species were collected, namely two individuals were selected within each pre-assigned diameter class of 10-20, 20-30, 30-50 and >50 cm DBH, if present. A total of 738 individuals was sampled, covering 105 species. All samples were collected between March and May 2012. Within the 5 hectares of mixed forest, all common species were measured (n = 43), 70% of rare species were measured (those with an abundance less than 5% of the maximal observed abundance across the species pool (following Mouillot *et al*. 2013); n = 30) and 23% of the highly rare species were measured (threshold at an abundance of 1% of the maximal observed abundance (following Mouillot *et al*. 2013); n = 16). For the monodominant forest, also all common species were measured (n = 12), 81% of rare species were measured (n = 21) and 59% of the highly rare species were measured (n = 47). Species-specific aboveground carbon (AGC) is estimated using the allometric equation of Chave *et al*. (2005) for moist tropical forest including height and wood density, with biomass assumed to be 50% carbon. Site and forest type specific height-diameter relationships (not species-specific) are used to estimate height based on diameter (*Chapter 3*). The species list including their relative abundance and AGC, for both forest types can be found in Supplementary Tables S8.1 & S8.2.

A selection of four traits was made to represent unique contributions to plant resource capture and growth. The selected functional traits are wood density (WD), specific leaf area (SLA), leaf nitrogen content (LNC) and leaf stable carbon isotope composition ($\delta^{13}C$). SLA and WD have been chosen because they are commonly studied traits and are of importance for different ecosystem processes (Lavorel & Garnier 2002; Wright *et al*. 2004; Chave *et al*. 2009). SLA affects primary production, carbon and nutrient cycling and litter decomposition (Poorter *et al*. 2009), and WD is a key trait for biogeochemical ecosystem processes such as carbon sequestration and turnover rates (Chave *et al*. 2009). LNC is included in this study to reflect nutrient status, with LNC also correlated to leaf phosphorus within this study (Pearson R^2 0.303, $p < 0.001$). Nutrient availability has a strong effect on photosynthetic carbon gain, as both phosphorus and nitrogen availability constrain leaf photosynthetic capacity (Domingues *et al*. 2010). $\delta^{13}C$ is measured as a proxy of the intrinsic water use efficiency, which is the ratio of photosynthetic carbon fixation to stomatal conductance (Farquhar *et al*. 1989).

From each individual tree, 10 leaves were sampled at various tree heights, which were fully expanded and no signs of pathogens or herbivory. Fresh weight of the leaf samples was measured as a composite sample, and high-resolution images were taken to determine leaf area while leaves were flattened between transparent Plexiglas. Leaf surface is determined by analyzing these images using ImageJ software (from the US National Institutes of Health; http:// www.nih.gov/). Leaves were subsequently dried at 60°C for 72h, or until no more weight change occurred, and dry mass was determined. Specific leaf area (SLA) was determined as leaf area divided by dry weight. Next, chemical analysis of the leaves was performed at the Isotope Bioscience Laboratory (Ghent University, Belgium). Composite leaf samples were ground to fine powder using a ball mill (ZM200, Retsch, Germany). Mass based nitrogen concentrations and carbon isotopic ratios were determined using an elemental analyzer (ANCA-SL, SerCon, Crewe, UK) coupled to an isotope ratio mass spectrometer (20-20, SerCon, Crewe, UK) (EA-IRMS). $\delta^{13}C$ is expressed in delta notation relative to Vienna Pee Dee Belemnite (VPDB) standard. Wood samples with an average size of 5x5x5 cm^3 are taken under the bark. The volume of the fresh sample was taken using the water displacement method. Samples were subsequently dried in an oven at 60°C until completely dry and dry weight was measured. Wood density could then be determined as the ratio of oven dry weight divided and fresh volume.

The Shapiro-Wilk test was used to test for normality of the individual traits. Skewed distributions of LNC and SLA were log transformed prior to the analysis and all traits were rescaled between zero and one to ensure an equal weight of each trait within this analysis. Correlations between all traits can be found in Supplementary Table S8.3.

Functional diversity indices and rarity

Functional diversity indices are assessed for the aggregate of all plots within each forest type, thus for the combined 5 hectares within mixed and monodominant forest. To determine the contribution of each species to functional diversity we calculated the community convex hull volume which quantifies the volume inside the minimum convex hull containing all the species belonging to the community (Cornwell *et al*. 2006). This volume can be interpreted as a four dimensional structure containing all four selected traits for each species represented in the community and corresponds to a multivariate functional range, namely the functional trait space (FTS). The FTS is only influenced by the presence of species and not by their abundance and is defined by the most extreme species in terms of traits. For example, adding a species outside the current range of trait values would increase the FTS. As such, species trait locations within the four dimensional FTS can be used to assess species-specific influence on the community divergence. The relative contribution of each species to the community divergence was quantified by separately removing each species and calculating the subsequent change in total FTS from the whole community.

However, relative changes in FTS do not quantify how different a species is from the other species in the community in terms of their functional traits. Therefore a distance-based functional diversity measure is calculated to address the functional distinctiveness (FD) of each species. Following Mouillot *et al.* (2013), the functional traits are used to estimate a Euclidian distance matrix between all species pairs and the most reliable functional dendrogram is used to link all species in functional space. The selection of this dendrogram is based on the similarity between the initial distance matrix and the cophenetic distance matrix using the cophenetic correlation, which indicates how good the dendrogram preserves the pairwise distances between the original unmodeled data points (Mouchet *et al*. 2008; Mouillot *et al*. 2013). The unweighted pair group method using arithmetic averages (UPGMA) was thereby selected for clustering. Subsequently, the FD of each species is estimated using an equal-split approach of the dendrogram which reflects how functionally isolated a species is and therefore approximates how functionally distinct it is from other species (Redding & Mooers 2006). The equal-split of the dendrogram was performed using the R package 'ade4' and the function 'originality' (Dray & Dufour 2007). The association between the FTS contribution and FD for all species is tested by Spearman correlation.

Two aspects of rarity are investigated, namely an abundance-based rarity and a carbon-based rarity. The abundance-based rarity is expressed as the relative number of stems of each species to the species with the highest number of stems, and represents rare species based on low number of occurrence. The carbon-based rarity is quantified using the species-specific AGC storage, with species-specific carbon as a percentage of the total AGC stock. The relationship between the abundance-based and carbon-based rarity is assessed to identify importance of occupancy and size within our definition of rare species. Additionally, a combined rarity rank with both relative abundance and AGC stock is addressed to quantify the functional contribution of species with both low presence and low AGC storage. This combined rarity rank is a normalized index calculated by multiplying log-transformed relative abundance and AGC stock.

The relationship between rarity ranking of species and FTS contribution and FD is assessed through linear and quantile regression. The linear relationship indicates trends of the means of the response variables, while quantile regressions (5th and 95th quantiles) quantify a linear relationship along upper and lower quantiles of the response variable (FTS or FD). The combination of both 5th and 95th quantile regressions will improve our understanding of the ranges of the two functional diversity indices along the rarity ranking.

In addition to this multivariate analysis, univariate analysis of all four traits are available in Supplementary Figures S8.1-4 to show how the raw trait data varies according to the different rarity rankings.

Hyperdominance, Dominance and Non-dominance

Next to the species-level analysis as described above, a summary of these results has been made to relate to the biomass ratio hypothesis (Grime 1998). Species are categorized as either being dominant or non-dominant (encompassed both subordinate and transient species, as defined in Grime (1998)), with the distinction between these two classes based upon the relative abundance of the species, with a threshold set at the arbitrary value of 10% (following Grime 1998). Subsequently, all dominant species with the highest carbon density, which together hold over 50% of the carbon stock in the forest are classified as hyperdominant. For each class, the contribution to functional diversity is summarized by portraying boxplots of FD and FTS of all species present.

8.3 Results

Abundant species are important contributors to the AGC storage, although abundance-based rare species can also contain large amounts of carbon (Figure 8.1). Within the mixed forest, several rare species with an abundance lower than 5% show similar AGC storage as species with a higher abundance (Figure 8.1a). Accordingly, the cumulative AGC starting with the rarest species shows a steady increase in AGC (Figure 8.1b). Rare species with a low AGC nevertheless contribute little to the carbon storage (Figure 8.1c). The contribution of large and abundant species to carbon storage is essential with only 11 species accounting for over half (51.3%) of the carbon stored. Within the monodominant forest the contribution of rare species to the total AGC is lower, with the dominant species *Gilbertiodendron dewevrei* containing 72.8% of the ecosystem carbon. Nevertheless, again several rare species show a high ACG stock similar to more abundant species (Figure 8.1d).

Rare species had a strong influence on FD in mixed forest (Figure 8.2). FD was negatively and significantly related to three rarity ranks (AGC stock, relative abundance or the combined rarity rank) for both the linear and 95th quantile regression within the mixed forest site. Generally, the highest FD is found for the rare species, while low FD occurs for, but is not exclusively limited to, more common species. Within the monodominant forest, a negative and significant trend is found when based on relative abundance and the combined rank (Figure 8.2). Specifically with rarity expressed as AGC stock, no trend is found. Accordingly, the FD of the monodominant species *Gilbertiodendron dewevrei*, the species contributing most to AGC storage, is relatively high with values just over the mean of the distinctiveness of all species.

Although a significant correlation ($r = 0.641$; $p < 0.001$; Supplementary Figure S8.5) is found between FD and FTS contribution, no consistent trends are found between contribution to FTS and rarity ranks in mixed forest (Figure 8.3). A significant negative relationship of the 95th quantile regression is only found between the combined rarity rank and FTS contribution. With rarity expressed as relative abundance and AGC, the rarest species show a low contribution, as do the common species, while less rare species show the highest contribution (Figure 8.3a & 8.3b). Even though no consistent trends are found, the first 6 species with the highest ranking for AGC stock, representing 38.4% of the total AGC storage (Figure 8.1c), show the lowest contribution to FTS (Figure 8.3a). Within the monodominant forest, significant negative trends for the 95th quantile regression are found based for the abundance-based, carbon-based and combined rarity (Figure 8.3e & 8.3f). The first 9 species with the highest AGC stock, representing 88.3% of the total AGC stock (Figure 1f), show no contribution to FTS (Figure 8.3d).

For the classes of hyperdominant, dominant and non-dominant species, no difference in the mean is found for either FD or FTS in both forest types.

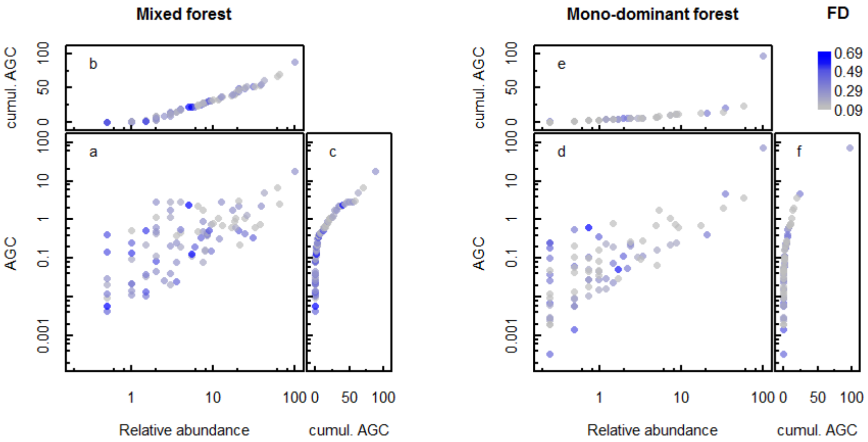


Figure 8.1: Species-specific aboveground carbon (AGC) compared to its relative abundance within the mixed and monodominant forest all 5 ha plots combined. The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Secondary plots show the cumulative AGC starting from rare species based on relative abundance (b, e) or based on species-specific AGC (c, f) to address the contribution of rare species to AGC along the two rarity axis. Color scheme indicates location of species with high and low functional distinctiveness (FD) in accordance with Figure 8.2.

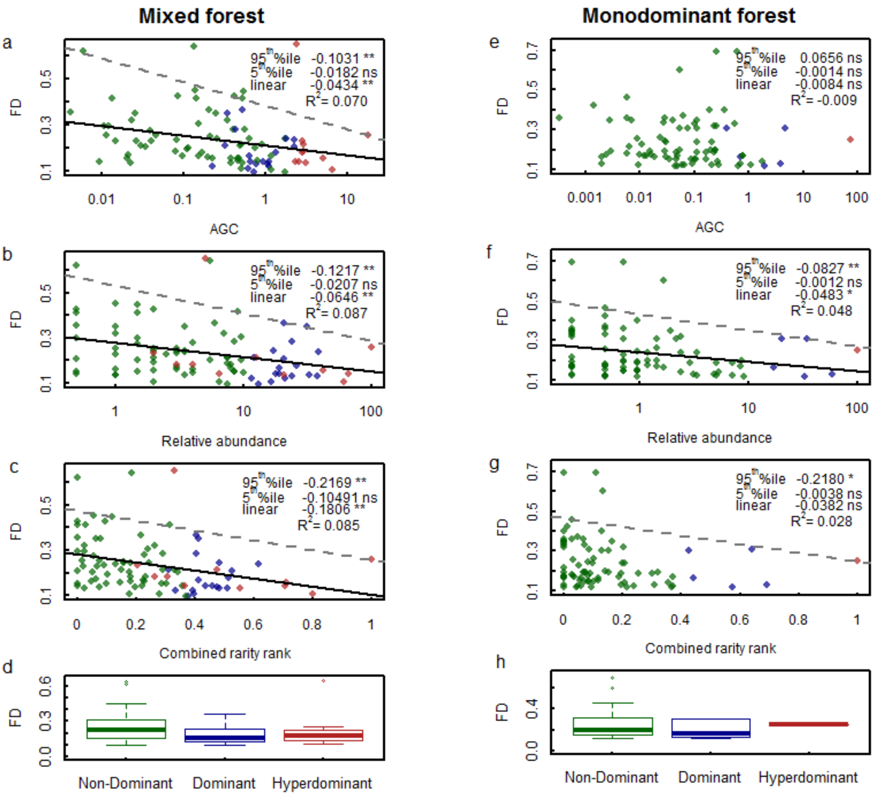


Figure 8.2: Functional distinctiveness (FD) of species within the mixed (a, b and c) and monodominant forest (e, f and g) for all 5 ha plots combined. All dots show the FD of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance. FD quantifies the uniqueness of species traits compared to the rest of the pool in the ecosystem. The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. FD of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.

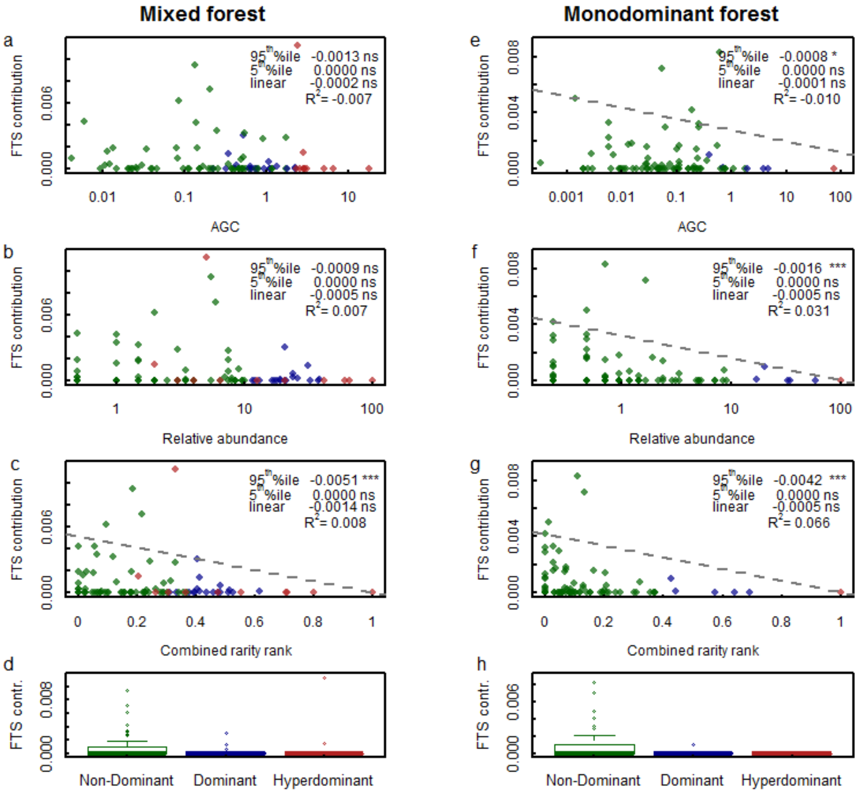


Figure 8.3: Contribution to the functional trait space (FTS) of species within the mixed (a, b and c) and monodominant forest (e, f and g) for all 5 ha plots combined. All dots show the contribution of a single species to FTS as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance. The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. Contribution to FTS of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.

8.4 Discussion

We examined the relationship between the rarity of species and their contribution to functional diversity by assessing the extremity of species trait locations within the functional trait space and by quantifying the distance between functional characteristics of different species or functional distinctiveness.

From a carbon stock perspective, a low number of highly abundant species and less abundant species with a large size maintain a large amount of the total AGC stock within each forest type. Eleven species in the mixed forest are classified as hyperdominant and contain over half of the AGC. Within the monodominant forest, only *Gilbertiodendron dewevrei* is classified as hyperdominant containing 73% of the total AGC. As these species contain a large fraction of the tropical tree community biomass, both theory (biomass ratio hypothesis) and experimental evidence have shown they highly determine ecosystem properties such as productivity, carbon sequestration, water relations, nutrient cycling etc. The large influence of hyperdominants, and to a lesser extent of dominants, does not exclude non-dominants from involvement in the determination of ecosystem function and sustainability.

Namely from a functional diversity perspective, we found that common species show a high degree of functional similarity and a low degree of functional divergence compared to other species within the community, both in mixed and monodominant forests. The presence of a strong habitat filtering could be the underlying cause of this difference. In particular, the establishment of monodominant forest could have been caused by environmental filters such as soil conditions, microclimate or disturbance, driving habitat filtering. This habitat filtering is subsequently reinforced by the dominance of *Gilbertiodendron dewevrei* which through specific trait combinations alters the environment favoring these traits (Peh *et al*. 2011b; Maire *et al*. 2012). As such, the high functional similarity could be advantageous for dominant species as it increases their importance as a competitor compared to less abundant species. Contrary, rare species benefit more by niche differentiation in order to coexist with competitors within a community which is passively or actively driven by strong habitat filtering (Maire *et al*. 2012). The high contribution to functional divergence of rare species suggests that species with a low occupancy in communities experiencing a strong habitat filtering need to specialize for a specific niche, with trait combinations diverging from the community mean. Consequently, these species are predominantly associated with extreme trait values. For example *Drypetes angustifolia* Pax & K. Hoffm., one of the rarest species in the mixed forest based on both abundance and AGC, shows the lowest SLA combined with lower LNC and δ^{13}C and a long leaf lifespan. Yet, the rare species *Isolona thonneri* (De Wild & Th. Dur.) Engl. & Diels does not show extreme trait values but has distinct trait relations, namely a low SLA combined with an above average LNC, which contrasts with the positive correlation that is generally observed (Wright *et al*. 2004). Furthermore, *I. thonneri* shows a longer leaf lifespan but combined with a higher LNC, potentially enhancing photosynthetic rates (Wright *et al*. 2004). In this study we have, nevertheless, limited understanding of the functional role of traits and trait combinations of particular rare species or their relationships across trophic levels / food webs.

The loss of rare species, supporting important traits, in tropical forests could affect long-term carbon storage by inducing shifts in carbon dynamics (Díaz *et al*. 2009). Consequently, the loss of species with distinct traits, adding to the functional diversity within the community (Cardinale *et al*. 2006), may affect ecosystem functioning more than would be expected as a result of numerical species loss (Mouillot *et al*. 2013). At the same time, rare species are more vulnerable due to their low abundances, restricted geographic distribution, susceptibility to habitat loss, overexploitation, invasion and climate change (Hansen *et al*. 2001; Brooks *et al*. 2002; Thomas *et al*. 2004). Yet, rare species with a high functional similarity with other species are found alongside rare species with distinct traits. This functional similarity suggests trait redundancy which might act as a buffer against species loss (Gaston & Fuller 2008) insuring ecosystem functioning through replacement with more common species following biodiversity erosion (Yachi & Loreau 1999; Fonseca & Ganade 2001). Conversely, rare species could maintain the stability of ecosystem functioning if they become more abundant (MacDougall *et al*. 2013) when common species go locally extinct due to environmental change (Walker *et al*. 1999; MacDougall *et al*. 2013). In short, functional redundancy in the context of biodiversity loss and environmental change safeguards the ecosystem against the loss of ecosystem functioning following biodiversity erosion, while the unique set of traits of rare species enables optimal ecosystem functioning and efficient use of resources.

We conclude that rare species show both unique and redundant functional traits, both of high importance for long-term stability of ecosystem functioning. Functions supported by rare species are however more vulnerable to extinction due to the low number of species and individuals supporting them. The loss of species with distinctive traits may thus affect ecosystem functioning more than would be expected. Within the context of forest conservation for carbon mitigation initiatives, limitation of biodiversity loss for long-term resilience of ecosystem functioning is crucial, beyond the classic motivations of preserving the diversity of life. Emphasis on common species with distinct functional traits is needed within monodominant forest systems of *Gilbertiodendron dewevrei* to ensure the stability of its ecosystem functioning. Combined efforts of conservation of rare and common species are needed for the success of carbon mitigation. Similar results to our African study in mixed forest are reported within the Neotropical forest (Mouillot *et al*. 2013) enabling a similar conservation policy, irrespective of the different dynamics in both tropical forests and highlighting the potential co-benefit within carbon mitigation projects (Greve *et al*. 2013) of safeguarding functional diversity.

8.5 Supplementary Information

Supplementary Table S8.1: List of species within the mixed old-growth forest including their relative abundance and aboveground carbon storage. Species are ranked according to their aboveground carbon (AGC). AGC values are the percentages each species contributes to the carbon stock of the studied plots (total 809.7 Mg C within 5 ha). The abundance is shown relative to the species with the highest abundance.

Species	Family	Abundance	AGC
Scorodophloeus zenkeri Harms	Fabaceae	100	17.852
Petersianthus macrocarpus (P. Beauv.) Liben	Lecythidaceae	60.7	6.573
Panda oleosa Pierre	Pandaceae	41.8	5.006
Tridesmostemon omphalocarpoides Engl.	Sapotaceae	20.4	3.1
Chrysophyllum lacourtianum De Wild.	Sapotaceae	12.4	2.961
Cynometra hankei Harms	Fabaceae	3	2.874
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	Irvingiaceae	2	2.858
Erythrophleum suaveolens (Guill. & Perr.) Brenan	Fabaceae	4	2.813
Staudtia kamerunensis (Warb.) Fouilloy	Myristiceae	65.2	2.553
Combretum lokele Liben	Combretaceae	5	2.404
Strombosiopsis tetrandra Engl.	Olacaceae	6.5	2.299
Tridesmostemon claessensii De Wild.	Sapotaceae	20.4	2.258
Anonidium mannii (D. Oliver) Engl. & Diels	Annonaceae	38.3	2.221
Turraeanthus africanus (Welw. ex C. DC.) Pellegr.	Meliaceae	16.9	1.767
Celtis mildbraedii Engl.	Ulmaceae	7.5	1.729
Irvingia grandifolia (Engl.) Engl.	Irvingiaceae	3	1.726
Strombosia grandifolia Hook. f.	Olacaceae	25.9	1.34
Ongokea gore (Hua) Pierre	Olacaceae	3	1.188
Entandrophragma utile (Dawe & Sprague) Sprague	Meliaceae	2	1.168
Drypetes gossweileri S. Moore	Euphorbiaceae	18.9	1.115
Trilepisium madagascariense Thouars ex DC.	Moraceae	11.4	1.088
Guarea thompsonii Sprague & Hutch.	Meliaceae	23.9	1.067
Greenwayodendron suaveolens (Engl. & Diels) Verdc.	Annonaceae	17.9	0.93
Strombosia pustulata Oliv. var. pustulata	Olacaceae	7.5	0.899
Dialium pachyphyllum Harms	Fabaceae	10	0.806
Microdesmis yafungana J. Léonard	Pandaceae	37.3	0.776
Trichilia gilgiana Harms	Meliaceae	9.5	0.737
Polyalthia suaveolens Engl. & Diels	Annonaceae	12.9	0.722
Pancovia harmsiana Gilg	Sapindaceae	32.3	0.65
Garcinia punctata Oliv.	Clusiaceae	18.9	0.632
Guarea cedrata (A. Chev.) Pellegr.	Meliaceae	2	0.628
Drypetes sp.	Euphorbiaceae	16.4	0.624
Cola lateritia K. Schum.	Sterculiaceae	4	0.563
Alstonia boonei De Wild.	Apocynaceae	1.5	0.535
Tessmannia africana Harms	Fabaceae	1	0.525
Microdesmis sp.	Pandaceae	20.4	0.524
Celtis tessmannii Rendle	Ulmaceae	9	0.516

Supplementary Table S8.1 continued

Species	Family	Abundance	AGC
Diospyros crassiflora Hiern	Ebenaceae	6.5	0.511
Chrysophyllum sp.	Sapotaceae	2	0.499
Synsepalum subcordatum De Wild.	Sapotaceae	7.5	0.489
Trichilia prieuriana A. Juss.	Meliaceae	8.5	0.468
Dialium sp.	Fabaceae	4	0.457
Piptadeniastrum africanum (Hook.f.) Brenan	Fabaceae	2	0.452
Cola griseiflora De Wild.	Sterculiaceae	23.9	0.428
Prioria sp.	Fabaceae	0.5	0.412
Chrysophyllum africanum A. DC.	Sapotaceae	8.5	0.409
Blighia welwitschii (Hiern) Radlk.	Sapindaceae	3.5	0.381
Trichilia sp.	Meliaceae	8.5	0.379
Carapa procera DC.	Meliaceae	30.8	0.346
Musanga cecropioides R. Br. ex Tedlie	Cecropiaceae	7	0.343
Pancovia laurentii (De Wild.) Gilg ex De Wild.	Sapindaceae	11.9	0.324
Pterocarpus soyauxii Taub.	Fabaceae	3.5	0.256
Symphonia globulifera L. f.	Clusiaceae	1	0.252
Dialium excelsum J. Louis ex Stey.	Fabaceae	1.5	0.226
Coelocaryon preussii Warb.	Myristiceae	20.9	0.224
Pentaclethra macrophylla Benth.	Fabaceae	3	0.214
Vitex welwitschii Gürke	Verbenaceae	6	0.205
Trichilia monadelpha (Thonn.) J.J.de Wilde	Meliaceae	4	0.196
Grossera multinervis J.Léonard	Euphorbiaceae	8	0.168
Prioria balsamifera (Vermoesen) Breteler	Fabaceae	9.5	0.154
Diospyros sp.	Ebenaceae	8	0.153
Vitex congolensis De Wild. & Durand	Verbenaceae	0.5	0.144
Ricinodendron heudelotii (Baill.) Heckel	Euphorbiaceae	1	0.138
Diospyros boala De Wild.	Ebenaceae	5.5	0.132
Rinorea oblongifolia (C.H. Wright) Marquand ex Chipp	Violaceae	5.5	0.113
Prioria oxyphylla (Harms) Breteler	Fabaceae	2	0.112
Tetrapleura tetraptera (Schumach. & Thonn.) Taub.	Fabaceae	1	0.097
Millettia drastica Welw. ex Baker	Fabaceae	2	0.084
Quassia undulata (Guill. & Perr.) F.Dietr.	Simaroubaceae	3.5	0.082
Pycnanthus angolensis (Welw.) Exell	Myristiceae	7.5	0.08
Monodora angolensis Welw.	Annonaceae	2	0.046
Garcinia smeathmannii (Planch. & Triana) Oliv.	Clusiaceae	3	0.04
Vitex sp.	Verbenaceae	1.5	0.039
Dacryodes edulis (G. Don) H.J. Lam	Burseraceae	1.5	0.034
Garcinia sp.	Clusiaceae	0.5	0.03
Rinorea sp.	Violaceae	2.5	0.026
Tabernaemontana crassa Benth.	Apocynaceae	3.5	0.026
Macaranga monandra Müll. Arg.	Euphorbiaceae	1	0.023
Allanblackia floribunda Oliv.	Clusiaceae	1	0.023

Supplementary Table S8.1 continued

Species	Family	Abundance	AGC
Drypetes leonensis Pax	Euphorbiaceae	3	0.021
Cola sp.	Sterculiaceae	0.5	0.021
Dialium corbisieri Staner	Fabaceae	1	0.015
Canarium schweinfurthii Engl.	Burseraceae	1.5	0.013
Hannoa klaineana Pierre & Engl.	Simaroubaceae	0.5	0.012
Tetrorchidium didymostemon (Baill.) Pax & K. Hoffm.	Euphorbiaceae	1	0.011
Monodora myristica (Gaertn.) Dunal	Annonaceae	1.5	0.011
Dacryodes osika (Guillaumin) H.J.Lam	Burseraceae	0.5	0.009
Drypetes angustifolia Pax & K. Hoffm.	Euphorbiaceae	0.5	0.006
Isolona thonneri (De Wild & Th. Dur.) Engl. & Diels	Annonaceae	0.5	0.004

Supplementary Table S8.2: List of species within the monodominant old-growth forest including their relative abundance and aboveground carbon (AGC) storage. Species are ranked according to their AGC. AGC values are the percentages each species contributes to the carbon stock of the studied plots (total 820.7 Mg C within 5 ha). The abundance is shown relative to the species with the highest abundance.

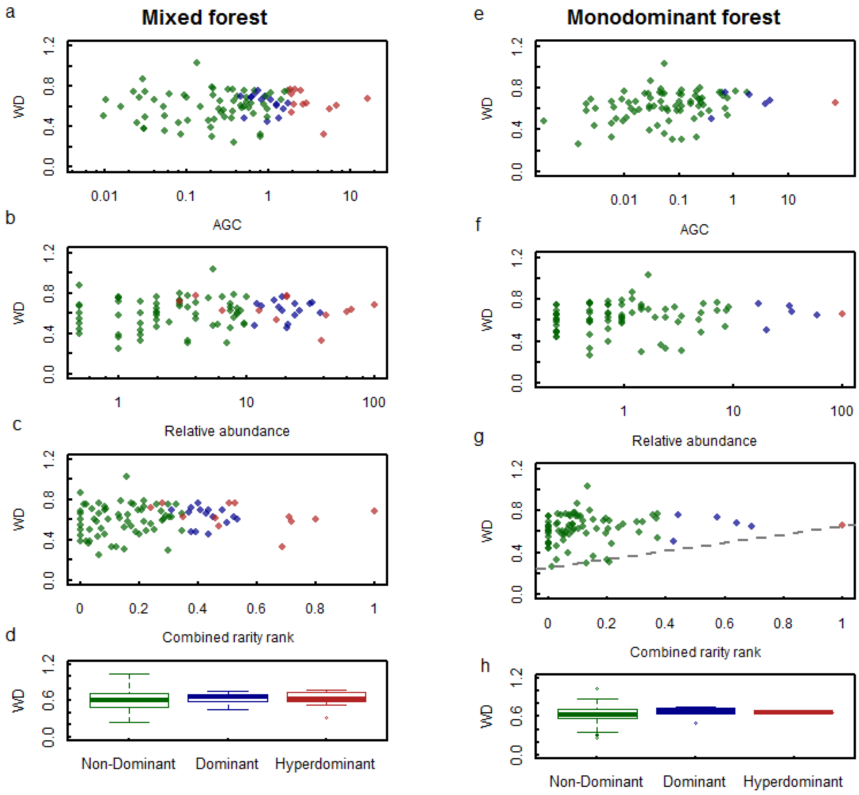
Species	**Family**	**Abundance**	**AGC**
Gilbertiodendron dewevrei (De Wild.) J. Léonard	Fabaceae	100	72.805
Scorodophloeus zenkeri Harms	Fabaceae	34.3	4.687
Cavacoa quintasii (Pax & K. Hoffm.) J. Leonard	Euphorbiaceae	57.6	3.768
Cleistanthus mildbraedii Jabl.	Euphorbiaceae	32.4	1.98
Dialium pachyphyllum Harms	Fabaceae	5.2	1.733
Tessmannia africana Harms	Fabaceae	7.1	1.068
Ongokea gore (Hua) Pierre	Olacaceae	1.4	0.788
Trichilia monadelpha (Thonn.) J.J.de Wilde	Meliaceae	8.3	0.766
Prioria oxyphylla (Harms) Breteler	Fabaceae	4.8	0.714
Garcinia punctata Oliv.	Clusiaceae	17.1	0.697
Drypetes sp.	Euphorbiaceae	9	0.625
Combretum lokele Liben	Combretaceae	0.7	0.62
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	Irvingiaceae	0.5	0.561
Isolona thonneri (De Wild & Th. Dur.) Engl. & Diels	Annonaceae	20.2	0.401
Entandrophragma candollei Harms	Meliaceae	1	0.356
Staudtia kamerunensis (Warb.) Fouilloy	Myristiceae	3.3	0.287
Dialium sp.	Fabaceae	2.4	0.269
Prioria sp.	Fabaceae	0.2	0.25
Pterocarpus soyauxii Taub.	Fabaceae	0.2	0.249
Carapa procera DC.	Meliaceae	8.6	0.248
Gilletiodendron mildbraedii (Harms) Vermoesen	Fabaceae	1.2	0.24
Strombosia pustulata Oliv. var. pustulata	Olacaceae	2.4	0.233
Cola griseiflora De Wild.	Sterculiaceae	7.1	0.23
Blighia welwitschii (Hiern) Radlk.	Sapindaceae	0.5	0.21
Anonidium mannii (D. Oliver) Engl. & Diels	Annonaceae	2.4	0.21
Cynometra hankei Harms	Fabaceae	1.4	0.204
Canarium schweinfurthii Engl.	Burseraceae	0.2	0.193
Drypetes sp. 1	-	5	0.168
Piptadeniastrum africanum (Hook.f.) Brenan	Fabaceae	1	0.167
Celtis tessmannii Rendle	Ulmaceae	1.9	0.113
Quassia undulata (Guill. & Perr.) F.Dietr.	Simaroubaceae	3.3	0.112
Dialium pentandrum Louis ex Steyaert	Fabaceae	0.7	0.112
Garcinia smeathmannii (Planch. & Triana) Oliv.	Clusiaceae	2.9	0.111
Panda oleosa Pierre	Pandaceae	0.5	0.107
Polyalthia suaveolens Engl. & Diels	Annonaceae	0.7	0.101
Drypetes louisii J. Leonard	Euphorbiaceae	0.2	0.1
Craterispermum sp.	Rubiaceae	3.1	0.094
Strombosiopsis tetrandra Engl.	Olacaceae	1	0.086
Musanga cecropioides R. Br. ex Tedlie	Cecropiaceae	1.4	0.077

Supplementary Table S8.2 continued

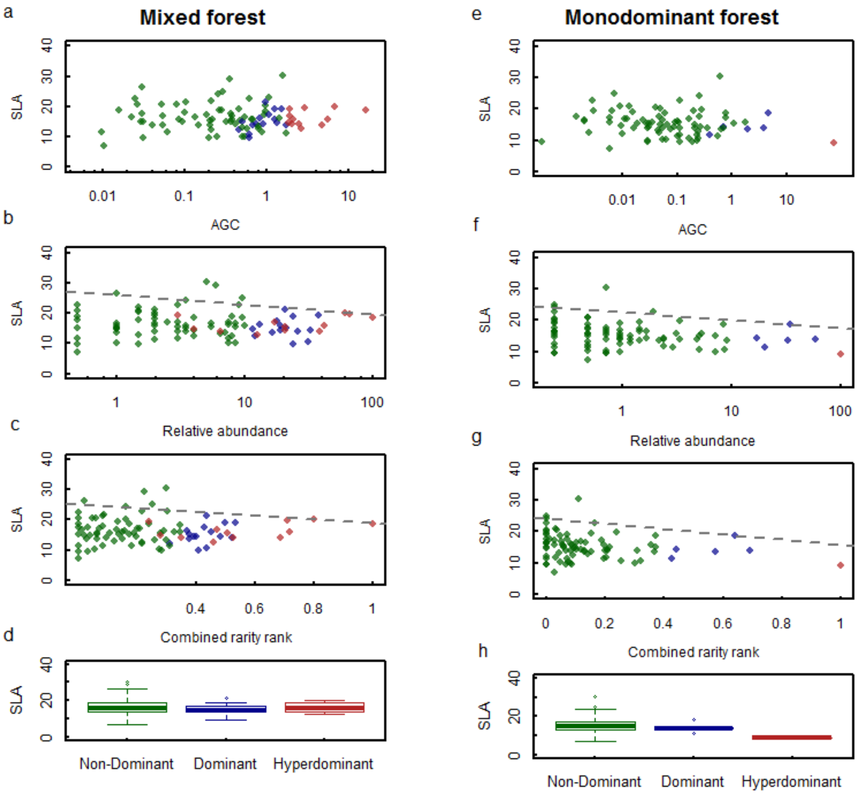
Species	**Family**	**Abundance**	**AGC**
Coelocaryon preussii Warb.	Myristiceae	5	0.066
Symphonia globulifera L. f.	Clusiaceae	0.5	0.062
Dacryodes osika (Guillaumin) H.J.Lam	Burseraceae	0.5	0.06
Macaranga monandra Müll. Arg.	Euphorbiaceae	2.1	0.055
Diospyros boala De Wild.	Ebenaceae	1.7	0.054
Aphanocalyx cynometroides Oliv.	Fabaceae	0.7	0.053
Petersianthus macrocarpus (P. Beauv.) Liben	Lecythidaceae	0.2	0.049
Allanblackia floribunda Oliv.	Clusiaceae	1	0.049
Diospyros sp.	Ebenaceae	1	0.047
Greenwayodendron suaveolens (Engl. & Diels) Verdc.	Annonaceae	0.7	0.046
Diospyros crassiflora Hiern	Ebenaceae	0.5	0.044
Vitex sp.	Verbenaceae	0.2	0.039
Drypetes gossweileri S. Moore	Euphorbiaceae	1	0.035
Pancovia harmsiana Gilg	Sapindaceae	1.7	0.03
Garcinia sp.	Clusiaceae	1.2	0.03
Chrysophyllum africanum A. DC.	Sapotaceae	1	0.029
Vitex congolensis De Wild. & Durand	Verbenaceae	0.7	0.028
Strombosia grandifolia Hook. f.	Olacaceae	0.7	0.028
Vepris louisii G.C.C.Gilbert	Rutaceae	0.2	0.027
Dialium corbisieri Staner	Fabaceae	1.4	0.024
Trichilia sp.	Meliaceae	0.7	0.019
Drypetes leonensis Pax	Euphorbiaceae	1.2	0.016
Guarea thompsonii Sprague & Hutch.	Meliaceae	1	0.016
Dacryodes edulis (G. Don) H.J. Lam	Burseraceae	0.5	0.013
Paramacrolobium coeruleum (Taub.) J. Léonard	Fabaceae	0.2	0.012
Rinorea sp.	Violaceae	0.7	0.011
Tessmannia anomala (M. Micheli) Harms	Fabaceae	0.5	0.01
Trilepisium madagascariense Thouars ex DC.	Moraceae	0.2	0.009
Cola sp.	Sterculiaceae	0.5	0.009
Prioria balsamifera (Vermoesen) Breteler	Fabaceae	0.2	0.007
Chrysophyllum sp.	Sapotaceae	0.2	0.006
Pycnanthus angolensis (Welw.) Exell	Myristiceae	0.5	0.006
Tabernaemontana crassa Benth.	Apocynaceae	0.5	0.006
Drypetes angustifolia Pax & K. Hoffm.	Euphorbiaceae	0.5	0.006
Microdesmis yafungana J. Léonard	Pandaceae	0.2	0.003
Hannoa klaineana Pierre & Engl.	Simaroubaceae	0.2	0.003
Pancovia laurentii (De Wild.) Gilg ex De Wild.	Sapindaceae	0.2	0.002
Craterispermum cerinanthum Hiern.	Rubiaceae	0.2	0.002
Trichilia prieuriana A. Juss.	Meliaceae	0.2	0.002
Parkia bicolor A. Chev.	Fabaceae	0.5	0.001
Bellucia grossularioides (L.) Triana	Melastomataceae	0.2	0.000

Supplementary Table S8.3: Spearman correlation coefficients between the selected traits: wood density (WD), specific leaf area (SLA), leaf nitrogen content (LNC) and leaf carbon isotope composition ($\delta^{13}C$). P-values are indicated: * p<0.05, ** p<0.01,*** p<0.001.

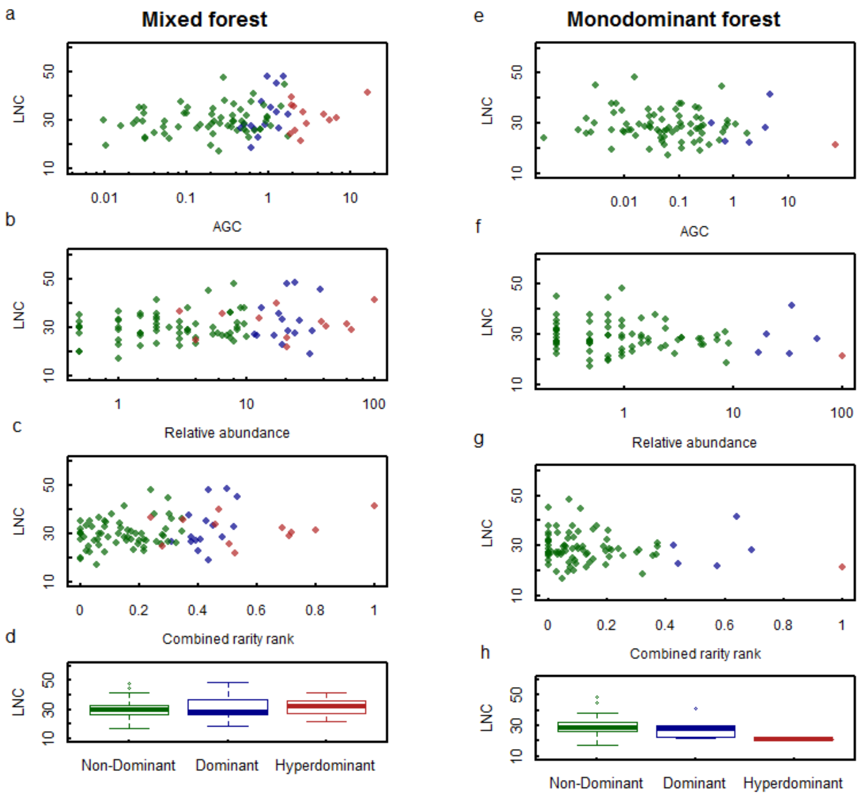
	WD	**SLA**	**LNC**	**$\delta^{13}C$**
WD	1	-0.079*	-0.143***	-0.227***
SLA		1	0.490***	-0.070***
LNC			1	0.002
$\delta^{13}C$				1



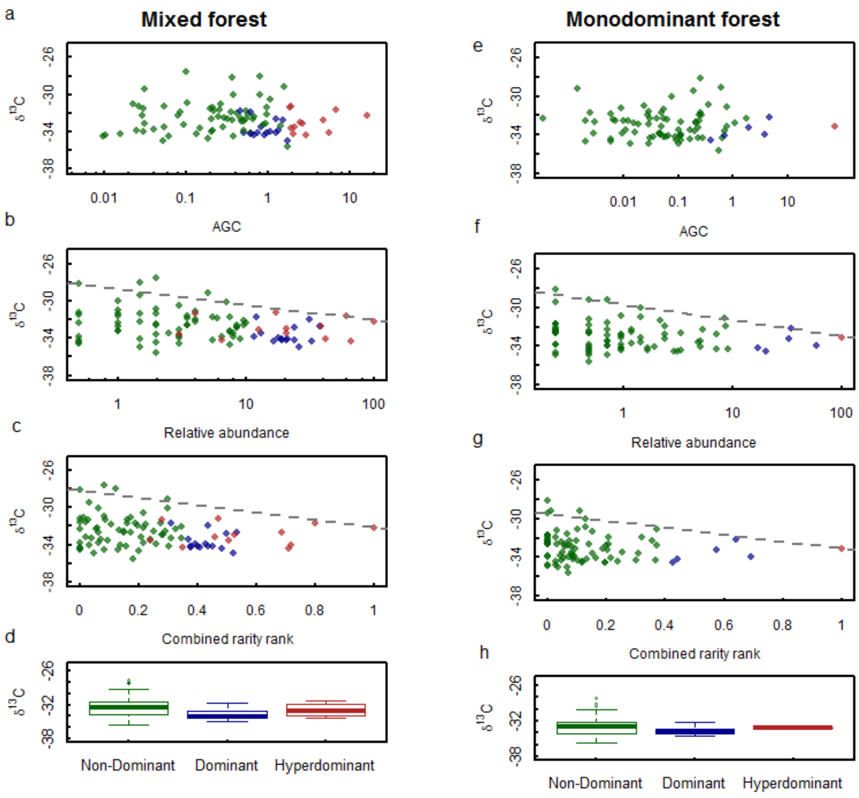
Supplementary Figure S8.1: Wood density (WD) of species within the mixed and monodominant forest for all 5 one ha plots combined. All dots show the WD of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. WD of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.



Supplementary Figure S8.2: Specific leaf area (SLA) of species within the mixed and monodominant forest for all 5 one ha plots combined. All dots show the SLA of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. SLA of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.



Supplementary Figure S8.3: Leaf nitrogen content (LNC) of species within the mixed and monodominant forest for all 5 one ha plots combined. All dots show the LNC of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. LNC of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.



Supplementary Figure S8.4: Leaf stable carbon isotope composition (δ^{13}C) of species within the mixed and monodominant forest for all one 5 ha plots combined. All dots show the δ^{13}C of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95th quantile regressions are presented as dotted grey lines. ns $p>0.05$, * $p<0.05$, ** $p<0.01$,*** $p<0.001$. δ^{13}C of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.

9

General conclusions and future perspectives

9.1 Research overview and future directions

Tropical forests represent a crucial carbon pool as they cover 7-10% of the global land area (Lewis *et al*. 2009) and, reportedly, store 40-50% of all terrestrial carbon (Houghton 2005; Lewis *et al*. 2006; IPCC 2007). These forests are an important component of the global carbon balance, with changes currently induced due to climate change (Pan *et al*. 2011) and direct anthropogenic disturbances (Harris *et al*. 2012). Increases in carbon storage over recent decades have been recorded in tropical forest indicating that they currently act as a carbon sink (Phillips *et al*. 1998; Baker *et al*. 2004a; Lewis *et al*. 2009; Pan *et al*. 2011) in part mediated by a CO_2 fertilization effect. On the ecosystem-level, increasing photosynthesis and net carbon uptake, and decreasing evapotranspiration have been observed, resulting a shift in the carbon- and water-based economics of the vegetation (Keenan *et al*. 2013). However, a more recent study showed a decline of this sink effect in the Amazon (Brienen *et al*. 2015).

Tropical land-use change

Tropical land-use change is an important source of carbon emission, mainly related to deforestation and forest degradation (Harris *et al*. 2012), and has important implications for biodiversity (Sala *et al*. 2000; Pereira *et al*. 2010). In our study area slash-and-burn agricultural activities and subsequent abandonment of the land had a larger effect on aboveground carbon storage compared to belowground carbon storage. Significant shifts in functional community structure and functional diversity are found as a result of the land-use change, providing important feedbacks to above and belowground carbon cycles. For example, within the first few decades of regrowth, the aboveground carbon stock does return to its initial state with species being limited to those with a lower wood density, although soil carbon stocks remain high even after degradation of the forest or land-use change. Yet, over time as part of the natural succession, the functional structure of the community changed significantly due to changes in light environment, resource availability and forest species composition. Deforestation in the Congo Basin is however limited compared to the Amazon and South-East Asia, with a net loss of forests (about 700 000 ha per year) over the period 2000–2010, and its rate of loss (0.23 percent per annum) considerably lower than that of the other two regions (both just over 0.4 percent per annum) (FAO 2011). However, shifting cultivation in the Congo Basin is substantial, resulting in a relatively large secondary forest area compared with other continents (FAO 2011) representing a significant component of carbon emissions in the Congo Basin (Zhuravleva *et al*. 2013).

Biomass in old-growth forest

Forests cover an area of over 300 million ha (FAO 2011) in the Congo Basin. However, the distribution of forest biomass or carbon storage over these forests is highly uncertain (Saatchi *et al*. 2007 & 2011). These uncertainties propagate and further decrease the reliability of estimates of carbon flux from land-cover and land-use change (Houghton 2005).

Our synthesis of aboveground carbon storage data across old-growth forest of Yangambi contributes to the extensive ground data required to increase this reliability. Here we show consistently lower values compared to the outer regions of the Congo Basin, due to a difference in tree height-diameter allometry. We estimated an average aboveground carbon stock of 162 ± 20 Mg C ha^{-1} for old-growth forest in Yangambi, which is significantly lower than stocks recorded in the outer regions of the Congo Basin, respectively 243 Mg C ha^{-1} and

259 Mg C ha^{-1} for western and eastern Congo Basin sites (Lewis *et al*. 2009). The best available tree height–diameter relationships derived for Central Africa (Feldpausch *et al*. 2012; Banin *et al*. 2012) do not render accurate canopy height estimates for our study area where the forests have a lower stature.

In addition, we explored the regional validity of this trend. Extending our study to new study areas in the region, Yoko and Yambela, confirmed the lower stature throughout the region. Our results hereby represent an important scientific contribution due to the central location of Yangambi, Yoko and Yambela within the Congo Basin. These results confirm earlier results by Saatchi *et al*. (2011), indicating that the Western Congo Basin in Gabon and Southern Cameroon, and Eastern D. R. Congo support higher carbon stocks. However, a high variability in local tree allometry between sites was found and results might not scale properly to the entire central Congo Basin. Increases of the spatial coverage of ground-based inventory plots as well as extensive remote sensing based measurements are therefore necessary to properly account for fine grained spatial variability. Yet, the expansion of a plot inventory network in the central Congo Basin is impeded mostly by logistical complications and poor infrastructure (Verbeeck *et al*. 2011; Malhi 2013).

Exploring the causes of this high local variability in tree allometry, we found differences in forest structure, species composition, soil texture and soil potassium levels as main explanatory variables. Forest structure and soil physical constraints are accepted variables influencing allometry (Poorter *et al*. 2003; Heineman *et al*. 2011). Furthermore, our results suggest that potassium might influence forest structure and above and belowground biomass. More so, a two-fold difference is found in soil organic carbon (SOC) stock between two old-growth tropical forest systems (Yoko: 44.2 ± 4.0 Mg C ha^{-1} and Yangambi: 109.5 ± 21.4 Mg C ha^{-1} respectively) with opposite asymptotic tree heights and aboveground biomass (Yoko: 42.5 m / 189 ± 28 Mg C ha^{-1}; Yangambi: 36.3 m / 157 ± 21 Mg C ha^{-1}), but very similar species composition, soil geochemistry and climate.

Our data indicates that small changes in nutrient availability can have large effects on the resulting biomass allocation in tropical lowland rainforest systems. We specifically propose that the differences in above and belowground carbon stock are a result of substantial variability in the root:shoot carbon allocation strategy of two similar tree communities for nutrient mining. We argue that adaptation of tree communities to nutrient limitation offer some explanation, as well as nutrient limitation as a constraint on microbial activity (Wright *et al*. 2011). Tropical forest soils are generally assumed to be phosphorus limited while limitation of potassium is often overlooked (Wright *et al*. 2011). This topic should be further developed by analyzing the relationships between leaf potassium concentrations, available soil potassium content and above and belowground biomass. Furthermore, quantification of root traits could also improve our knowledge on the functional structure of a community as they provide information on anchoring of a plant, water and nutrient absorption, transportation and storage (Jackson *et al*. 2007). However, root traits are not easily measured and a number of challenges still have to be addressed (Lavorel et al. 2007). Namely, an evaluation needs to be made of which root traits best represent certain root functions such as nutrient acquisition, anchoring, rhizospheric activity, decomposition rate. Additionally, the identification of relationships between root traits and aboveground traits (i.e. leaf or stem) could allow for the use of these second group of traits as proxies, which are more easily measurable (Lavorel *et al*. 2007).

These findings of highly variable SOC stocks have important consequences for the assessment of total carbon stored in tropical forests leading to different conclusions regarding the carbon storage capacity of the entire system, i.e. above and belowground carbon mass combined. The large and unaccounted variability in SOC stocks introduces additional uncertainty in the response of tropical forest systems to climate change and its contribution to the current terrestrial carbon budget.

Functional groups

Predicting future growth responses and the overall carbon budget of tropical forests is currently limited by, amongst others, a proper understanding of how different species are limited by various resources and their interactions (Prentice *et al*. 2007). Both light requirement and adult stature are two frequently used traits to classify tropical tree species (Swaine & Whitmore 1988; Turner 2001; Gourlet-Fleury *et al*. 2005; Poorter *et al*. 2006; Valladares & Niinemets 2008), which capture a large portion of the variation in functional traits found among tropical tree species (Loehle 2000; Turner 2001; Poorter *et al*. 2006). These classifications are also expected to form distinct groups within the leaf economics spectrum (Wright *et al*. 2004), which contrasts inexpensive short-lived leaves with rapid returns on carbon and nutrient investments vs. costly long-lived leaves with slow returns on investments.

Our work however provides new insights orthogonal to the current paradigm regarding these classifications. The site-specific classification of trees made in this study, irrespective of species identification, shows that these classifications do not show distinctly different trait values, mainly of leaf traits reflecting resource acquisition and stress tolerance. Our classifications of trees based on their individual traits allow us to better understand the origin and the functioning of species-rich ecosystems (Gitay *et al*. 1999). It also provides ways to model the dynamics of such ecosystems more realistically (Köhler *et al*. 2000; Picard *et al*. 2009 & 2012; Fyllas *et al*. 2012), with a more accurate description of community-level trait variation.

Biodiversity

Not all tropical forest types display the known high species diversity as often observed in most tropical forests. For example, the species *Gilbertiodendron dewevrei* dominates riparian forests within the Congo Basin, shaped by environmental filtering. *Gilbertiodendron dewevrei* in particular shows a combination of functional traits highly suitable for gaining dominance over other species, where the remaining species present in this forest show trait combinations that increase their likelihood for competition and survival in this forest type. Our trait-based analysis corroborates mechanisms of monodominance proposed by Peh *et al*. (2011b), and support the mechanism suggesting that the slow leaf decomposition rate of *Gilbertiodendron dewevrei* aids in attaining monodominance. Furthermore, our data also indicates that mechanisms related to xylem and WUE traits could be beneficial in adaptation to the moist soils of riparian forests.

On the other hand, high species diversity in tropical forest is maintained by rare species which rely on niche differentiation. Consequently, these species are predominantly associated with extreme trait values. The high contribution to functional divergence of rare species suggests that species with a low occupancy in communities, even within communities experiencing a strong environmental filtering, need to specialize for a specific niche, with trait combinations diverging from the community mean. As such, rare species benefit from niche differentiation in order to coexist with competitors within a community, which is passively or actively driven by strong environmental filtering (Maire *et al*. 2012).

Although these results are well established in literature (Belyea & Lancaster 1999; Cornwell & Ackerly 2009; Kraft *et al*. 2008; Maire *et al*. 2012), we show that rare species show both unique and redundant functional traits, both of high importance for long-term stability of ecosystem functioning. In contrast more common species mainly support redundant traits. Our study provides accurate descriptions of (rare) species composition and functional community structure related to the local environmental conditions of African tropical forests, which will allow us to better understand current and future species distributions and biodiversity in the African tropical forest.

Although a growing number of studies are investigating the relationship between functional diversity and ecosystem functions (Loreau *et al*. 2001; Balvanera *et al*. 2006; Cardinale *et al*. 2006; Díaz *et al*. 2007), only a limited amount of studies are performed in tropical forests. Most studies are conducted in grassland ecosystem (e.g. Balvanera *et al*. 2006; Clark *et al*. 2012; Maire *et al*. 2012), and the conclusions are not easily transferable to tropical forest systems. It is therefore obvious that additional work on functional diversity in tropical forests is needed, especially within the Congo Basin. We therefore emphasize that protection of rare species, or highly biodiverse areas, is imperative to safeguard the ecosystem against the loss of ecosystem functioning.

Conclusions and Implications

This work presents an improved estimation of above and belowground carbon storage in an underexplored central area of the Congo Basin, together with a quantification of its local variability. We have shown that forest structure and aboveground carbon storage should not be viewed independently. We therefore propose that upscaling of the estimates made in this study would be most appropriately done in combination with remote sensing methods mapping stand structure (e.g. LIDAR). Notwithstanding we acknowledge that a large and unaccounted variability in belowground carbon stocks is to be expected in tropical rainforests. This introduces a high uncertainty in predictions of the response of tropical forest systems to climate change and feedbacks to the global carbon budget. An increased effort, with new sampling plots and remeasurement of existing plots, is needed to better quantify these stocks and its stability in order to better predict changes induced by climate and land-use change.

This work is a key element in improving the accuracy of regional and basin-wide estimation of carbon storage in tropical forest (Saatchi *et al*. 2011; Baccini *et al*. 2012) as well as the functional understanding of the tropical tree community, providing useful information regarding ecosystem dynamics. The implications range from basic research assessing the impact on the global carbon cycle over policy making through the REDD+ mechanisms (Somorin *et al*. 2012) to ecosystem conservation where functional understanding of the forest ecosystem could allow us to better predict its resilience for land-use change and climate change (Pereira *et al*. 2010).

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Kearsley, E., Hufkens, K., Beeckman, H., Steppe, K., Boeckx, P., Verbeeck, H. Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. EGU General Assembly, Vienna, Austria, 28 April – 2 May 2014

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