Promotoren:

Prof. dr. ir. Joris Van Acker
Faculteit Bio-Ingenieurswetenschappen
Vakgroep Bos- en Waterbeheer
Laboratorium voor Houttechnologie
Coupure Links 653, 9000 Ghent

Dr. ir. Hans Beeckman
Koninklijk Museum voor Midden-Afrika
Afdeling Biologie
Laboratorium voor Houtbiologie & Xylarium
Leuvensesteenweg 13, 3080 Tervuren

Decaan:

Prof. dr. ir. Guido Van Huylenbroeck

Rector:

Prof. dr. Paul Van Cauwenberge

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FACULTEIT BIO-INGENIEURSWETENSCHAPPEN

Tree-ring analysis and stem biomass estimation of limba (*Terminalia superba* Engl. & Diels) in the framework of sustainable forest management

by

Maaike De Ridder

Proefschrift voorgedragen tot het bekomen van de graad Doctor in de
Bio-Ingenieurswetenschappen.

Thesis submitted in fulfilment of the requirements for the degree of Doctor (Ph.D.) in
Applied Biological Sciences.

Op gezag van de rector,
Prof. Dr. Paul Van Cauwenberge.

Dutch translation of the title:

Jaarringanalyse en schatting van de stambiomassa van limba (*Terminalia superba* Engl. & Diels) in functie van duurzaam bosbeheer

De Ridder M. (2013). Tree-ring analysis and stem biomass estimation of limba (*Terminalia superba* Engl. & Diels) in the framework of sustainable forest management. Ph.D. dissertation, Ghent University, Ghent, 167 p.

ISBN 978-90-5989-619-2

Dankwoord

De eerste stappen richting doctoraat werden ergens in 2006 gezet, omringd door duizenden xylariumstalen en straffe Congolese veldwerkverhalen. Na mijn studies kon ik bij Hans Beeckman aan de slag binnen dit fascinerende kader aan het Koninklijk Museum voor Midden-Afrika. Het platte Vlaand'renland werd prompt omgeruild voor Vlaams-Brabantse heuvels en de liefde voor tropisch hout bleef groeien. Bedankt Hans om me op sleeptouw te nemen in die ongekende, mysterieuze wereld en me de ruimte te geven om zelf accenten te leggen. Waar ikzelf nooit echt doctoraatsambities had, wist jij me met de limba plantages te motiveren om mijn kans te wagen. Joris Van Acker van het Gentse 'parallelle houtlab' tekende met plezier bij als promotor voor mijn doctoraat en de tandem Gent-Tervuren was klaar voor het kronkelende pad der doctoraatsonderzoek. Joris, dankjewel om enthousiast mee te gaan in mijn toch weer iets minder technologisch onderwerp en voor de joviale aanmoedigingen bij alle wetenschappelijke en administratieve knopen. Ook toen ik thuis werkloos verder werkte de laatste maanden, bleven jullie beide geduldig en positief in mails, telefoons en andere vormen van lange-afstandscommunicatie. Merci!

Geen onderzoek zonder financiële steun, zeker niet als daar veldwerk in de tropen bij komt kijken. Gelukkig hebben ze bij de VLIR ervaring met al dit soort zaken en hielpen Helke Baeyens en Stefan Wellens me door die andere jungle aan papierwerk heen. Ook Kathrien Verhanneman verdient hier een plaatsje voor het vlotte geregel van alle papierwerk toen Elodie onverwacht een hele winter moest thuisblijven. Dankjewel voor zoveel flexibiliteit! Ook mijn welgemeende dank voor de bijdragen van het Koning Leopold III fonds voor Natuuronderzoek en Natuurbehoud, de COST actie IE0601, Thanry en Bomaco. Zowel in Congo als in Ivoorkust heeft dat veldwerk wel wat voeten in de aarde gehad. Daarom wil ik graag iedereen bedanken die mijn pad kruiste tijdens de voorbereidingen en op het terrein zelf. We beginnen in Congo, waar WWF België en DRC trouwe partners waren. Merci Geert Lejeune, om mij op 1, 2, 3 te overhalen om mee te gaan met het inventarisatieteam, het was een ware ervaring. Merci Yolente Delaunoy om mij de knepen van het vak te leren, zijnde je mannetje te staan in een ploeg potige mannen. Et aussi merci à Laurent Nsenga et Prof. Mutambwe pour s'occuper des routines administratives, incompréhensible pour une petite maman belge. Benjamin Toirambe, merci pour les rencontres chaleureux à Kin et pour ton sourire royal. Et bien sûr, l'équipe de terrain, les hommes forts qui travaillent sans avoir peur des vipers ou des maringouins: Jean-Maron, Fils, Lidjo, Mbenza, les policiers et les éco-gardes de Luki. Merci à Papy et André pour l'accueil sympa à Luki. J'aimerais aussi remercier les gens de Soforma qui m'ont fourni des disques bien précieux et m'ont offert un séjour agréable à Tshela. Maar ondanks alles bewogen die Congolese stalen zich heel traag naar België en ging ik op zoek naar nieuwe opties. Zo mailde ik Guido Bayens die me kort daarop belde. Ik vroeg of hij me stamschijven kon bezorgen en hij vroeg of ik ze niet liever zelf wou komen halen. En zo geschiedde. Een enorm dikke dankjewel Guido! Zelfs toen de crisis toesloeg, liet je me het bos intrekken en stamschijven verzamelen voor wetenschappelijk onderzoek. Mensen met jouw ervaring, kalmte en liefde voor dit heel specifieke vak zijn zeldzaam, chapeau! Aussi un grand merci à Mr Thanry et les familles Girardeau, Blanca et Filion pour les moments de détente et l'organisation pratique du travail de terrain. Et de nouveau, l'équipe de terrain forte et amusante: merci à Mabea, Alexis, Marius, Sam, Rhodes et les autres que j'ai oublié ici. Merci à Hamidou pour ta gentillesse et les plats riches et merci à Seka, pour les promenades à Abidjan et pour les repas délicieux.

Toch was thuis komen na zo'n tropische trip ook best fijn, zeker met een rits leuke collega's als daar zijn Imke, Nele, Marijke, Griet, Rik, Dries, Piet, Wannes, Stijn, Wanzhao en Tom. Altijd paraat voor een babbel, een knabbel en zoveel meer. Ook voor de X-stralen scans was ik steeds in goed gezelschap. Bedankt Manu en Denis voor alle hulp bij het opstarten en verwerken van de beelden. In Tervuren kon ik altijd terecht bij José, Ilse, Camille, Claire, Nele, Lies, Joëlle, Lore, Julie, Elizabeth en Thalès. Agathe et Harisoa, merci de votre soutien. Ook een pluim voor de mannen van de technische dienst die met de glimlach elke klus klaarden. Als laatste pluk ik er nog even twee heren uit. Wim, je hebt me als pas afgestudeerd snotneusje onder je vleugels genomen, me alle do en don'ts binnen de musée geduldig bijgebracht en dat alles gekruid en op smaak gebracht met veel humor en veel liefde voor mens en natuur. Muchas gracias! En in Gent had ik de eer en het genoegen om een piepklein bureau te delen met Jan, de ik-brainstorm-en-programmeer-alles-man. Fijne babbels, altijd enthousiast en vooral vol goesting om het onderste uit de kan te halen en de ander ook zover te krijgen om zichzelf te overtreffen. Het is er niet zoveel gegeven maar je hebt echt die gave. Merci voor de laatavondmails, het weekendwerk en het aanhoren van alle ups en downs als er weer iets in de soep draaide. Je doet dat super!

Verder wil ik ook mijn dendro-collega's bedanken die me leerden dat geduld een schone deugd is. Kristof Haneca zette me op weg en Ilse Boeren, Anouk Verheyden en Valerie Trouet effenden het pad naar de tropen onder het allesomvattende motto: niet plooien! I would also like to thank my fellow scientists who motivated me along the way (this list is not at all complete): Ute Sass-Klaassen, Pieter Baas, Dieter Eckstein, Katharina Cufar, Patrick Fonti, Achim Brauning, Eberhard Lehmann, Kathy Steppe, Ingvar Bauweraerts, Martin Hallinger and all the others at Eurodendro, TRACE or COST meetings, I owe you all big time!

Dat de boog soms gespannen stond, hoeft geen betoog. Een luisterend oor, een gezellige koffieklets, afspreken met een hele hoop of een ontspannen loopje. Het kon allemaal. Dankjewel Katelijne, Jordi, Heidi, Pascal en de rest van de 'woodlab' bende voor die gezellige avonden en middagen. Dankjewel land- en bossers van het eerste uur om die liefde voor het buitengevoel verder te sterken, dankjewel vrienden van het jeugdhuis en dankjewel lieve buren om van Bertem een warme thuis te maken. Dankjewel aan Lientje en Ronny, die mij al lopend wegwijs maakten in Leuven en ver daarbuiten. Ook aan de rest van het lopende volkje van HRC (Vera, Dirk, Lies, Kris, Chrisje, Christine, Jo, Agnes…) en de gezellige open water bende van SWEM (Eric, Christiane, Sofie, Hilda, Ludwig…), een sportieve pluim op jullie hoed. Aan Sylvie en Pieter voor de onvergetelijke backstage en andere avonturen en aan Delphine (Fientje) voor alle doldwaze fratsen, onze gedeelde lachjes en traantjes en de weekendjes ertussen uit, dankjewel! Aan Kaya, Marc en de kinderen, voor al die uren 'therapie' voor, naast en achter de naaimachine, voor al die keren dat we bijna in ons broek deden van 't lachen en voor al die andere keren dat we zomaar mochten binnenvallen en aanschuiven aan jullie tafel. Jullie (en alle anderen die hier nog thuishoren maar me nu ontglippen) zijn me een bende lieverds, waarvoor oprechte dank!

Last but not least, mijn veilige opvangnet waarvan ik gretig gebruik maakte, soms om zelf wat stoom af te laten of soms om de rest van ons gezinnetje te verwennen terwijl ik achter de computer zat. Dankjewel! Jullie hebben me bijna voelbaar gesteund en hard mee geduimd hebben voor deze goeie afloop. Een dikke zoen voor de mémés en pépés, tantes en nonkels, neefjes en nichtjes, moeke, vake en oma en opa. Ook een dikke knuffel voor mijn zus(je) Elke, Koen, Lowiek en Babette. Onze belletjes, blitsbezoekjes onder de baan en de dolle pret die onze kindjes samen hebben, maakten de iets donkerdere dagen meteen een pak vrolijker. En dan mama en papa die mijn studiekeuze zeker aanmoedigden maar dat vertrek naar Afrika ineens veel minder vanzelfsprekend vonden. Dankjewel om me los te laten en toch dichtbij te blijven, om telkens opnieuw in te springen als er eentje ziek werd, om samen met Lieven ons huisje af te werken, om voor het hele gezin op zondag heerlijk te koken of om eventjes te bellen en pas een uur later in te haken. Er is veel veranderd sinds de start van mijn doctoraat. Mijn vriend werd mijn man, Bertem werd onze thuis en Elodie en Otto-Jan vulden de slaapkamers. Kleine kapoenen van me, jullie hebben het me niet altijd even gemakkelijk gemaakt hoor. Maar tegelijkertijd zetten jullie alles in het juiste perspectief en leerden jullie me (toch in zekere mate) relativeren. Die lach op jullie snoetjes was soms effectief genoeg om even die vastgelopen pc te vergeten. De pc die jullie papa dan prompt weer aan de praat kreeg. Lieven, lieve schat, een pretje is het niet altijd geweest hé, zo'n doctoraatsstudente en je eigen job, twee kindjes en nog meer werk naast je avondschool, al onze hobby's en bezoekjes aan familie en vrienden. Maar we bleken toch wel heel complementair ☺ en hebben het rond gekregen met z'n tweetjes, iets waar ik ontzettend trots op ben. Bedankt voor al je liefde, je geduld, het geruisloos overnemen van mijn deel als het even niet meer ging, de gezellige momenten samen op de zetel, de ettelijke wandelingen met de kindjes in het bos... Bedankt voor alles, deze thesis draag ik op aan jou, Elodie en Otto-Jan!

Samenvatting

Duurzaam bosbeheer is sterk afhankelijk van de beschikbaarheid van kwantitatieve data. Deze data ontbreken echter vaak in tropische bossen. Dit tekort aan gegevens over boomgroei, houtproductie en koolstofopslag verhindert niet alleen de implementatie van duurzaam bosbeheer maar ook de financiering ervan door programma's als REDD+ en Clean Development Mechanisms, beiden gerelateerd aan het Kyoto Protocol. Duurzaam beheerde bossen zijn wereldwijd het minst vertegenwoordigd op het Afrikaanse continent. Vooral de tropische bossen van Afrika maakt zelden deel uit van veldwerk in dit kader.

Gegevens over houtproductie en koolstofopslag kunnen op vele manieren verzameld worden hoewel de meeste gegevens afkomstig zijn uit grootschalige bosinventarisaties of herhaalde metingen van permanente proefvlakken. Deze methodes zijn tijdrovend en arbeidsintensief, zeker in tropische bossen. Bovendien zijn inventarisatiegegevens momentopnames zonder tijdskader, wat beheersplanning op lange termijn bemoeilijkt. De bovengrondse biomassa van bomen en dus ook de opslag van koolstof worden gemeten door nauwkeurige weging van de verschillende delen van de boom. Deze destructieve metingen vormen de basis voor pantropische biomassamodellen die gebruik maken van eenvoudige variabelen als diameter, hoogte en houtdichtheid. Pantropische modellen zijn gebaseerd op biomassametingen van een groot aantal tropische soorten over een ruim diameterbereik en lijken daarom toepasbaar op alle tropische bossen. Aangezien Afrikaanse metingen van biomassa slechts een beperkt deel uitmaken van de gegevens voor pantropische modellen, houdt het gebruik van deze modellen in Afrikaanse bossen grote onzekerheden in voor de schatting van koolstofopslag.

Dankzij de studie van groeiringen en gedetailleerde informatie over de dichtheid van hout kunnen nauwkeurige gegevens rond houtproductie en koolstofopslag over langere tijdsspanne verzameld worden en dit op een minder dure en minder destructieve manier. Deze twee methodes worden toegepast op een langlevende pioniersboomsoort, *Terminalia superba* Engl. & Diels. Boorspanen en stamschijven uit natuurlijke bossen en plantages werden geselecteerd in Ivoorkust en het zuidelijkste deel van het Mayombe bos in de Democratische Republiek van Congo. Groeiringen hebben een jaarlijks karakter in beide studiegebieden. De groei van *T. superba* is in beide studiegebieden gerelateerd aan globale klimaatsvariabelen zoals de El Niño 3.4 index terwijl de relatie met lokale neerslagpatronen enkel duidelijk is in het Mayombe bos. Groeicurves kunnen, naast klimaatsgebonden studies, ook op concrete wijze informatie leveren voor duurzaam bosbeheer. Zo werden variabelen zoals de minimum diameter voor exploitatie en de biologische rotatieleeftijd bepaald aan de hand aan de hand van groeicurves en vergeleken met de wettelijk bepaalde waarden. Deze waarden zijn sterk gebonden aan het type bos (plantages of natuurlijk bos) en het studiegebied (Ivoorkust/Mayombe). De analyse van veranderingen in groeipercentages doorheen de tijd toont ook aan dat *T. superba* doorgroeit tot de bovenste boomlagen zonder periodes van bv. extreme onderdrukking. Hiermee wordt ook wetenschappelijk bewezen dat deze boomsoort geen nood heeft aan intensief bosbeheer. Toch blijft duurzaam bosbeheer van *T. superba* sterk gebonden aan het bostype en kan het niet zomaar uitgebreid worden tot het gehele verspreidingsgebied van de soort.

Microdensitometrische profielen van boorspanen uit Ivoorkust werden bepaald aan de hand van X-stralen (3D-helix-scans met een resolutie van 50 µm). Het gebruik van een houder uit referentiemateriaal met een gekende dichtheid laat directe inschattingen van dichtheid toe, zonder bijkomende calibratie. Jaarlijkse dichtheidswaarden kunnen afgeleid worden uit de combinatie van dichtheidsprofielen van merg tot schors en jaarringreeksen. De dichtheid van hout stijgt van merg naar schors en de toevoeging van jaarringreeksen maakt het mogelijk om gedetailleerde schattingen te maken van de jaarlijkse evolutie in koolstofopslag. Op die manier wordt de vermoedelijke overschatting van koolstofopslag in Afrika bevestigd en toegeschreven aan het gebruik van vaste (literatuur)waarden voor houtdichtheid in plaats van jaarlijkse dichtheidsgegevens. Het gebruik van pantropische modellen veroorzaakt waarschijnlijk nog grotere overschattingen, zelfs indien houtdichtheid kan ingegeven worden in het model.

Deze studie bevestigt het enorme potentieel van jaarringanalyse en gedetailleerde gegevens rond houtdichtheid in functie van de planning van duurzaam bosbeheer en koolstofopslag op lange termijn. Beide methodes zijn complementair met klassieke bosinventarisaties en kunnen op een groot aantal boomsoorten toegepast worden. De diversiteit van variabelen uit inventarisaties (hoogte, mortaliteit, verjonging) wordt aangevuld met jaarringen die toelaten om tot enkele eeuwen terug te gaan in de tijd en beter inzicht te krijgen in evoluties van houtproductie en koolstofopslag. Een grotere steekproef, inclusief oudere bomen, is aanbevolen om regionale jaarringchronologieën uit te breiden, bvb. voor toekomstige dendroclimatologische studies en vergelijking met de groei van andere tropische boomsoorten. Systematische fouten worden sneller gedetecteerd bij grotere steekproeven, wat op zijn beurt leidt tot een meer betrouwbare inschatting van de culminatie van groeivariabelen en een betere basis voor bootstrapping. Tot slot kan toekomstig onderzoek ook toegespitst worden op variaties van microdensitometrische profielen binnen een groeiseizoen. Hierbij kunnen variaties in houtdichtheid ondermeer in verband gebracht worden met klimatologische en houtanatomische variabelen.

Résumé

La gestion durable des forêts dépend de la disponibilité des données quantitatives. Ces données manquent en ce qui concerne les forêts tropicales. Le manque de données sur la croissance, la production de bois et le stockage de carbone empêche non seulement l'implémentation de la gestion durable des forêts mais également le financement des recherches par des initiatives telles que le REDD+ et le Clean Development Mechanisms, qui sont liés au protocole de Kyoto. Les forêts soumises à une gestion durable sont le moins représentées sur le continent africain. De ce fait, les forêts tropicales africaines font rarement partie d'exploration et de recherches sur le terrain.

Les données sur la production de bois et de stockage de carbone peuvent être récoltées de différentes manières. Notamment, la plupart des données proviennent d'inventorisations forestières à grande échelle ou de mesures répétées sur des parcelles permanents. Ces méthodes prennent beaucoup de temps et sont intensif, en particulier pour les forêts tropicales. En plus, les données d'inventorisations sont prises à un moment donné sans cadre temporel ce qui rend la gestion de ces forêts difficile sur le long terme. La biomasse terrestre des arbres, ainsi que le stockage de carbone, sont mesurés en pesant minutieusement différentes parties de l'arbre. Cette méthode destructive est à la base des modèles de biomasse pantropicaux qui utilisent des variables simples tels que le diamètre, la hauteur et la densité du bois. Ces modèles sont basés sur des mesures de biomasses effectuées sur un grand nombre d'espèces tropicales englobant des diamètres très différents. Etant donné que les mesures de biomasses d'espèces africaines ne représentent qu'une partie des données nécessaire pour les modèles pantropicaux, il existe des incertitudes dans l'estimation du stockage de carbone.

Grace à l'étude des cernes de croissance et l'information détaillée sur la densité du bois, des données précises concernant la production de bois et le stockage de carbone peuvent être récoltés sur le long terme d'une manière moins couteuse et moins destructive. Ces deux méthodes sont appliquées sur une espèce pionnière à grande longévité, *Terminalia superba* Engl. & Diels. Des carottes et des rondelles de bois ont été sélectionnés dans des forêts naturelles ainsi que dans des concessions forestières à la Côte d'Ivoire et dans la partie sud de la forêt de Mayombe en République Démocratique du Congo. Les cernes de croissance ont un caractère annuel dans les deux zones d'études. La croissance de *T. superba* est relatée, dans les deux zones d'études aux variables climatologiques globaux tels que le « El Nino » index 3.4, tandis que la relation avec les précipitations locales est seulement visible dans la forêt du Mayombe. Des courbes de croissances peuvent aussi donner d'une manière concrète des informations concernant la gestion durable des forêts. De cette manière, des variables tels que le diamètre minimal d'exploitation et l'âge biologique de rotation peuvent être déterminés à l'aide des courbes de croissances et comparés au valeurs imposées par la législation. Ces valeurs sont fortement liées au type de forêt (plantation ou forêt naturelle) et de la zone d'étude (Côte d'Ivoire/Mayombe). L'analyse des changements de croissance, évalué en pourcentage, montre que *T. superba* croit jusqu'à la canopée sans montrer de périodicité spécifique p.e. d'oppression extrême. Ceci démontre scientifiquement que cette espèce n'a pas besoin d'une gestion intensive. La gestion durable de *T. superba* est néanmoins fortement liée au type de forêt et ne peut pas être étendue sur toute la zone de répartition de l'espèce.

Les profils micro densimétriques des carottes de bois de la Côte d'Ivoire ont été déterminés à l'aide de rayons X (scans hélicals 3D d'une résolution de 50 µm).L'utilisation d'un matériel

de référence avec une densité connue permet de faire des estimations directes de la densité sans avoir besoin d'une calibration supplémentaire. Les valeurs de densité annuelles peuvent être déduites de la combinaison entre les profils de densités de la moelle à l'écorce et les séries de cernes annuels. La densité du bois augmente de la moelle à l'écorce et l'ajout de séries de cernes annuels rend l'estimation détaillée de l'évolution annuelle du stockage de carbone possible. De cette manière, la probabilité de surestimation du stockage de carbone en Afrique est du à l'utilisation de valeur fixe (provenant de la littérature) de densité du bois au lieu de données annuelles sur la densité. L'utilisation de modèles pantropicaux cause probablement de plus grandes surestimations, même si la densité du bois peut être ajoutée au modèle.

Cette étude confirme le potentiel de l'analyse des cernes annuelles et des données détaillées sur la densité du bois en fonction de la planification de la gestion durable des forêts et des stocks de carbones sur le long terme. Les deux méthodes sont complémentaires avec les méthodes classiques d'inventorisation forestière et peuvent être appliquées sur un grand nombre d'espèces ligneuses. La diversité des variables utilisées dans les inventorisations (hauteur, mortalité, rajeunissement) est complémentées par les cernes de croissances qui permettent de retourner quelques siècles en arrière et permet également d'avoir une meilleure compréhension sur l'évolution de la production de bois et du stockage de carbone. Un grand échantillonnage, incluant de vieux arbres, est recommandé pour développer des chronologies régionales sur les cernes de croissance, par exemple, pour les futures études dendroclimatiques et pour la comparaison avec la croissance d'autres espèces tropicales. Des fautes systématiques peuvent être détectées plus rapidement avec un nombre d'échantillonnages plus élevées, ce qui permet d'avoir des estimations plus fiable pour les paramètres de croissances et forme une meilleure base pour le bootstrapping. Pour finir, la future recherche peut être axée sur les variations des profils micro densimétriques dans une même saison de croissance. Des variations de densités du bois peuvent être mises en relation avec des variables climatiques et avec l'anatomie du bois.

Summary

Sustainable forest management primarily depends on the availability of quantitative data, often not available in tropical forests. The lack of long-term data on tree growth, wood production and carbon stocks hampers the implementation of sustainable forest management and possible financing by Kyoto Protocol related tools like REDD+ and Clean Development Mechanisms. Africa is the continent with the lowest percentage of sustainably managed forests and especially African rainforests are currently poorly sampled.

Data on wood production and carbon stocks can be collected in several ways but mostly originate from large-scale inventories or repeated measurements of permanent sample plots. These methods are time- and labour-intensive in tropical forests. Moreover, the inventory data require a temporal scale that enables long-term planning. Measurements of carbon stock include the weighing of aboveground biomass of complete trees. Pantropical models are based on these destructive measurements and use variables such as diameter, height and wood density to estimate aboveground biomass in the world's tropical forests. These models are based on biomass measurements of a large range of tree species and diameters. African rainforests remain underrepresented in these datasets, creating large uncertainties on their carbon stock estimates.

Tree-ring observations and detailed information of wood density enable the collection of long-term, accurate data on wood production and carbon stocks in a less destructive, less expensive way. Both approaches are performed on *Terminalia superba* Engl. & Diels, a long-lived pioneer species. Stem disks and increment cores of planted and natural forest trees were collected in Ivory Coast and in the southernmost part of the Mayombe Forest in the Democratic Republic of Congo. Annual tree rings are observed in both study regions. Growth of *T. superba* appears to be related to global climate variables like the El Niño-Southern Oscillation in both study regions but a clear link with local precipitation patterns is only found in the Mayombe Forest. Growth curves were also more directly used to document sustainable forest management. On the one hand, growth curves offer the opportunity to calculate growth-based variables for sustained yield like biological rotation ages and associated minimum logging diameters, variables that appeared site-specific. On the other hand, a study on growth changes revealed that *T. superba* generally reaches the canopy without releases or suppressions, validating that this species does not demand for intensive silvicultural management. Sustainable forest management of *T. superba* nevertheless appears dependent on forest type and cannot just be scaled up to the species level.

Wood density was measured directly at high resolutions (50 μm) on increment cores from the Ivorian sample trees, using state-of-the-art helical X-ray scanning. Combining annual tree-ring data and pith-to-bark wood density profiles enables the extraction of annual wood densities. Wood density increases from pith to bark and allows for detailed estimates of carbon stocks over time using individual ring data. The assumed overestimation of carbon stocks in tropical Africa was confirmed and related to the use of fixed instead of annual wood densities. Furthermore, pantropical models, including those with wood density as a variable, probably even lead to higher overestimates.

This work confirms the huge potential of tree-ring analysis and detailed wood density data for long-term planning of sustainable forest management and carbon stocks. Both methods can be used complementary to inventories, combining the diversity of inventory variables (height, recruitment, mortality) with tree rings that extend decades to centuries into time. A larger sample size, including older trees, is recommended to lengthen regional tree-ring chronologies for future dendroclimatological studies. It would also enable a better detection of sampling biases, more reliable estimates of the culmination of growth variables and serve as a solid base for bootstrapping. Apart from the tree level and the inter-annual level, the obtained high-resolution wood density profiles offer also possibilities to study intra-annual density variations and their possible relation with climate and wood anatomy.

List of abbreviations

AC: autocorrelation
AGB: aboveground biomass
BA: basal area
BRA: biological rotation age
CAI: current annual increment
CDM: Clean Development Mechanism
CI: confidence interval
CT: computed tomography
CTFT: Centre Technique Forestier Tropical
DAB: diameter above buttresses
DBH: diameter at breast height
DRC: Democratic Republic of Congo
ENSO: El Niño-Southern Oscillation
ERAIFT: Ecole Régional postuniversitaire d'Aménegement et de gestion Intégrés des Forêts et Territoires tropicaux
EPS: expressed population signal
FAO: Food and Agriculture Organization of the United Nations
GC: growth change
ITTO: International Tropical Timber Organization
KNMI: Koninklijk Nederlands Meteorologisch Instituut
LLV: log-likelihood value
MAI: mean annual increment
MC: moisture content
MLD: minimum logging diameter
MS: mean sensitivity
ppr: percentage of parallel run
PSI: Paul Scherrer Institute
PSP: permanent sample plot
REDD: Reduced Emissions from Deforestation and forest Degradation
RMCA: Royal Museum for Central Africa
RSE: residual standard error
SD: standard deviation
SINQ: Swiss spallation neutron source
SST: sea surface temperature
TSAP-Win: Time Series Analysis and Presentation for Windows
TV_BP: t-value of Baillie-Pilcher
UGCT: Universiteit Gent Centrum voor X-stralen Tomografie
VLIR: Vlaamse Interuniversitaire Raad
WWF: World Wide Fund for Nature

Table of content

Chapter 1

Introduction and outline

This introduction provides a concise overview of the framework in which this study was performed. In paragraph 1.1, the origin of sustainable forest management (SFM) and related concepts are described, along with the actual situation in African rainforests, the analyzed forest region. The conditions and necessary data for SFM are listed and current bottlenecks are identified. Finally, the main objective of this work is formulated as well as arguments for the two approaches under consideration. In paragraph 1.2, the tree species under study is discussed into detail, including ecological and economical characteristics that illustrate the species' suitability for the given research objective. In paragraph 1.3, the different chapters of this study are briefly mentioned and the relations between the separate chapters are clarified.

1.1 Sustainable forest management and the use of tree-ring analysis and wood density: state-of-the-art and potential in tropical Africa

‘Sustainability’ is a concept with roots in forestry and dates back exactly 300 years. At that time, Hans Carl von Carlowitz (1713), defined ‘Nachhaltigkeit’ of forests as: *Die Consumtion des Holtzes müsse sich in Rahmen dessen bewegen, was der Waldraum / zu zeugen und zu tragen vermag. Dass man das Holtz, das so wichtig sei wie das tägliche Brot, mit Behutsamkeit nutze, sodass eine Gleichheit zwischen An- und Zuwachs und dem Abtrieb des Holtzes erfolget und die Nutzung immerwährend, continuirlich, und perpetuirlich stattfinden könne.* This term was recycled as ‘sustainable forest management’ at The United Nations Conference on Environment and Development in Rio de Janeiro in 1992, as a part of the ‘Forest Principles’. One of these principles states that *forest resources and forested lands should be sustainably managed to meet the social, economic, ecological, cultural and spiritual needs of present and future generations*. A crucial condition for SFM is the collection of quantitative data or as it is formulated in the ‘Forest Principles’, *the provision of timely, reliable and accurate information on forests and forest ecosystems is essential for public understanding and informed decision-making and should be ensured*.

The collection of these data needs to be representative for different forest types and forest regions and should measure variables that are not only useful for SFM but also for the estimation of carbon stocks in the framework of Clean Development Mechanisms (CDMs) and REDD+ files (Reducing Emissions from Deforestation and forest Degradation). Forests contain more than 80 % of the terrestrial biomass (Breckle 2002) of which half is considered carbon (Rowell 2005). Tropical forests cover 7 to 10 % of the total forest surface but store 40 to 50 % of the carbon in vegetation (Lewis et al. 2009). Intact tropical forests cover about 70 % of this total tropical forest surface but represent two third of the carbon sink (Pan et al. 2011). A considerable amount of studies were launched the last decade aiming at quantification of the global carbon cycle and the options of carbon sequestration in natural forests and plantations under the CDM of the Kyoto Protocol (Jepsen 2006; Oelbermann et al. 2004). This CDM comprises a global market for carbon credits, earned by investments that offset or reduce carbon emissions and offers a powerful, but not yet fully refined, tool to finance improved forest management and sustainable development (Glenday 2006).

On a global scale, studies and data on carbon stocks and cycles in tropical forests are not evenly distributed. Most studies focus on tropical forests in South and Central America (Asner et al. 2009; Chave et al. 2001, 2003, 2004, 2006; Clark and Clark 2000; Fonseca et al. 2011) and to a lesser extent, South East Asia (Basuki et al. 2009; Chaturvedi et al. 2010, 2012). Brown et al. (1993) only report historic carbon data in South America and Asia. Ciais et al. (2011) pinpoint at this lack of long term measurements in Africa although African rainforests are among the least disturbed forests on earth with carbon stocks up to 255 ton C ha^{-1}. Furthermore, Lewis et al. (2009) reported a significant increase in carbon storage during the last 40 years throughout intact African rainforests. Fortunately, two large long-term projects were recently enrolled in Africa, aiming at the evaluation of the carbon cycle on the continent. The CarboAfrica project was launched in 2006 by the European Commission (Bombelli et al. 2009) and the University of Leeds started the Afritron network (Lewis et al. 2009). Still, the Congo Basin (especially in the Democratic Republic of Congo, DRC) is not sufficiently sampled and a lot of effort is needed to install and maintain permanent sample plots (PSPs) and connect them to the global networks (Verbeeck et al. 2011). Consequently, the introduction of SFM in tropical Africa is also lagging on inventories of tropical forests in Latin America and South East Asia. In their ‘Status of Tropical Forest Management 2011’, the International Tropical Timber Organization (ITTO) reports a significant increase in the area included in management plans but this area remains the lowest for Africa. In 2005, the management plans including SFM principles only covered 6 million ha in Africa or about 1 % of the African forest area (Siry et al. 2005). Although the forest area under SFM slightly increased worldwide and even tripled in Africa between 2005 and 2010, it represents less than 8% of the world’s forests (Blaser et al. 2011). The area managed sustainably even decreased in Central African Republic, Gabon and Ivory Coast. African certified forests implement SFM principles and increased from 1.5 to 4.6 hectares. This increase should be regarded as hopeful although the increases between 2005 and 2010 were, to a very large extent, the result of better availability of information (Blaser et al. 2011).

As stated before, quantitative data are essential for SFM and estimates of carbon stocks. The lack of these data, especially in Africa, is caused by a combination of, e.g., complex forest structures (Whitmore 1990), unstable political situations (Blaser et al. 2011), but also by a lack of efficient methods for data collection in tropical conditions. The ITTO criticizes that there is no methodology for measuring forest carbon thus large uncertainties remain. In its recommendations concerning SFM, the ITTO urges the international community to assist countries to improve the quality of data on forest management as several countries lack the capacity to collect, analyze and make available comprehensive data on the status of forest management (Blaser et al. 2011). Large-scale inventories and the installation and maintenance of PSPs are highly recommended as a multitude of variables can be measured during periodical inventories (diameter, height, often survival/mortality rates), contributing to or evaluating the implementation of silvicultural treatments that promote SFM (Herault et al. 2010; Peña-Claros et al. 2008; Schulze et al. 2008). However, these long-term research plots are scarce, mostly situated in South and Central America (Alvarez-Buylla and Martinez-Ramos 1992; Kammesheidt et al. 2001), and are labor, time and as such capital intensive. All of these are limited in tropical countries, especially in tropical Africa (Verbeeck et al. 2011). Furthermore, Valle et al. (2006) reviewed the use of PSPs for repeated diameter measurements and subsequent modeling critically and observed overestimates that are caused by the limited length of the monitoring period, the diameter at which first measurements take place and the impact of stem defects.

Additionally, measurements of above-ground biomass (AGB) are destructive and time-consuming because trees need to be logged and all parts weighed, which is not straightforward in developing countries (Brown 2002), certainly not on a national scale (Gibbs et al. 2007). Therefore, a wide range of growth models and AGB models with simple input variables such as diameters were constructed, e.g., Brown (1997), Chave et al. (2001, 2005), Djomo et al. (2010). The debate on the use of specific or pantropical models is ongoing (Ciais et al. 2011). Nonetheless, most of these models are not based on African forests and several studies revealed that general compared to site-specific models often introduce large uncertainties on carbon stock estimates for tropical forests in Africa (Bombelli et al. 2009; Ebuy et al. 2001; Henry et al. 2010).

Keeping in mind the knowledge gaps and the needs formulated, **the main objective of this work is to assess the potential of tree-ring and wood density measurements in documenting and planning long-term SFM in addition to optimizing the estimation of carbon stocks. Our aim is to collect accurate and reliable information on growth and wood density over large time spans in West and Central Africa in a fast, less destructive way than carbon stock measurements and at low cost.** Although we worked on a number of stem disks, the sample trees were used locally or exported after felling, contrary to trees for destructive carbon stock measurements. Furthermore, we used a high number of semi-destructive increment cores. The potential of these cores for our objectives was studied in order to further limit the impact of measurements on the forest in the future.

Since long, the use of tree-ring analysis in the tropics was the subject of debate as tree rings were considered to be absent in tropical trees without clear seasonal variations in climate (Schweingruber 1988). Nowadays, tree-ring analysis in the tropics already looks back on more than a century of studies (Worbes 2002) but especially for Africa, the potential is not yet fully known and is limited to exploratory work of a few very committed scientists in the 1970s (Détienne and Mariaux 1970, 1975, 1976, 1977). Only recently, new dendrochronological studies in West and Central Africa revealed age structure and wood production of a natural forest in Cameroon (Worbes et al. 2003) and successfully linked growth to local and regional climate variables in the DRC, Benin and Ivory Coast (Couralet et al. 2010; Schöngart et al. 2006). Nevertheless, the explicit use of tree-ring data for forest management planning was never studied in tropical Africa to our knowledge, neither was the relation between climate and tree growth of one species in two distant regions at both sides of the equator.

Secondly, wood density is an important variable in wood biology and wood technology. Wood density variations can be related to wood anatomical structures like vessel and fiber characteristics (Roque and Filho 2007) whereas wood density is also often used to determine wood quality, due to its strong correlation with, e.g., the modulus of elasticity (Kästner and Niemz 2004). Average wood density values are numerous in literature and in databases but often lack important metadata (sample location, number of samples, method for measurements). Furthermore, these average wood densities are also used in models on biomass and carbon content and decrease the uncertainty of carbon stocks estimates considerably (Chave et al. 2005; Djomo et al. 2010). Yet, variations in wood density of any kind (radial, in age, in height, juvenile and mature wood, cavities) are less studied (Henry et al. 2010; Nock et al. 2009) and not considered if carbon stocks are estimated. This work will therefore explore the possible advantages of including this variable into the calculation of cumulative carbon stocks and their optimum increments.

1.2 *Terminalia superba* as a model tree species

The long-lived African pioneer species *Terminalia superba* Engl. & Diels is the tree species under study, sampled in both natural and planted forests in Ivory Coast and the DRC. *T. superba* is a light-demanding, semi-deciduous tree that sheds its leaves during the dry season. Trees are characterized by large buttresses and typically found in secondary forests and fallows (Groulez and Wood 1985; Hawthorne 1995; Humblet 1946; Swaine and Whitmore 1988). *T. superba* is a valuable species for our research objectives for several reasons:

- *Large distribution area and abundant presence.* The distribution area stretches from Sierra Leone to Angola (Groulez and Wood 1985) (Fig. 1.1). This huge area enables comparison of data over considerable distances at both sides of the equator. Results could as such be valid for large areas if, e.g., common tree-ring patterns are found in West and Central Africa. Recommendations for SFM could possibly be formulated at the species level instead of the site level. The species under study has a dominant character in terms of tree density because of its heliophilous character and fast growth in cleared areas. *T. superba* is therefore the flagship species of natural forests like the Mayombe Forest that covers parts of Gabon, the Republic of Congo, the DRC and Angola (Donis 1948), making the tree species an excellent representative for the analysis of our research objectives.

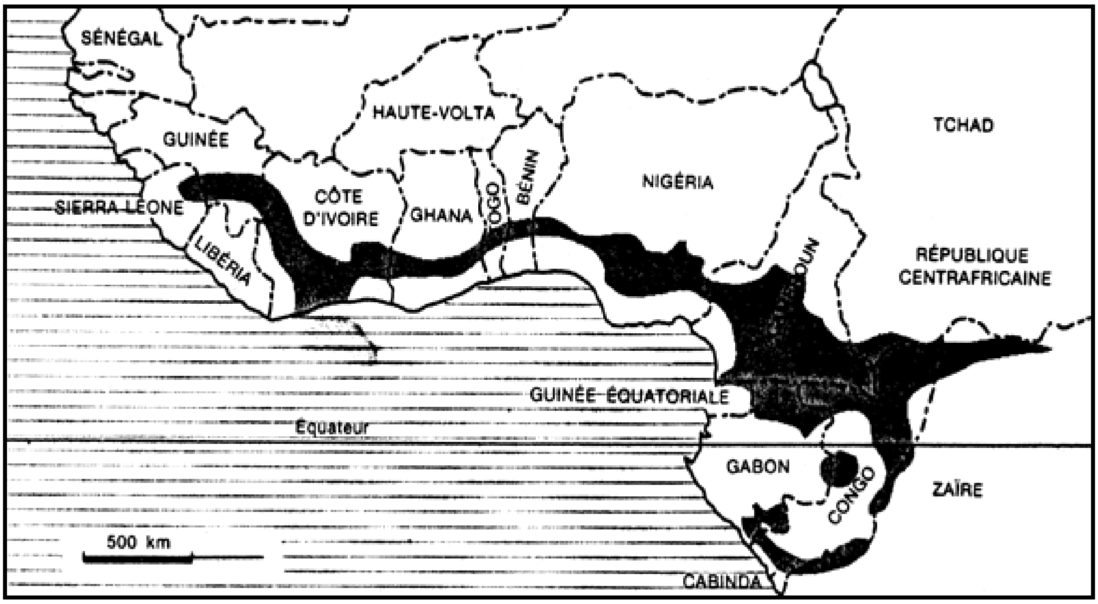


Fig 1.1. Distribution area of *T. superba* (after Groulez and Wood 1985).

- *Ease of silvicultural treatment and use in large-scale plantations*. *T. superba* is characterized by fast growth, straight stems, and high commercial heights. Additionally, the species has good natural pruning capacities and homogenous stands facilitate logging (Groulez and Wood 1985, Humblet 1946). The ease of installing seedbeds and nursing seedlings also illustrates the potential of *T. superba* as a plantation species. The largest plantations were installed in the DRC (ca. 7500 ha), the Republic of Congo (ca. 6500 ha) and Ivory Coast (ca. 11000 ha) (Groulez and Wood 1985).

Trees for this study were sampled in the DRC plantations (Fig. 1.2). These large-scale plantations were established in the Lower Congo Province (DRC) since the early 1940s (Humblet 1946) to replete the large harvests of *T. superba* during the 1930s in the Mayombe Forest. These plantations were not managed apart from some small-scale replanting to replace trees that died shortly after the installation of the plantation. Contrary to these early tree losses caused by inferior planting material, recent population increases in this province go along with considerable (illegal) removal of firewood (Iloweka 2004) and clearings for agriculture, putting enormous pressure on the natural and planted forests (Nsenga 2001). Certainly, settings for research are unique: 50-year-old plantations with an indigenous species, also occurring naturally in the same region. In addition, data on wood production and carbon stocks could offer new grounds for sustainable management planning and financing through CDM, lifting pressure off the natural forests and generating income for local and international economies.

Fig 1.2. The Congolese plantations of *T. superba* in the Luki Biosphere Reserve.

- *Annual tree rings.* The climate within the distribution area (dry season with at least three months < 60 mm monthly precipitation (Worbes 1995)) is considered to induce yearly tree-ring formation. This was confirmed by Mariaux (1969), who used cambial pinning and dendrometers to monitor tree growth in Cameroon, the Republic of Congo and Ivory Coast. His study, however, was limited to 13 trees, younger than 20 years, hampering classical dendrochronological procedures like cross-dating and relations with climate. Worbes et al. (2003) studied *T. superba* disks and wood cores from Cameroon but without climate matching or the calculation of variables for SFM such as minimum logging diameter and biological rotation age.

- *Presence of false heartwood and cavities.* Cavities are always unwanted, but the darker heart caused by false heartwood (*limba noir*, Bauch et al. 1982) is appreciated if occurring over considerable diameters (flame-like pattern for veneer; Groulez and Wood 1985). Normally, heartwood gets its colour from extractives by oxidation of phenols. Heartwood of which the colour is the result of injury or damage, is defined as false heartwood by Shigo (1979). Bauch et al. (1982) did not find a relation between diameter and the occurrence of false heartwood in *T. superba*. For *T. superba*, false heartwood and cavities only become visible after logging trees. Mostly, such logs remain in the forest because they cannot be sold or exported, representing an ecological and economic loss. The Food and Agriculture Organization (FAO; 2004) reports that volumes of exploited wood that is not evacuated can be as high as 50% of the logged volume. However, these volumes are not only left because of discolorations or cavities but also because of, e.g., severe logging damage to trunks. Furthermore, hollow or rotten trees affect measurements of AGB and carbon stock but are ignored in current estimates (Nogueira et al. 2006). From a commercial and ecological point of view, the assessment of a tree's density and its density variations before harvesting is important in order to limit the impact of exploitation on tropical forests. Again, *T. superba* is a model species for density fluctuations because information on these variations might be relevant to judge the presence of cavities and false heartwood and estimate the importance of these phenomena for carbon stocks.

- *One of the major African tree species traded. T. superba* is not only selected for research because of ecological reasons, it is also of economic importance. The trade name is limba (south of the equator) or fraké (north of the equator) and the species is listed by the International Tropical Timber Organisation (ITTO) as one of the major tropical species traded. This also strengthens the need for data to support the introduction of sustainable forest management.

The first limba logs arrived in Belgium in 1925 but the export volumes became significant from 1933 onwards. Trade in this species increased significantly from 1948/1949 onwards, leading to the depletion of forests in the DRC and the Republic of Congo, the largest exporters, by 1965. In the meantime, the northern countries (in particular Ivory Coast) increased their exports and took the lead from 1973 onwards. The total export volume increased from 206 000 m^3 in 1953 to 296 000 m^3 in 1958 (Groulez and Wood 1985) and was mainly imported by Belgium, Germany and the Netherlands. Data on exported wood volumes are scarce in the post-colonial era and the most recent (fragmented) data on export are found in the reports of the ITTO (Annual Review and Assessments of the World Timber Situation) from 1992-1993 onwards. Through the years, exported wood products shifted from logs to sawn wood and a few years later to plywood (Fig. 1.3). The most important exporting countries currently are Cameroon, Ghana and Ivory Coast. Wood of *T. superba* is mostly imported by Sahelian countries such as Senegal and by South European countries such as Greece, Italy and Spain (ITTO 1993-2011). As a result of supply problems and changes in prices, the Asiatic species *Gonystylus bancanus* (Miq.) Kurz started to replace *T. superba* on the international market (Von Karsten 1997). But even though export volumes were lower than in the 1950s (Fig. 1.4), these volumes only recently decreased to less than 50 000 m^3. Over the last decade, the revenues of limba export ranged between 7 and 60 million dollar. The most important cause of the decrease after 2004 is the worldwide economic crisis, also strongly present in the wood sector (Guy Bayens, Alex Dedeckel, pers. comm.). Even today, this species is still on the limited list of African export species (about 20 different tree species) (ITTO 2011). In addition, it should be noted that abovementioned data only contain registered quantities of international traded *T. superba*, yet the amount of wood from legal and illegal loggings of *T. superba*, and wood used by local people for charcoal, furniture, moldings and framings (pers. obs.) is considered substantial as well.

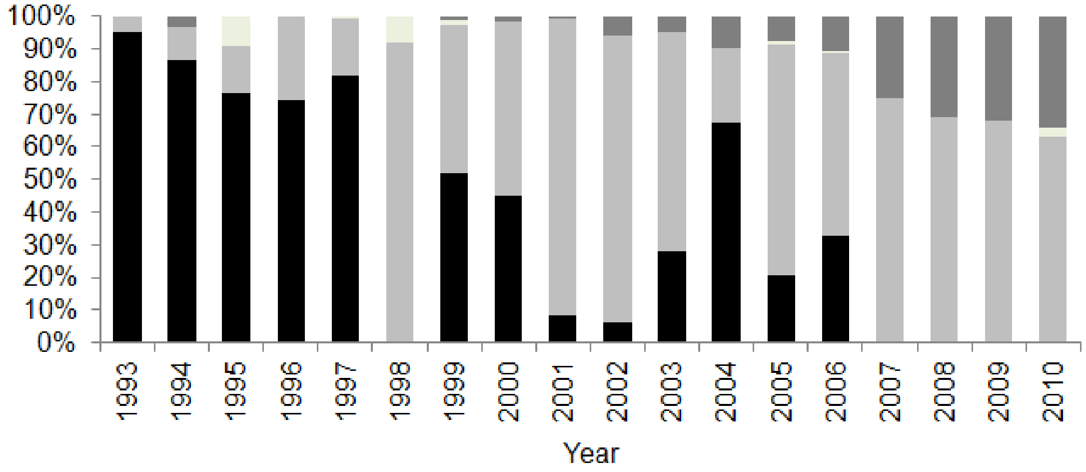


Fig 1.3. Percentages of different wood products of *T. superba*: logs (black bars), sawn wood (grey bars), plywood (dark grey bars) and veneer (light grey bars).

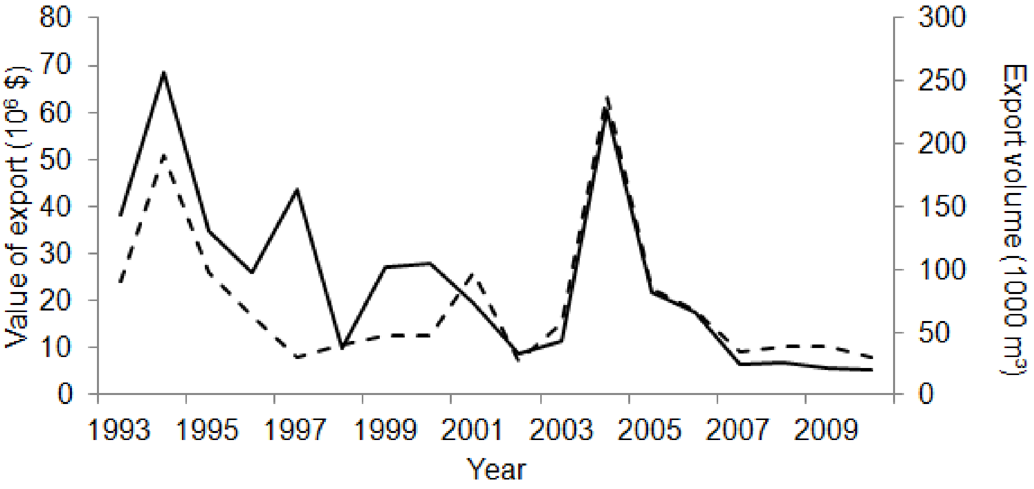


Fig 1.4. Value and volume of exports of *T. superba*. The solid curve represents the export volumes, the dashed curve represents the value of exports.

- *Multiple wood use*. *T. superba* is mainly used for indoor applications because of its low resistance to fungi and insects. Timber applications are skirting boards, interior joinery and also doors (Groulez and Wood 1985). It was one of the major veneer timber species exported by African timber producers (Lamprecht 1989). The peeled veneer is mainly used for plywood and furniture. *T. superba* is also chosen for the fabrication of moldings during the construction of buildings, especially locally. Trees with decorative false heartwood are still used for coffins in southern Europe (Guy Bayens, pers. comm.). The main physical and mechanical wood properties are listed in Table 1.1.

Table 1.1. List of physical and mechanical properties of *T. superba* (after Paradis et al. 2011)

Properties (measuring units)	Mean value and standard deviation
Specific gravity (-) [a]	0.54 ± 0.07
Monnin hardness (-) [a]	2.4 ± 0.9
Coefficient of volumetric shrinkage (%)	0.42 ± 0.07
Total tangential shrinkage (%)	6.1 ± 0.9
Total radial shrinkage (%)	4.3 ± 1.1
Crushing strength (MPa) [a]	47 ± 8
Static bending strength (MPa) [a]	80 ± 16
Modulus of elasticity (MPa) [a]	11750 ± 2480

[a] Measurements at 12 % moisture content, with 1 MPa = 1 N mm^{-2}.

Although other African tree species with relative low densities and light-colored wood (e.g., *Triplochiton scleroxylon* K. Schum., trade names: ayous or obeche) can replace *T. superba* for certain uses, research on new uses was launched by, e.g., Plato®, a company that introduced modified boards of *T. superba* for cladding (Fig. 1.5). This way, limba can be used for outside applications. The Plato® process is a thermal modification process resulting in reduced hygroscopicity and thus, increased resistance to different types of biodegradation and improved dimensional stability, without the use of biocides. Development of suitable thermal modification techniques focused on optimization of the process for a maximum increase of the dimensional stability and durability, while minimizing the decrease of strength. Plato® collaborates with a logging company in Cameroon that has the FSC certificate (Forest Stewardship Council) and listed 200 tree species in their concessions. Plato® selected 10 tree species based on literature and high abundance in the forest but not on the wood markets. *T. superba* had the highest score during the testings of the Plato® process and is now commercialized for cladding, without the need for additional coatings (Edo Kegel and Michiel Boonstra, Plato®wood, pers. comm.). This is an example of the new economic opportunities for *T. superba* and how logging companies are encouraged to introduce sustainable management in their concessions. Again, the need for accurate growth data on *T. superba* is evident.

Fig 1.5. An example of thermally modified *T. superba* boards by Plato® (left) and two applications of cladding in the Netherlands (copyright: Plato®hout).

All of the above mentioned reasons document and support the use of *T. superba* for our research objectives. The methods tested in this work, however, are of use for tropical trees in general and should allow similar research on other tropical tree species.

1.3 Outline

While the introduction focused on the importance of *T. superba* in general, **Chapter 2** describes the results of a classical inventory of *T. superba* that was conducted in the Congolese large-scale plantations of the southern Mayombe Forest to gain insights on the potential of this species for wood production and carbon stocks. A site-specific volume model was constructed based on detailed diameter, height and form factor measurements, whereas carbon stock was estimated using different existing pantropical models.

In chapter 3 and 4, tree growth is studied on stem disks and increment cores from West and Central Africa. Data collected at one point in time (inventories) are transformed into time series (tree-ring series) that allow for retrospective growth analysis over larger time spans than those covered by repeated inventories. In **chapter 3**, regional tree-ring chronologies were constructed for both Ivory Coast and the Congolese Mayombe Forest. Both chronologies were compared to local (precipitation), regional (sea surface temperatures) and global (El Niño-events) climate variables in order to analyze common or different responses of tree growth on climate. The link with climate is crucial, since tropical regions often do not dispose of long time-series of meteorological data. Dendrochronology offers a powerful tool to develop dated proxies for climate reconstruction. Next to dendroclimatology, tree-ring data could also provide direct links to SFM. In **chapter 4**, tree-ring patterns were used as a base for the calculation of minimum logging diameters and biological rotation ages in planted and natural forests of the Mayombe and Ivory Coast. The variability of these harvesting variables was also tested with a bootstrap method developed for tropical tree-ring series. Finally, growth releases and growth suppressions were derived from growth curves to analyze if tree-ring patterns are useful in determining the need and timing of silvicultural treatments.

As a final step towards reliable estimates for carbon storage, measurements of wood density and its variations were analyzed in chapters 5 and 6. In **chapter 5**, three methods to study wood density estimates at high resolution were tested: helical X-ray computed tomography scanning, neutron scanning and drilling resistance. It is possible to calculate direct wood densities based on X-ray scans when using a sample holder made from a material with a density close to that of wood cell wall density. Drilling resistance was added as this method could offer a less destructive, low budget and portable alternative in the field. The actual mean wood density values and profiles of wood density from pith to bark of *T. superba* increment cores were analyzed in **chapter 6**. Variations of wood density were not only compared with age and length of the X-ray scans but also the location of the wood density sample was evaluated (radial density variations, variations of density with increasing age...), along with differences between juvenile, mature and false heartwood regions in the wood. One of the important objectives was to review the use of a fixed wood density value for the calculation of carbon stock, as it is done nowadays. The use of wood density as a function of age also enabled the calculation of the time at which carbon increments are optimized, similar to volume increments in chapter 4. As such it is possible to gain insight into optimum volume as well as carbon stock increments, allowing for a better integration of carbon stock in SFM plans. Finally, the results of resistance drillings as a field method for wood density variations were critically reviewed.

Because different chapters do not always use the same samples, the type and number of samples, along with the location and chapter in which the samples are used, is visualized in Fig. 1.6.

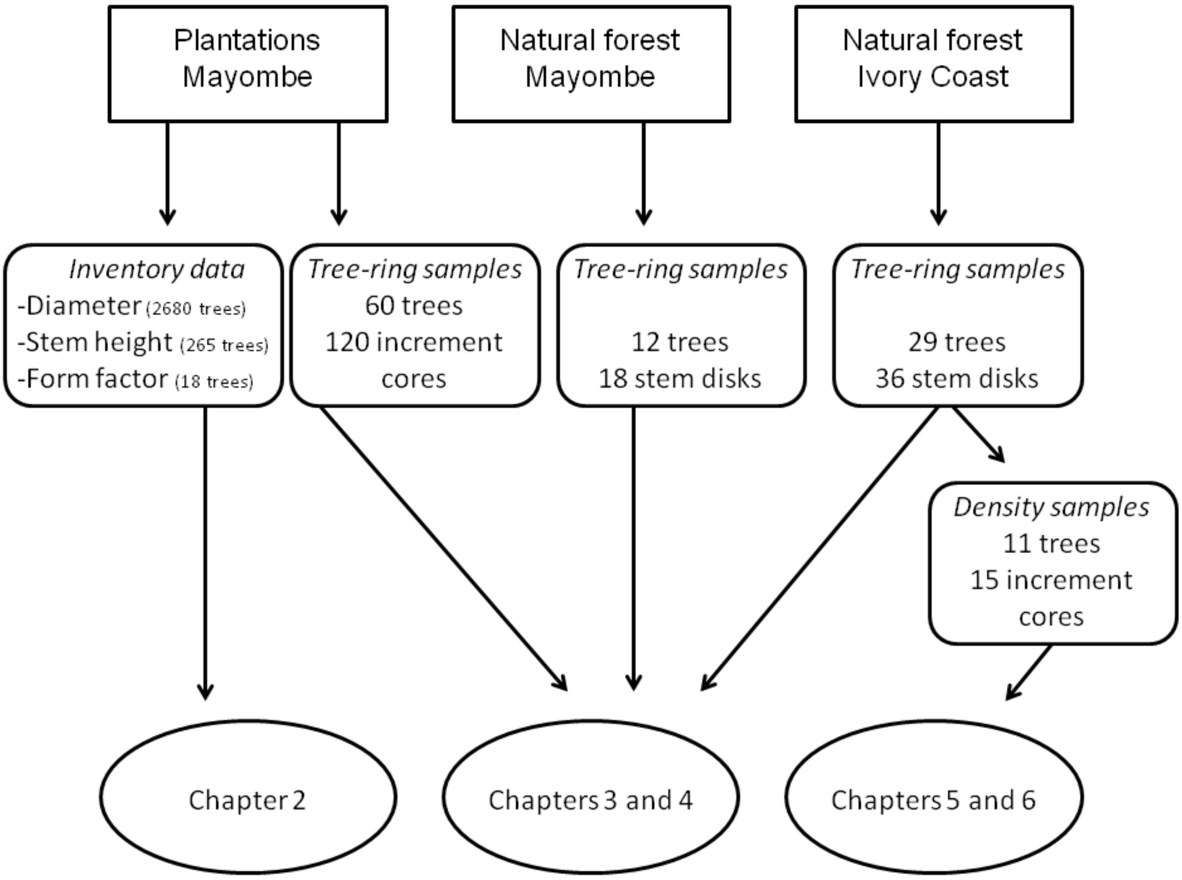


Fig 1.6. Overview of the studied forest regions/types (rectangular boxes), the type and number of samples (rounded rectangular box) and the chapters in which these data are analyzed (oval boxes). Two separate boxes were drawn for the plantations of the Mayombe because inventory data and tree-ring samples were not collected at the same location. Density samples originated from a subset of Ivorian trees.

Chapter 7 concludes on the potential that temporal tree-ring and wood density data have for tropical forests and the challenges for future research regarding, e.g., bootstrapping and wood density data at an intra-annual level.

Chapter 2

The potential of plantations of *Terminalia superba* Engl. & Diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo)

Abstract

In the 1940s-1950s, large limba (*Terminalia superba* Engl. & Diels) plantations were established in the Democratic Republic of Congo to reduce the pressure on the natural forests. The objective of this study was to evaluate the potential of these long-rotation plantations as production forests (timber) and carbon sinks. Five different plantations, between 50 and 58 years old, were sampled. Over a sample surface of more than 73 ha, the diameter above buttresses of 2680 trees, bole height of 265 trees and tree height of 128 trees was measured. To estimate the commercial volume, a nonlinear power law regression was used (R^2=0.95). A power law variance function was applied to counter heteroscedasticity of the residual plot. Estimates of commercial tree and stand volume at 50 to 58 years were 5.6 ± 4.1 m^3 and 183.9 ± 135.0 m^3 ha^{-1}. Stand volumes appear low but are explained by a large decrease in tree density. However, the mean volume increment of 3.2 – 3.7 m^3 ha^{-1} y^{-1} corresponds well with teak plantations of a similar age. For limba, aboveground biomass and carbon estimates of this study (resp. 108.4 and 54.2 Mg ha^{-1}) differ significantly from those of existing aboveground biomass models (resp. 135.7 – 143.9 Mg ha^{-1} biomass and 67.9 – 72.0 Mg ha^{-1} C). All aboveground biomass and carbon estimates for *T. superba* stands were lower than for the estimates of young fast-growing plantations like *Tectona grandis* L. f., *Eucalyptus* spp. and *Acacia* spp. (≤ 30 years).

Published in Annals of Forest Science

De Ridder M, Hubau W, Van den Bulcke J, Van Acker J, Beeckman H (2010). The potential of plantations of *Terminalia superba* Engl. & Diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo). Annals of Forest Science 67:501

2.1 Introduction

The Congo Basin is the second largest tropical forest in the world, second in extension only to Amazonia (FAO 2005). Within this basin, the Democratic Republic of Congo (DRC) has the largest forest surface in continental Africa, covering 134 million hectares and including many different forest types (FAO 2005). Still, deforestation and forest degradation in the tropics continue at an alarming rate. Between 1990 and 2000, 0.21 % of the Central African forest disappeared annually and almost 0.15 % was degraded every year (Duveiller et al. 2008).

Ecologically, sustainable forest management means that the management should not impair the ecological functions of the forest. This general concept, however, is quite difficult to achieve and to monitor and gives rise to controversy. Therefore the concept of sustained yield is being advocated as a more robust means to evaluate the non-detrimental character of timber logging and trade (Sands 2005). Applying the principle of sustained yield implies that log removals should not exceed the capacity of the growing populations to replace them (annual growth = annual allowable cut). It probably is not the single unique condition (as other factors such as sociological and ecological parameters could also be taken into account), but the concept is generally accepted as a the basic principle of forest management aiming at sustainability (Sands 2005).

Tropical plantations seemed to play a minor role in the debate on sustainable management. However, when these plantations are created on degraded or agricultural land and carefully designed with respect to the local people, they can provide several environmental and socio-economic benefits (Evans and Turnbull 2004). Lugo (1992) showed that the understory of older plantations can develop a high species richness with many native tree species. Thus, plantations can help in maintaining and restoring the diversity and productivity of forests after human-induced disruption. On the other hand, they can also provide a way to meet the national and international wood demand and to contribute to the country's economy (Marien and Mallet 2004). According to the Forest Resources Assessment of 2005, forest plantations cover 140 million ha or 4 % of the global forest area. About half of that area is located in the tropics and subtropics with no more than 10 % in Africa (FAO 2005).

Other arguments in favour of plantations are often found in the ongoing debate on climate change and global warming. Indeed, forests contain a large fraction of the terrestrial biomass, which underlines their importance as carbon sinks. The elemental composition of wood regarding the main components is relatively similar for all wood species, with carbon as the main component accounting for 50 % of the woody biomass (Rowell 2005). Kraenzel et al. (2003) measured a mean carbon content of 49.2 % in teak. Elias and Potvin (2003) measured the carbon content of 32 neotropical species and found similar results although the wood carbon fraction may exhibit some small across species variations. Still, carbon content can be considered as half of the woody biomass. There is an increased interest to quantify this global carbon cycle under the Clean Development Mechanism (CDM) of the Kyoto Protocol because it offers an interesting tool to finance sustainable forest management.

Volume and aboveground biomass (AGB) may be considered as the two main estimates within the framework of sustainable management and the mitigation of climate change. Measurements of both volume and AGB are difficult and time consuming (especially in tropical conditions), so often they are estimated from tree characteristics such as diameter or height, using allometric equations. The selection of the appropriate allometric model is a key element in the accurate estimation of volume and biomass (Navar 2009). The requirements for these allometric equations are identical, so classical forest inventories provide all the necessary data (Brown 1997). Still, allometric equations are a simplified way of estimating volume and biomass by taking measures of diameter and/or height. The actual measurements of volume and biomass (including carbon content) are more complex.

In tropical regions, most figures on volume, productivity and AGB are derived from natural forests (Brown 1997; Chave et al., 2001, 2005) or younger plantations with exotic tree species (up to 30 years). In these short-rotation plantations, teak (Kraenzel et al. 2003; Ola-Adams 1993), *Eucalyptus* spp. (Fonweban and Houllier 1997; Forrester et al. 2004) and *Acacia* spp. (Bernhard-Reversat et al. 1993; Forrester et al. 2004) make up the majority of research projects. A few studies on AGB of short-rotation plantations with indigenous tree species like *Terminalia superba* Engl. and Diels (DRC and Nigeria) and *Nauclea diderichii* (De Wild.) Merr. (Nigeria) have also taken place (Ola-Adams 1993; Onyekwelu 2007; Pendje 1993). However, these data were collected from other climate regions (Ola-Adams 1993; Onyekwelu 2007) or from small plots (< 1 ha) (Pendje 1993).

The objective of this study is to evaluate the potential of limba plantations around the Reserve of Luki in terms of wood and biomass production, including the sequestration of carbon. The combination of large-scale plantations in Central Africa with an indigenous tree species and an age of more than 50 years offers a unique opportunity to answer the following research questions. What is the ranking of limba among different indigenous and/or exotic plantation species, planted for timber production? And, can these plantations lower the pressure on the surrounding natural forests? Can limba play an important role as a carbon sink, compared to the other plantation species?

2.2 Material and methods

2.2.1 Study area

The Mayombe Forest covers the most southern part of Gabon, the western parts of the Republic of Congo and the DRC, and Cabinda (Angola). The plantations of *Terminalia superba* were located at the southern border of the Mayombe Forest, within a drier semi-evergreen Guineo-Congolian rainforest (White 1983) with large parts of secondary forests where former cultivation took place. In 1976, a relic of the Mayombe Forest in Luki -about 400 km coastward from Kinshasa- was assigned as a UNESCO Man and Biosphere Reserve. This reserve, located between 05°30' to 05°45'S and 13°07' to 13°15'E, has a typical zonation pattern (Fig. 2.1): a strictly protected core area, a buffer zone with human settlements where conservation is emphasized and a surrounding transition area with the limba plantations where sustainable development is encouraged by several projects. The plantations were established 50 to 58 years ago following planting schemes with planting densities of 104 trees ha^{-1} (8 x 12 m). The total surface of the plantation area under study was 5952 ha. The exact age of each individual limba tree is mostly unknown but always included within the range of 50 to 58 years. Planting activities were not always executed on time and borders between different plantations are unclear.

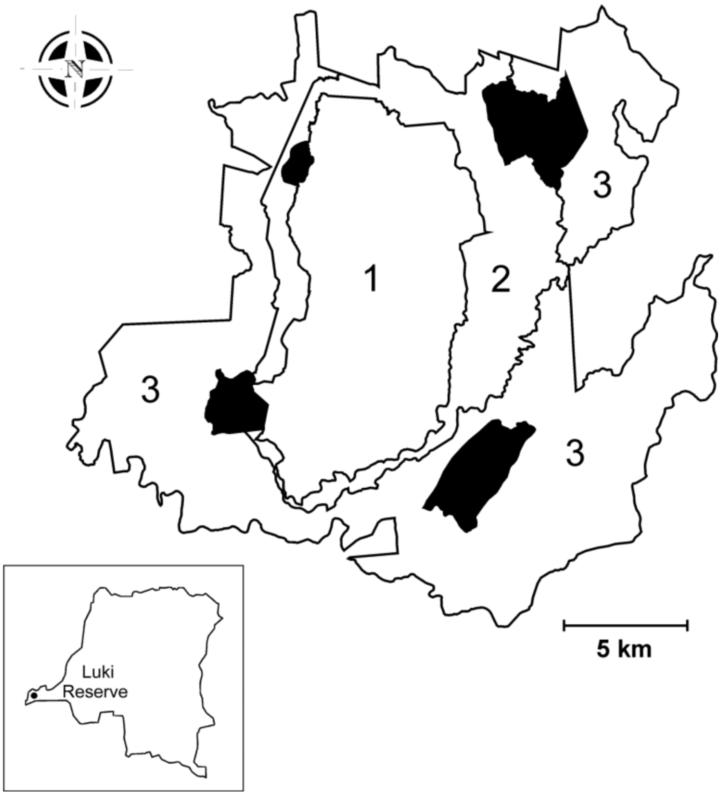


Fig 2.1. Location of the study area and division of the Luki Reserve (Lower Congo Province, DRC) in (1) a central zone, (2) a buffer zone, and (3) a transition zone with limba plantations. The black zones represents the four official enclaves within the Reserve. The presence of three of these enclaves in or near the plantations explains the human induced losses within the sample plots.

A dry season of four to five months (May - October) and a short period with lesser rainfall (January – February) characterize the region. The proximity of the ocean, manifest by a strong nebulosity, buffers the intensity of this dry season. The mean yearly rainfall fluctuates between 1100 and 1400 mm (Humblet 1946) but some particularly dry years exist. Temperatures oscillate around 26 °C in the rainy season and drop to a minimum of 20 °C in the dry season. The altitude is between 500 and 600 m above sea level. Soils belong to the so-called system of the Mayombe, consisting of four layers with schists, quartzites, gneiss and sandstone. Within this system, the Luki Reserve is located on substrates of fertile and schists with graphite. Most soils are argillaceous with a porosity of 35 to 55 %, a C/N ratio between 4 and 9 and pH between 4 and 6. In general, soils are classified as humified Ferralsols with small local variations (Mukendi 1973; Tutula 1968).

2.2.2 Inventory

Within the homogeneous plantations in the Luki Reserve, strip sampling was chosen in five different plantations using a width of 48 m and a length varying from 250 to 1000 m (Fig. 2.2(a)). A minimal distance between two strips and plantation borders was respected. This way, the total inventory of 21 strips covered 73.3 ha, slightly more than 1 % of the total surface of the limba plantations.

The circumference above buttresses of every limba tree was measured (n = 2680). Within this main sample, two subsamples were chosen: the buttress height of 2365 trees was noted while the bole height of 265 trees was measured. From this last subsample, 128 trees were selected to measure total tree height (Fig. 2.2(b)).

Measurements of circumference and buttress height were performed with a measuring tape in February and August-September 2007. Due to the fairly circular circumference of the stem, transformation to diameter above buttresses (DAB) is meaningful. During the dry season, when limba trees were mainly defoliated (April and August-September 2007), the bole height and total tree height were measured by using DAB classes of 10 cm as strata. All height measurements were performed with a Blume-Leiss hypsometer at a measuring distance of 30 m.

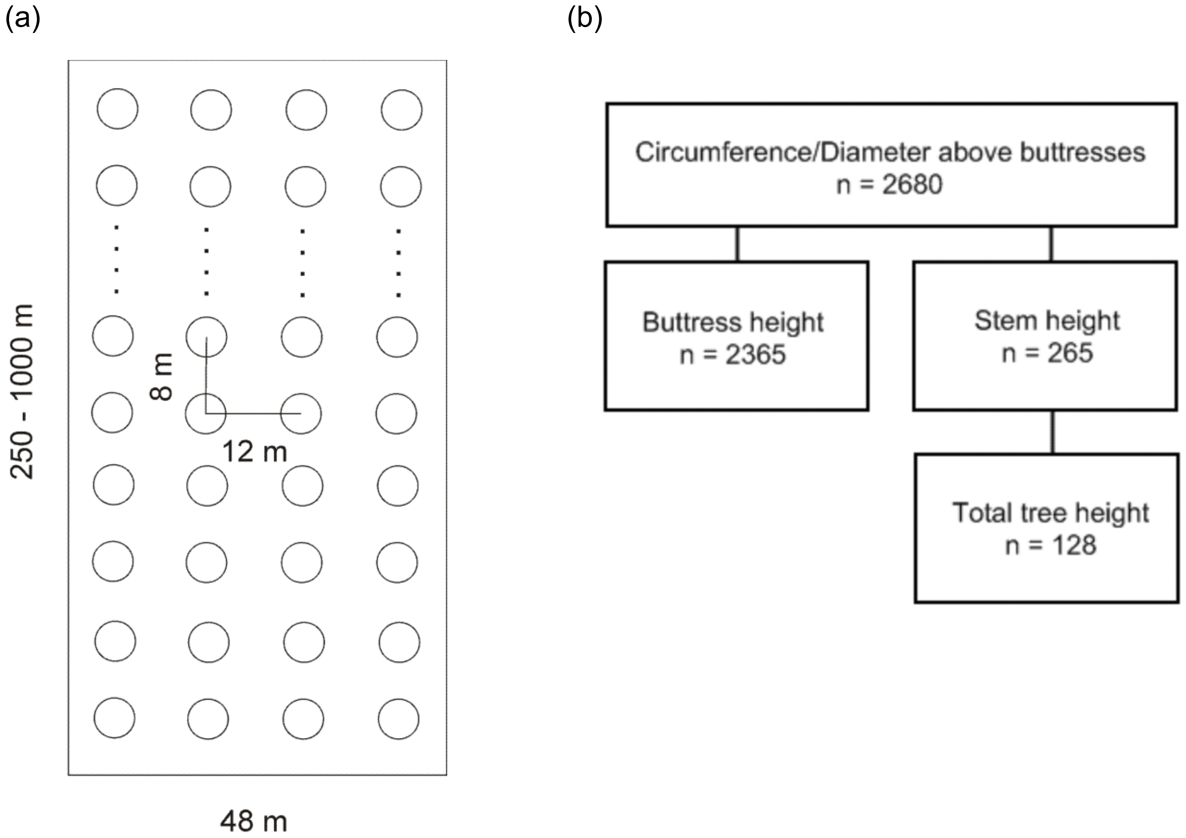


Fig 2.2. Sampling strategy. (a) Original planting distances were 8 x 12 m (O = tree). Sampling was done in strips of 48 m in width and 250 to 1000 m in length. The length is depending on the presence of roads, rivers, savannah or secondary forest areas, encountered during the inventory. (b) Schematic view on the number of samples for the different variables. Boxes with subsamples originate from larger samples and are connected by lines.

2.2.3 Felled trees

Apart from the inventory, 18 trees were felled within the plantations. All felled trees were subjected to repeated circumference measurements every 2 m until the first large branch. This way, the commercial volume was measured and form factors were calculated using the methods of Rondeux (1999). Form factors were calculated for every DAB class of 10 cm. Trees larger than the largest DAB of the felled trees receive the same form factor as the largest felled tree. The diameter and length of large branches were also measured on a selection of eight of the felled trees.

2.2.4 Allometric relations for volume and aboveground biomass

A model for commercial volume

In plantations, the most important volume is the commercial volume. The aim is to estimate this volume quickly and with a good accuracy. Measurements of the commercial volume were made on the 18 felled trees. Using those trees, the commercial volume was calculated with the classical volume equation:

$$V = G\ H\ F \tag{2.1}$$

where V is the commercial volume (m³), G the basal area above buttresses (m²), H the bole height (m) and F the form factor. By means of statistical analysis (one way ANOVA), the measured and calculated commercial volume of these 18 trees were compared. If there were no significant differences, the calculated volume is in this particular study a good approximation of the volume measurement. In that case, the commercial volume was calculated with the classical Eq. 2.1 based on 265 trees with a known DAB and bole height and a form factor derived from the 18 felled trees. The sample of 265 trees could then form the starting point for allometric equations. If differences were significant, the 18 felled and measured trees would be used.

Based on the adjusted determination coefficient (R²), the residual standard error (RSE), goodness-of-fit and distribution of residuals, one allometric equation was selected to estimate the commercial tree volume. All tested allometric equations, based on DAB only or DAB and bole height, were already successfully used under tropical conditions by, e.g., Segura and Kanninen (2005) and Tewari and Singh (2006).

Estimates of aboveground biomass using models and field data

Direct measurement of the biomass and enclosed carbon were not possible due to an interdict on the exploitation of a representative sample of trees and the lack of adequate means to measure biomass (oven/weighing scales). Therefore, indirect methods were used. First, stem biomass was defined as the product of the estimated commercial stem volume and wood specific gravity. Specific gravity is defined as the oven-dry weight divided by the green volume and expressed in g cm^{-3}. For limba, a wood specific gravity of 0.55 g cm^{-3} is used (Groulez and Wood 1985). Then, the product of the volume of the measured branches of eight felled trees and wood specific gravity was added. To calculate the volume of the branches, the classical formula (Eq. 2.1) with a form factor of 1/3, typical for cones, was used. Comparing the sum of stem biomass and biomass of the largest branches with data on AGB would lead to small underestimates because this study did not consider the biomass of twigs and leaves. According to Ola-Adams (1993) and Pendje (1993), small branches and leaves in limba plantations represent only 3 % of the total AGB. This percentage was also added to the stem and branch biomass.

On the other hand, AGB models – based on destructive measurements – already exist. Unfortunately, most models on AGB are limited in use because of a small diameter range (diameter at breast height, DBH) and a limited number of sample trees. Moreover, they are often based on young plantations (Forrester et al. 2004; Kraenzel et al. 2003; Ola-Adams 1993; Onyekwelu 2007). Until now, no species-specific allometric equation for old limba plantations (> 40 years) exists. Therefore, the use of general models for the estimation of

AGB in natural forests is accepted. Navar (2009) also stimulates the use of allometric equations for the estimation of biomass and carbon content. Both Brown (1997) and Chave et al. (2001, 2005) collected a broader data set and created models for dry to wet tropical forests. The model by Chave et al. (2005) is supposed to be consistent within the DBH range of 5 and 156 cm:

$$AGB = \rho \, exp\,(-1{,}499 + 2{,}148\, ln(D) + 0{,}207(ln(D))^2 - 0{,}0281(ln(D))^3) \qquad (2.2)$$

where AGB is the aboveground biomass (kg), D is the DBH (cm) and ρ is the wood specific gravity (g cm^{-3}). This model already includes the correction factor for the log-transformation of the AGB. Without this correction factor, the log-transformation of the data entails a bias in the final biomass estimation that could lead to an underestimate of the real biomass (Chave et al. 2005). Next to this rather complex model, three other widely used models, based on simple measurements of DBH were used.

$$AGB = 42.69 - 12.8\,(D) + 1.242\,(D^2) \qquad (2.3)$$

$$AGB = exp\{-2.134 + 2.530\ln(D)\} \qquad (2.4)$$

both in moist forests (Brown 1997),

$$\ln(AGB) = -2.19 + 2.54\ln(D) \qquad (2.5)$$

in regions with an annual rainfall below 3000 mm y^{-1} (Chave et al. 2001). Because the present results are based on DAB (≤ DBH), the AGB could be slightly underestimated, depending on the height of buttresses. However, this might be compensated by incorporating the biomass of these large buttresses.

The results of the used AGB models (Eqs. 2.2-2.5) were compared with the sum of stem biomass, biomass of the largest branches and the percentage of biomass in twigs and leaves. Carbon is considered as half of the AGB estimates.

2.2.5 Statistical analysis

Data were analyzed with the statistical software packages SPSS® 16.0 (Analysis of Variance, Linear and Nonlinear Regression) and S-Plus® 8.0 (Generalized Nonlinear Least Squares Analysis with variance functions). The threshold probability level was 0.01 for determining significant differences and 0.001 for significant regressions. During the analysis of variance, conditions of normality and homogeneity were tested. The selection of regressions was based on the determination coefficient, goodness-of-fit, the distribution of residuals and the residual standard error.

2.3 Results

2.3.1 Actual structure of the plantations

The actual mean density is 33 stems ha^{-1} which means that almost 70 % of the original stand has disappeared due to natural dieback and illegal cuttings. The variation in DAB is very high (11 – 155 cm) and the distribution of DAB is not normal ($p < 0.001$, Fig. 2.3). The mean DAB of 60.3 ± 20.7 cm (standard deviation) coincides with the originally proposed minimum logging diameter (MLD) (Humblet 1946). Exactly 50 % of the trees reached this MLD. The basal area (BA) of barely 10.5 ± 7.4 m² ha^{-1} also illustrates the decrease in density.

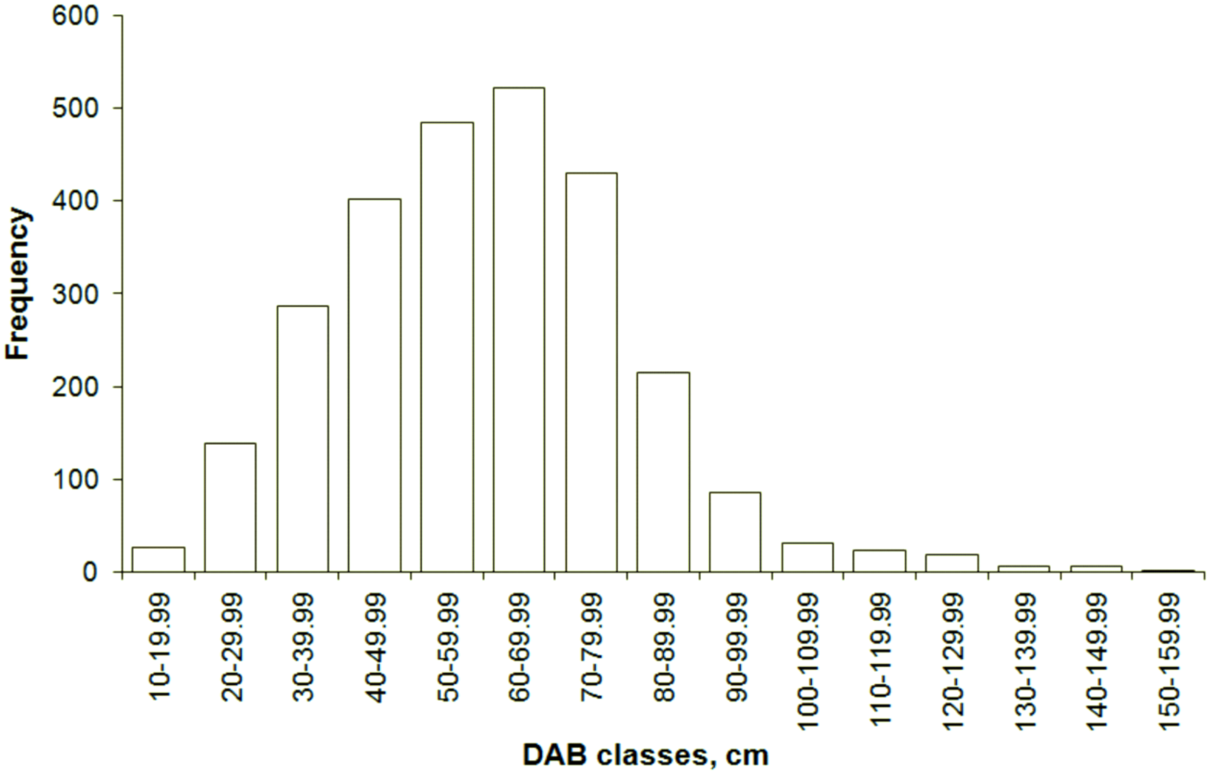


Fig 2.3. Distribution of the DAB of 2680 limba trees. The normal distribution, typical for even-aged plantations, is not found. The DAB class, containing the mean DAB of 60.3 cm, is best represented throughout the sample area.

The mean height of the buttresses was 202.5 ± 69.2 cm. Almost 72 % of all measured individuals had buttresses higher than breast height. There exists a clear relation between the height of the buttresses and DAB. The larger the trees, the higher the buttresses (Fig. 2.4):

$$H_{buttress} = 96.16\, e^{0.012DAB} \quad (\text{Adjusted } R^2 = 0.46,\ p < 0.001) \qquad (2.6)$$

where $H_{buttress}$ is the height of buttresses (cm).

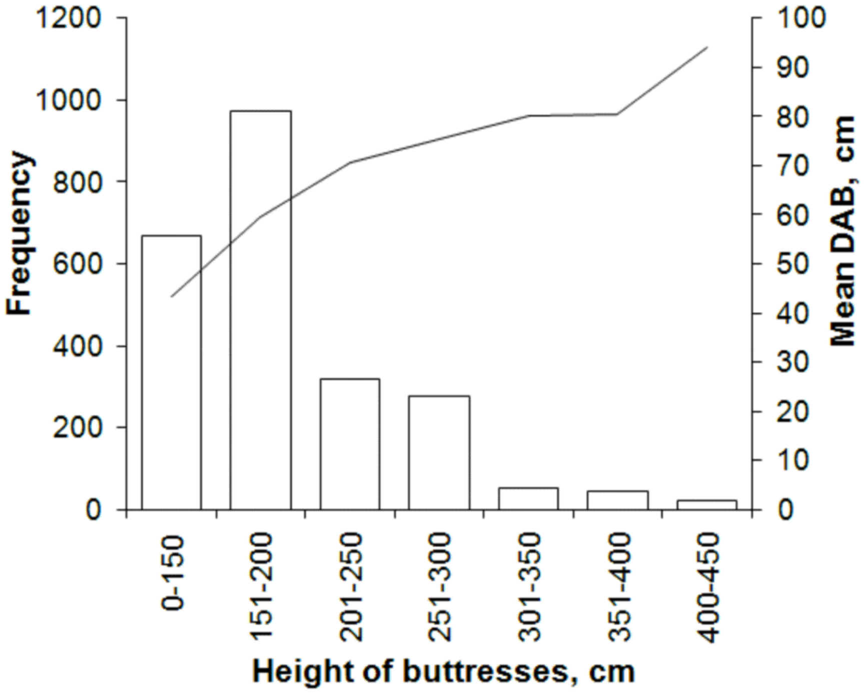


Fig 2.4. The relation between the height of the buttresses, the frequencies of trees within classes of buttress height and the mean DAB within those classes (n = 2365). Buttress height increases significantly with DAB.

The mean bole height of 265 trees is 25.2 ± 6.4 m while the mean total tree height of 128 trees is 31.5 ± 6.7 m. Looking at the heights cited by Groulez and Wood (1985), the plantations can be considered mature, i.e. reaching exploitable dimensions. The mean ratio between bole and total tree height of 128 trees is 0.78, indicating that almost 80 % of the trunk has a commercial value.

The DAB-height curves were constructed for bole height (n = 265 trees) and total tree height (n = 128 trees). A selection of four robust models gave the best results: logarithmic, quadratic, inverse and linearized power law regressions. All regressions are significant ($p < 0.001$) and show comparable adjusted determination coefficients (R^2) for the estimate of bole height (0.35-0.39). Based on the goodness-of-fit, logarithmic and power law relations revealed quite similar results but a slightly better distribution of the residuals supports the decision to choose the logarithmic regression (Fig. 2.5).

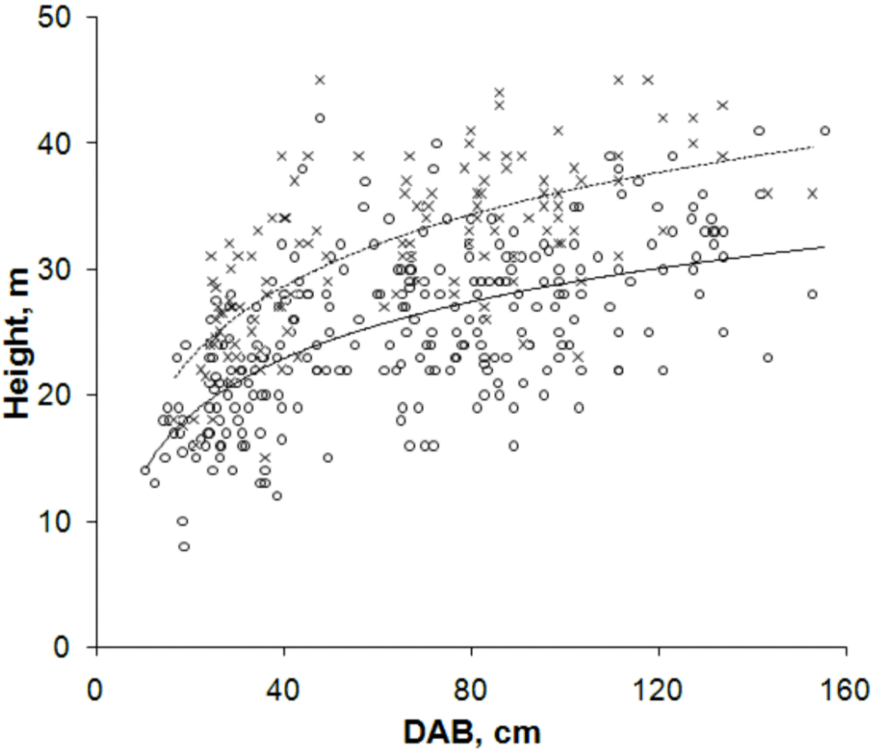


Fig 2.5. DAB-height curves for stem and total tree height (plain line: Bole height = -1.08 + 6.51 ln(DAB), R² = 0.38, p < 0.01 and dotted line: Total tree height = -1.64 + 8.22 ln(DAB), R² = 0.49, p < 0.01). Dots and crosses respectively represent measurements of bole and total tree height.

2.3.2 Commercial volume

No significant differences were found between the 18 measured and computed volumes with Eq. 2.1. In addition, the data set of 265 trees with measured heights and DAB covers the whole range of DAB (11 – 155 cm) while the 18 felled trees only cover a range of DAB from 18 to 91 cm. Therefore, all tested models are based on 265 trees of which the commercial volume was calculated by Eq. 2.1. The mean form factor is 0.68.

Inserting height in volume models only made them more complex and did not add any significant value to the performance of the model (R², RSE, goodness-of-fit, residuals). From the used linear, quadratic, cubic and (nonlinear and log-log transformed) power law equations, the most robust simple models all have a $R^2 \geq 0.90$. More complex cubic equations didn’t result in significant differences in R², RSE, goodness-of-fit or distribution of residuals and were therefore abandoned for further analysis. Notwithstanding the widely used log-log regression, Tausch and Tueller (1988) found that this type of regression is less precise and accurate than nonlinear regression. This study also contributes towards the establishment of nonlinear regressions, selecting a nonlinear power law model as the most appropriate for the commercial volume estimates of limba trees within a DAB range from 11 to 155 cm (Table 2.1):

$$V = 3.24 \times 10^{-4} DAB^{2.35} \qquad (p < 0.001) \qquad (2.7)$$

This model uses a variance function that counters the heteroscedastic character of the residual plot:

$$\mathrm{var}(V_i) = |V_i|^{1.83} \tag{2.8}$$

With $\mathrm{var}(V_i)$ the variance of the estimated commercial volume of the *i*th sample tree.

In addition, the use of this variance function leads to a better value for log-likelihood and RSE and smaller standard deviations of the coefficients of Eq. 2.7 (Table 2.1 and Fig. 2.6).

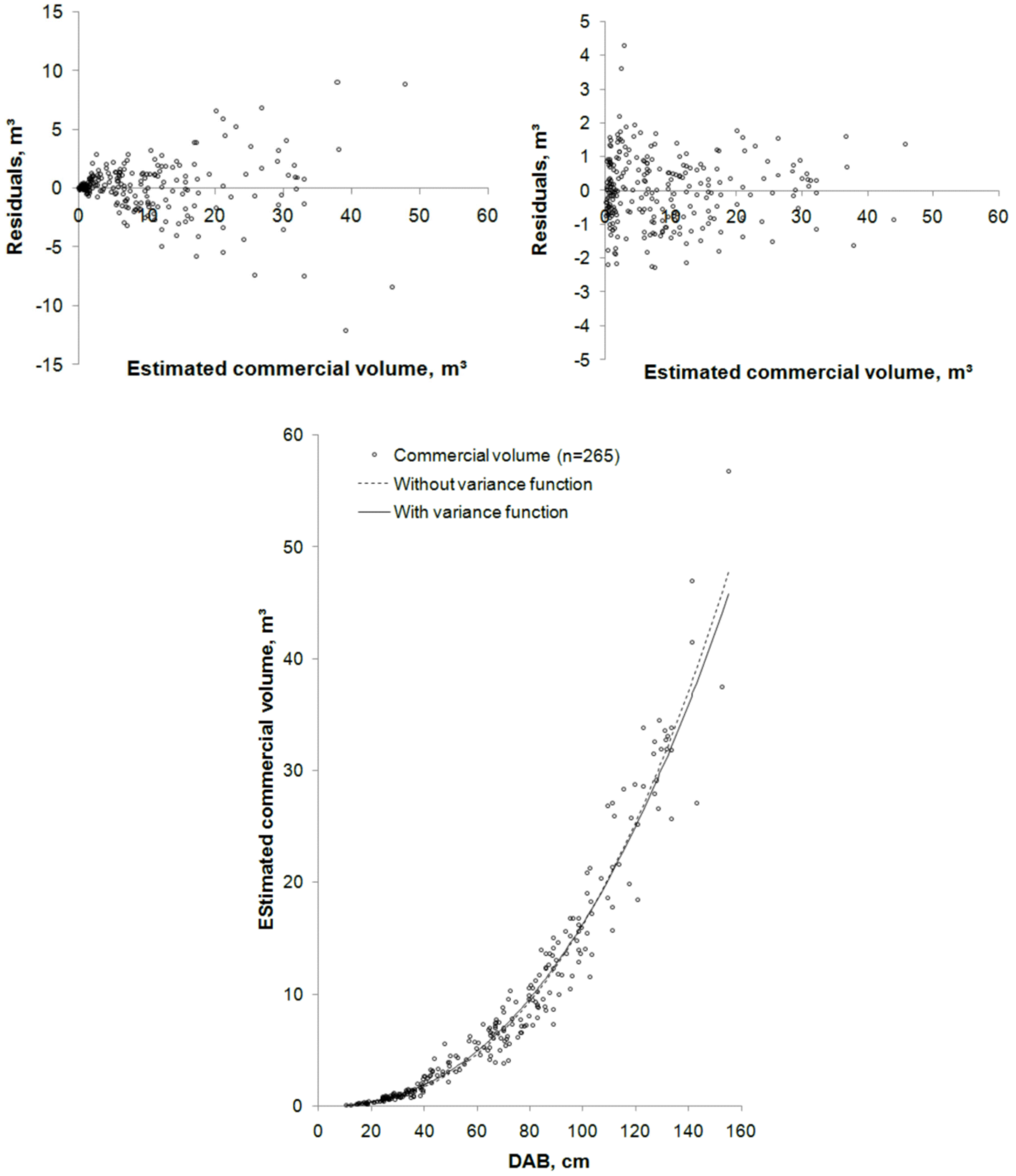


Fig 2.6. Residual plot of the power law regression (upper left) before, and (upper right) after applying the variance function (Eq. 2.8), and (lower) goodness-of-fit of both power law regressions. It is clear that the use of a power law variance function counters the heteroscedasticity of the residual plot.

This model (Eq. 2.7) was used to estimate the volume of the rest of the main sample (n = 2415). The estimated mean commercial volume was 5.6 ± 4.1 m³ per tree. Multiplied by the actual stand density, this results in a commercial stand volume of 183.9 ± 135.0 m³ ha^{-1}. Multiplied by the planned density (52 trees ha^{-1}) leads to values of 290.3 m³ ha^{-1} (Table 2.2). 'Planned density' is the final density that former foresters had proposed at the end of the rotation, after one thinning operation (Humblet 1946).

Table 2.1. Statistical characteristics of the nonlinear power law model (Eq. 2.7). SD = standard deviation, CI = confidence interval (95%), LLV = log-likelihood value, $p < 0.001$ (with and without variance function, Eq. 2.8).

	a	*b*	*SD (a)*	*SD (b)*	*CI (a)*		*CI (b)*		*LLV*	*RSE*	*Adj.* R^2
Without variance function	1.96 x 10^{-4}	2.458	4.42 x 10^{-5}	0.047	1.09 x 10^{-4}	2.83 x 10^{-4}	2.365	2.552	-583.944	2.220	0.95
With variance function (Eq. 2.8)	3.24 x 10^{-4}	2.351	3.14 x 10^{-5}	0.023	2.62 x 10^{-4}	3.85 x 10^{-4}	2.305	2.396	-347.658	0.241	0.95

Table 2.2. Volume estimates of limba plantations, using the power law regression (Eq. 2.7) (age between 50 and 58 years).

Mean commercial volume (m^3 per tree)	5.6 ± 4.1
Mean stand volume (m^3 ha^{-1})	183.9 ± 135.0
Minimum annual increment (m^3 ha^{-1} y^{-1}) [a]	3.2 ± 2.3
Maximum annual increment (m^3 ha^{-1} y^{-1}) [b]	3.7 ± 2.7
Mean planned stand volume (m^3 ha^{-1})	290.3 ± 213.2
Minimum annual increment (m^3 ha^{-1} y^{-1}) [a]	5.0 ± 3.7
Maximum annual increment (m^3 ha^{-1} y^{-1}) [b]	5.8 ± 4.3

[a] Mean annual growth if the plantations were 58 years old.

[b] Mean annual growth if the plantations were 50 years old.

2.3.3 Aboveground biomass

The use of existing models results in AGB estimates between 135.7 and 143.9 Mg ha^{-1} (or 4.1 to 4.4 Mg per tree) (Table 2.3). This corresponds with carbon content estimates between 67.9 and 72.0 Mg ha^{-1} (or 2.1 to 2.2 Mg per tree). Variances were not equal so the Tamhane's test was used to reveal significant differences between the models. Although the difference in AGB estimates is significant for Eqs. 2.3 and 2.4 (Brown, 1997), the difference between the lowest and highest estimates of AGB is only 6 %. Both models of Chave et al. (2001, 2005) result in very comparable estimates, situated between the two models of Brown (1997).

The mean stem biomass was 3.1 Mg per tree or 101.1 Mg ha^{-1}. The portion of volume and biomass from large branches of 8 measured crowns is very small (4.2 %). The portion of twigs and leaves is quite constant throughout time and a fraction of 3.0 % is added (Ola-Adams 1993; Pendje 1993). Considering the sum of the mean stem biomass, the biomass portion of the measured large branches (8 trees) and the portion of leaves and twigs (Ola-Adams 1993; Pendje 1993), the AGB would be 3.3 Mg per tree or 108.4 Mg ha^{-1} (or 1.7 Mg C per tree and 52.4 Mg C ha^{-1}). This is significantly lower than the estimates produced by Eqs. 2.2-2.5.

2.4 Discussion

2.4.1 Past and present structure of the plantations

It is clear that the initial density of 104 stems ha^{-1} has declined heavily due to human pressure and natural dieback. An exponential decrease in density did not only occur during the last three decades (unpubl. data). Tutula (1968) and Mukendi (1973) already noted a large decrease in density, ranging from 20 to 54 %, depending on the location of the sample plot. As the first losses in density can be assigned to the inferior quality of planting material or problems on steep slopes, the main cause during the last decades is the increasing population pressure in the Lower Congo Province, also increasing the need for fuelwood and the production of charcoal (L. Nsenga, pers. comm., 2007). In 2007, many charcoal furnaces, together with illegally cut limba trees for timber use were observed during the field sampling campaigns. Combined with the establishment of large agricultural areas for manioc (*Manihot esculenta* L.) and rice (varieties of *Oryza glabberima* Steudel and *Oryza sativa* L.), the pressure on the natural forests and the limba plantations is extremely high.

Table 2.3. Estimates of the above-ground biomass of limba plantations by using field data and existing models (age = 50 - 58 years).

	Stem biomass + large branches + twigs and leaves[c]	Eq. 2.2	Eq. 2.3	Eq. 2.4	Eq. 2.5
Mean AGB tree^{-1} (Mg per tree)	3.3 ± 2.4	4.3 ± 3.2	4.1 ± 2.8	4.4 ± 3.5	4.3 ± 3.5
Mean stand AGB (Mg ha^{-1})	108.4 ± 79.6	141.5 ± 104.3	135.7 ± 90.7	143.9 ± 114.8	142.0 ± 113.8
Minimum annual increment (Mg ha^{-1} y^{-1})[a]	1.9 ± 1.4	2.4 ± 1.8	2.3 ± 1.6	2.5 ± 2.0	2.5 ± 2.0
Maximum annual increment (Mg ha^{-1} y^{-1})[b]	2.2 ± 1.6	2.8 ± 2.1	2.7 ± 1.8	2.9 ± 2.3	2.8 ± 2.3
Mean planned stand AGB (Mg ha^{-1})	171.2 ± 125.7	223.5 ± 164.7	214.3 ± 143.2	227.2 ± 181.3	224.1 ± 179.7
Minimum annual increment (Mg ha^{-1} y^{-1})[a]	3.0 ± 2.2	3.9 ± 2.8	3.7 ± 2.5	3.9 ± 3.1	3.9 ± 3.1
Maximum annual increment (Mg ha^{-1} y^{-1})[b]	3.4 ± 2.5	4.4 ± 3.3	4.3 ± 2.9	4.5 ± 3.6	4.5 ± 3.6

[a] Mean annual growth if the plantations were 58 years old.
[b] Mean annual growth if the plantations were 50 years old.
[c] Data for twigs and leaves originates from Ola-Adams (1993) and Pendje (1993).

After 50 to 58 years, the mean DAB of 60 cm corresponds with the planned MLD (Humblet 1946). The 23-year old limba plantations already reached a DAB of approximately 37 cm, confirming the fast-growing character of this tree species (Mukendi 1973). While even-aged plantations are known for their normal diameter distribution, that distribution has become a normal curve with a right-hand tail, representing a few larger trees. Several causes could explain the large variation in DAB: presence of large, old natural limba trees (already present at time of initiating the plantations, cf. maximum DAB 155 cm), natural regeneration or small scale replanting with small understory trees (lack of light) (cf. minimum DAB of 10 cm), grouping of sample plots of slightly different ages (50-58 years) and different soil characteristics (amount of organic material, carbon, nitrogen, pH and soil texture). Sarlin (1963) found a correlation between tree growth and soil characteristics such as exchangeable bases and pH. However, this correlation is stronger in young plantations as older trees modify the soil, enriching it with some of the elements contained in its leaves, this process being in proportion to its rate of growth (Sarlin 1963). Finally, uncontrolled cuttings result in uneven competition, also contributing to the asymmetry of the diameter distribution.

A recent inventory (Maloti 2009, unpubl. data) of 29 ha within the core area of the Luki Reserve (natural primary and secondary forest) lead to a basal area of 21.6 m² ha^{-1} (diameter trees ≥ 15 cm), twice the value of the current basal area in the plantations (10.5 m² ha^{-1}). Of course, this inventory occurred in a natural forest with a vertical stratification (even without measuring the smallest diameters) while plantations are mostly characterized by one tree layer (with no or little understory growth) and fixed planting distances.

One of the main characteristics of limba is the presence of large buttresses. As trees grow taller, their crowns get exposed to the stronger winds in the upper canopy layer, resulting in larger buttresses to assure mechanical stability. The significant correlation between DAB and the height of buttresses also occurs in other tree species (Woodcock et al. 2000). While Woodcock et al. (2000) fitted a second-order polynomial with an upper limit around 450 cm, the exponential regression model based on DAB and buttress height of limba trees doesn't impose an upper limit. The largest limba tree in this inventory had a DAB of 155 cm and can be considered as rare (only 2 trees with D > 150 cm). The calculated upper height of buttresses is 580 cm, an estimate that still corresponds with the inventory results. The type of regression can be considered as species-specific.

The maximum total tree heights of 40 to 50 m, found in natural forests (Groulez and Wood 1985), are met in 9 % of the total tree height measurements so planted limba trees can reach heights comparable to those of natural trees. Groulez and Wood (1985) and Lamprecht (1989) mention normal heights for adult trees of 30 m thus the studied plantations can be considered as mature and appropriate for exploitation. For commercial purposes, bole height and ratio between bole height and total tree height are more important. Bole heights varying from 20 to 25 m are considered as high and found in mature forests as well as the plantations under study (Groulez and Wood 1985). Tutula (1968) measured heights in 14- to 18-year old plantations, resulting in portions of 72 to 79 % branch-free tree height. The corresponding bole heights were 17 to 21 m (0.8 to 1.2 m y^{-1}), once more confirming the pioneer character of the species, i.e. fast growth during the first years. The current value of 78 % indicates that the portion of bole height remains constant after the first 20 years and corresponds with the values of Groulez and Wood (1985), namely between 0.7 and 0.8. Notwithstanding the wide planting distances, this species has an excellent natural pruning capacity and a high percentage of valuable stem timber. Compared to teak (*Tectona grandis* L. f.), where only a 60 % ratio was obtained after an intensive pruning program (Víquez and Pérez 2005), the management of limba plantations might be less labour-intensive and costly.

Furthermore, the DAB-height curve of natural uneven-aged forest has a typical point of inflection (Rondeux 1999). Although the plantations are not perfectly even-aged (50-58 years), the DAB-height curve has the classic shape of even-aged forests, without a point of inflection.

2.4.2 Commercial volume

In tropical regions, the determination of form factors is not obvious and therefore, little information is available, leading to significant overestimates in volume and biomass. Very often, limba is described as a tree species with a cylindrical stem (e.g. Humblet 1946). However, Mabela (1978) suggested a form factor of 0.7 for limba, very close to the mean measured value of 0.68.

The objectives at the time of initializing the plantations differ considerably depending on the author. Humblet (1946) estimated the mean total tree volume of a mature tree at 6 m³. Limba trees would reach maturity around 50 – 60 years in plantations where half of the original density was cut by thinning interventions, leaving 52 trees ha^{-1} for the final exploitation (Humblet 1946). Tutula (1968) and Lamprecht (1989) estimated the total volume without defects not less than 200 m³ ha^{-1}. Groulez and Wood (1985) predict rotation periods of 40 years in the most favourable conditions and 65 years in less favourable conditions. In general, a final density around 52 trees ha^{-1} with a total tree volume around 6 m³ is assumed after 50 – 60 years. The expected total stand volume would fluctuate around 300 m³ ha^{-1}, hence the estimated commercial volume would be about 230 m³ ha^{-1}. Today, the mean DAB of 60 cm coincides with the MLD at an age between 50 and 58 years, obtaining the expected values without the support of the scheduled management interventions. The actual mean commercial volume easily passes 5 m³ per tree so the mean total tree volume will also reach the proposed 6 m³ per tree, taking into account the bole/tree height ratio of 0.78.

Most likely, the commercial volume per tree was not heavily influenced by recent density losses, i.e. after the first 30 years following the installation. Within that period, limba has terminated its main growth period and the largest losses in plant density took place. Cutting trees after 30 years won't have a major impact since growth already culminated (pioneer species). In addition, the canopy closure is incomplete so multiplying the individual volume with the actual (n=33) or the planned density (n=52), can only create small or no overestimates of the planned volume. Thus, the estimated planned commercial volume (290 m³ ha^{-1}) could be larger than the proposed commercial volume of 230 m³ ha^{-1} (Table 2.2).

In reality, illegal harvesting and natural die-off even surpassed the number of trees that would have been cut by thinning operations, so that the present volume of the plantations is lower than the proposed commercial volume. At the tree level, all expectations were fulfilled. Where management seemed to have no major impact on the accomplishment of the MLD, thinning operations are recommended to obtain the proposed commercial volume. The hypotheses of Humblet (1946) and Tutula (1968) proved to be very accurate but did not entirely succeed at the stand level without a minimum of forest management.

One of the main reasons in the 1950s to install plantations, was the low density of exploitable trees, only 15 - 35 m³ ha^{-1} in natural forests (Humblet 1946; Tutula 1968). The present mature plantations with commercial volumes of 184 m³ ha^{-1} offer an alternative that can lower the pressure on natural forests by providing enough exploitable trees.

When comparing volume estimates with other plantations and natural forests, one should always keep in mind forest characteristics that determine the volume: age, soil, climate, elevation, purpose and presence of management. Table 2.4 lists volume estimates for other limba plantations, plantations with other African indigenous species, hardwood plantations (teak), pulp and fuelwood plantations (*Eucalyptus* and *Acacia* sp.) with exotic species and natural secondary forests.

Table 2.4. Commercial volume estimates in tropical plantations and natural forests. Comparison with the current results is based on this table.

Forest type	Country	Density (ha^{-1})	Age (y)	Tree volume (m³)	Stand volume (m^3 ha^{-1})	Volume increment (m^3 y^{-1} ha^{-1})	Author
Limba plantation	Rep. of Congo	-	35 – 40	-	180.0	4.0 – 4.5	Marien and Mallet (2004)
Limba plantation	Rep. of Congo	72	41	1.8	130.1	3.2	Groulez and Wood (1984)
Limba plantation	Ivory Coast	-	20	-	240.0	12.0	Dupuy et al. (1999)
Terminalia ivorensis plantation	Ivory Coast	-	32	-	192.0	6.0	Dupuy et al. (1999)
Aucoumea klaineana plantations	Gabon	-	15 – 51	-	-	2.0	Marien and Mallet (2004)
Triplochiton scleroxylon plantation	Ivory Coast	-	24	-	264.0	11.0	Dupuy et al. (1999)
Teak plantation	Ivory Coast	-	68	-	231.2	3.4	Dupuy et al. (1999)
Teak plantation[a]	India	-	60 – 80	-	240.0 – 640.0	4.0 – 8.0	Evans and Turnbull (2004)
Teak plantation[a]	India	-	40 – 60	-	40.0 – 360.0	1.0 – 6.0	Beghagel and Monteuuis (1999)
Eucalyptus globulus plantation[a]	Australia	1515	11	< 0.1	71.3	6.5	Forrester et al. (2004)
Eucalyptus saligna plantations[a]	Cameroon	Ca. 1000	11 - 19	Ca. 0.2 – 1.0	154.5 – 980.5	14.1 – 51.6	Fonweban and Houllier (1997)
Pinus caribaea plantation	Australia	2204	9.3	0.1	145.1	15.6	Evans and Turnbull (2004)
		1680	9.3	0.1	130.9	14.7	
		747	9.3	0.1	103.2	11.1	
Acacia mearnsii plantation[a]	Australia	1515	11	< 0.1	76.3	6.9	Forrester et al. (2004)

[a] Total instead of commercial volume.

Primary forest is not neighbouring the plantations but the presence of secondary forest in plantation gaps allows comparing with secondary forests and woodlands. While middle-aged limba plantations in the Republic of Congo have lower or similar volumes (Marien and Mallet 2004), younger plantations in Ivory Coast have exceptional high growth values (Dupuy et al. 1999). Management interventions, together with other climate and soil conditions, explain the success of these plantations. Framiré (*Terminalia ivorensis* A. Cheval) and obeché (*Triplochiton scleroxylon* K. Schum.) plantations also produce more volume at a younger age in West Africa (Dupuy et al. 1999) while the production of okoumé is inferior to the limba plantations (Marien and Mallet 2004).

Teak (*Tectona grandis* L. f.) is a widely planted species, known for its durable timber. Although the applications of limba and teak differ considerably, they both are hardwood species, found in plantations with a rather long rotation period (40 to 60 years). In Ivory Coast, the situation of teak plantations is highly comparable to limba (Dupuy et al. 1999). The volume production of the limba plantations also falls within the range of volume production of teak plantations in India, keeping in mind that the total volume production is higher than the commercial volume production (Beghagel and Monteuuis 1999; Evans and Turnbull 2004). Unfortunately, no or little information is available on planting densities.

Species for the production of pulp or fuelwood should grow very fast but criteria like merchantable height, straightness of stem or presence of defects are less important. Enormous densities are planted to obtain a large stand volume with very high volume increments in a short period of time. Considering the different purposes of these plantations, comparison should be made with caution.

2.4.3 Aboveground biomass

Compared to other species, limba has a very low portion of crown biomass (large branches, twigs and leaves). For 30 year old *Nauclea didderichii* plantations, the crown biomass accounts for 16 % (Onyekwelu 2007). The crown biomass of teak plantations varies from 18 to 25 % (Kraenzel et al. 2003).

Pendje (1993) measured a crown biomass of 19 % in the 35 years old limba plantations of Luki. The older the plantations, the smaller the crown portion as a result of good natural pruning capacities. Ola-Adams (1993) estimates the crown biomass around 3 % in very dense and 7 % in the less dense Nigerian stands of limba. The larger the planting distances, the higher the portion of crown biomass (power law regression based on Ola-Adams (1993)), leading to a percentage of approximately 11 % for the crown biomass in the old plantations under study (with a plant density of 33 trees ha^{-1}). This is higher than the results of the 8 measured crowns (7.2 %), possibly because these trees were on average less vital. The exact age of the 8 sample trees is not known. Although the trees reach comparable heights, their DAB is always inferior to the mean DAB in the old plantations. Thus, the real crown portion for old limba plantations is most likely higher than 7 % but no more than 11 % in vital trees.

The range of AGB estimates based on field data and existing models (Eqs. 2.2-2.5) is quite large (108 to 144 Mg ha^{-1}). Without weights and direct measures of the specific gravity, it is difficult to decide which method should be used. Therefore, the range of AGB estimates will be compared with previous studies.

In comparison to most African natural forests (Table 2.5) (Brown, 1997), the stored AGB of limba plantations is low. The estimated planned AGB (52 trees ha^{-1}) is slightly smaller than the AGB of natural forest in the Luki Biosphere Reserve before silvicultural treatment (C. Couralet, pers. comm., 2008).

Unfortunately, other biomass estimates for old plantations are rare. Therefore, comparisons could only be made with younger plantations. Ola-Adams (1993) proves that the largest density of limba trees results in the largest stand biomass. Most teak plantations (Kraenzel et al. 2003; Ola-Adams 1993) and pulp and fuelwood plantations with *Acacia* spp. and *Eucalyptus* spp. accumulate AGB at a faster rate than limba plantations (Bernhard-Reversat et al. 1993; Forrester et al. 2004). Thus, the old limba plantations with only 33 trees ha^{-1} are less favourable for biomass and carbon storage.

A higher planting density for limba trees would increase the AGB and carbon stored (as confirmed by Ola-Adams (1993)) but a study on the trade-off between commercial and conservation issues is necessary to determine which planting density still produces trees with an acceptable DAB and quality for industrial processing. Kalonji (1968) concluded that small planting distances (5 x 5 m or 400 trees ha^{-1}) result in closed stands with excellent natural pruning and straight stems. Limba plantations with large (12 x 12 m) or intermediate planting distances of 4 x 8 m (313 trees ha^{-1}) showed more stem deformations and were suppressed by natural secondary species. Nevertheless, when plantations with intermediate planting distances were managed, they had the highest DAB and bole height (Kalonji 1968). Kalonji (1968) conducted his study in the same area and the same species as in the current study. So adapting Kalonji's intermediate planting distances with a management plan (as proposed by Marien and Mallet (2004)), could promote diversity (natural occurrence of secondary species) as well as creating larger commercial stand volumes and more AGB and carbon storage.

Table 2.5. AGB estimates in tropical plantations and natural forests. Comparison with the current results is based on this table.

Forest type	Country	Density (ha^{-1})	Age (y)	Tree AGB (Mg)	Stand AGB ($Mg\ ha^{-1}$)	AGB increment ($Mg\ y^{-1}\ ha^{-1}$)	Author
Limba plantations	Nigeria	3086	13	< 0.1	127.7	9.8	Ola-Adams (1993)
		1276	13	0.1	112.0	8.6	
		567	13	0.2	82.7	6.4	
		269	13	0.3	77.0	5.9	
Nauclea diderrichii plantations	Nigeria	496	30	0.6	279.1	9.3	Onyekwelu (2007)
Teak plantation	Panama	624	20	0.3	209.0	10.5	Kraenzel et al. (2003)
Teak plantation	India	-	30	-	76.9	2.6	Karmacharya and Singh (1992)
Teak plantations	Nigeria	5328	18	0.1	288.2	16.0	Ola-Adams (1993)
		2551	18	0.1	275.1	15.3	
		1189	18	0.3	360.1	20.0	
		638	18	0.3	199.5	11.1	
Acacia mearnsii plantation	Australia	1515	11	< 0.1	75.8	6.9	Forrester et al. (2004)
Acacia sp. plantations	Rep. of Congo	698	7.5	0.1	94.6	12.6	Bernhard-Reversat et al. (1993)
Eucalyptus globulus plantation	Australia	1515	11	< 0.1	47.1	4.3	Forrester et al. (2004)
Moist forest	Cameroon	-	-	-	310.0	-	Brown (1997)
Gallery forest	Gambia	-	-	-	140.0	-	Brown (1997)

2.4.4 Conclusion and perspectives

The planned commercial volume for the final exploitation wasn’t entirely realized, especially due to the low density. Still, individual commercial volumes exceeded the planned values, while 80 % of the planned stand volume is present in the plantations. Thus, the mature limba plantations are quite successful with regard to the initial goals. Looking at commercial volume and the production of quality timber with merchantable dimensions, limba can compete with other indigenous species (e.g. *Terminalia ivorensis, Aucoumea klaineana*) and also teak plantations of the same age, having the advantage of larger merchantable heights and less intensive management interventions. Other exotic species as *Eucalyptus* spp. and *Pinus caribaea* Morelet have higher production rates, but can not be used for the same applications as limba and teak. In Central Africa, where the means for an intensive management of exotic plantations are often absent, indigenous species like limba will continue to play an important role due to their natural pruning capacities, the absence of infections and the ease of installing tree nurseries. In addition, the mature limba stands provide a sufficient volume production to lower the pressure on the surrounding natural forests.

Limba plantations store AGB, including carbon (especially in their stems due to the large merchantable height and small crowns), but are not preferred when sequestration is the main goal. In this case, *Nauclea diderrichii* is the preferred indigenous species (unpubl. data; Onyekwelu 2007), next to exotic species as teak, *Eucalyptus* spp. and *Acacia* spp.

Homogeneous plantations are still installed but regarding the public pressure on the Congolese limba plantations, it is advisable to add other secondary species -already naturally present- creating mixed plantations (e.g. *Albizia ferruginea* (Guill. and Perr.) Benth., *Musanga cecropioides* R. Br. ex Tedlie and *Petersianthus africanus* (Welw. ex Benth. and Hook. f.) Merr.). Dupuy and Mille (1993) wrote a comprehensive manual on the association and compatibility of species (e.g. *Terminalia superba* and *Triplochiton scleroxylon*), the comparative growth and the silvicultural consequences of mixed African plantations. Mixed plantations can also store a larger amount of volume, AGB and carbon compared to homogeneous plantations (Forrester et al. 2004). Within a sustainable management plan, secondary species could be used at the local and national scale (sustainable livelihood, charcoal), leaving limba for industrial applications and export. Additionally, limba trees will quickly create a forest climate and, together with this, optimal conditions for the germination of tree species of climax forests.

Chapter 3

A tree-ring based comparison of *Terminalia superba* climate-growth relationships in West and Central Africa

Abstract

Tropical lowland forests are characterized by humid climate conditions with interannual variations in amount of precipitation, length of dry season, and relative humidity. The African tree species, *Terminalia superba* Engl. & Diels has a large distribution area and potentially incorporates these variations in its tree rings. Tree ring analysis was performed on 60 plantation trees (increment cores) and 41 natural trees (stem disks) from Ivory Coast and the Congolese Mayombe Forest. Natural forests and old plantations (50-55 years) showed similar growth patterns. Regional chronologies were developed for the two sample regions and showed a long-distance relationship for the period 1959-2008. Growth in the Mayombe was associated with early rainy season precipitation, but no relation was found between tree growth and precipitation in Ivory Coast. Congolese trees possibly show a higher climate-sensitivity than Ivorian trees, because precipitation in the Mayombe is more limiting and Congolese *T. superba* trees are found closer to the margins of their distribution. Likewise, tree growth in the Mayombe was also influenced by the SSTs of the Gulf of Guinea and the South Atlantic Ocean during the early rainy season. However, tree growth was influenced by ENSO in both regions. In the Mayombe, La Niña years were associated with stronger tree growth whereas in Ivory Coast, El Niño years corresponded with stronger tree growth. The presented relation between ENSO, precipitation and tree growth is original for equatorial African forests, suggesting an influence of global climate variability on tree growth.

Published in Trees

De Ridder M, Trouet V, Van den Bulcke J, Hubau W, Van Acker J, Beeckman H (2013). A tree-ring based comparison of *Terminalia superba* climate-growth relationships in West and Central Africa. Trees (doi: 10.1007/s00468-013-0871-3, online since March 2013)

3.1 Introduction

Tropical climates are characterized by high temperatures, humidity and precipitation, light frosts and an average temperature of at least 18°C during the coolest month (McKnight and Hess 2000). However, tropical climates are far from homogeneous and large differences in precipitation periodicity, amount of precipitation, air humidity and annual temperature occur, related to the distance from the equator, ocean and altitude (McKnight and Hess 2000; van Oldenborgh and Burgers 2005). Within the Köppen–Geiger climate classification, these differences result in three tropical climate subtypes: equatorial, monsoon and savannah climates (Köppen and Geiger 1930). Notwithstanding these climatic difference, several tree species have a broad distribution area within the tropics and are able to grow in diverse climate types. Furthermore, they can grow in a large range of local site conditions, including dense mixed forest stands and widely spaced manmade plantations (CTFT 1983). Light-demanding species such as *Terminalia superba* Engl. & Diels (Groulez and Wood 1985) are expected to be sensitive to such variability in climate and site conditions. The link between light-demanding trees and significant climate correlations was already presumed in the 1920s (Douglass 1920).

Dendrochronology in tropical regions has a history of more than 100 years (Worbes 2002), but a lot more tree-ring research was conducted in tropical forests of Latin America and Asia than in Africa. Several studies on different species resulted in tree-ring chronologies that were verified with radiocarbon dating (Worbes et al. 2003) or with relations to climate (Bräuning et al. 2009; Brienen and Zuidema 2005; Dünisch et al. 2003; Pumijumnong et al. 1995; Worbes 1999). For the African continent, tree-ring chronologies were mostly developed for semi-arid savannas (Fichtler et al. 2004; Gebrekistos et al. 2008; Gourlay 1995), the miombo woodlands in southern Africa (Stahle et al. 1999; Trouet, et al. 2001, 2006, 2010) and Ethiopia (Couralet et al. 2005; Sass-Klaassen et al. 2008; Wils et al. 2011). However, the number of exactly dated tree-ring chronologies from West and Central African species is limited (Couralet et al. 2010; Schöngart et al. 2006; Worbes et al. 2003), despite clear potential as pointed out by the exploratory research by Hummel (1946) and Détienne and Mariaux (1970, 1975, 1976, 1977). For the tropics, especially the work of Détienne and Mariaux was important because they showed the existence of annual tree rings in different climates and countries by applying cambial wounding, phenological observations, and monthly diameter measurements. More recently, Tarhule and Hughes (2002) published a list of West African species with dendrochronological potential. Only 7 out of more than 70 species were labelled ‘potentially useful’. This means that these species have distinctive annual rings that are consistent throughout the stem cross section (easy to identify and verify by independent persons), have minimal or absent ring wedging, were successful cross-dated at least for some radii and show variable ring-widths, indicating possibilities for dendroclimatology. All of this indicates that potential exists but the choice of study species is limited.

The majority of dendroclimatological studies in tropical regions focus on one climate type and compare tree growth of different species within this climate, e.g. Devall et al. (1995) and Brienen and Zuidema (2005). Still, when tree ring analysis is applied and results in long time-series, it offers a powerful tool to analyze the responses of trees, species and stands to different and changing climatic conditions. Detailed knowledge on the growth patterns of tropical tree species can thus be obtained, that is necessary for reforestation programs and REDD+ files (reduced emissions from deforestation and degradation). In addition, tree ring time-series enable the development of dated proxies for climate reconstruction (Schöngart et al. 2006; Therrell et al. 2006) and can extend instrumental climate time-series that are often sparse in tropical regions. The comparison of those climatic reconstructions based on tree rings with atmospheric circulation patterns, sea surface temperatures (SSTs) and the El Niño – Southern Oscillation (ENSO) provides a useful bridge between past and future trends in global climate change and its implications for human welfare and socio-economic development (Boninsegna et al. 2009).

The interannual precipitation variability in West Central Africa is extremely complex, contrary to the rest of tropical Africa, where the variability is coherent over very large sectors (Balas et al. 2007). Research on the causes of this variability has been focused on teleconnections with tropical SSTs rather than on land-atmosphere interactions (Joly et al. 2007). The SSTs of the equatorial Pacific (Balas et al. 2007; Camberlin et al. 2001; Joly et al. 2007; Paeth and Friederichs 2004), the tropical Atlantic in general (Camberlin et al. 2001; Paeth and Friederichs 2004), and the Benguela Coast including the Gulf of Guinea in particular (Balas et al. 2007; Paeth and Friederichs 2004; Joly et al. 2007) are among the most important factors governing the interannual variability in western and equatorial Africa. The influence of these oceans is seasonally dependent (Balas et al. 2007) and resulting relations also vary between studies based on the season, the time span, the study region, and the methods selected for analysis.

Moreover, the abovementioned anomalies of SSTs of the equatorial Pacific Ocean are generally used to calculate ENSO indices (Trenberth 1997). ENSO is the result of the coupling between oceans and the atmosphere (Nicholson and Entekhabi 1987), but most ENSO indices, including the Niño3.4 index, are based on anomalies of SSTs in the region between 5°N–5°S and 120°–170°W (Trenberth 1997). Camberlin et al. (2001) studied the gridded response of African precipitation on Niño3 indices and found no consistent large-scale relation in West Africa. Surprisingly, they observed a clear negative relation in March-June and August-November in western equatorial Africa (Cameroon, Gabon, Republic of

Congo and the coastal region of the Democratic Republic of Congo (DRC)), a region which had never before been shown to exhibit significant correlations with ENSO.

The studied species is *T. superba*, a long-lived pioneer tree species, characterized by large buttresses and typically found in secondary forests and fallows (Groulez and Wood 1985; Hawthorne 1995; Humblet 1946; Swaine and Whitmore 1988). This tree species has a large range of distribution on both hemispheres (from Sierra Leone to Angola) (Groulez and Wood 1985). The climate within this region (dry season with < 60 mm monthly precipitation in at least three months (Worbes 1995)) is believed to provoke the formation of yearly growth rings. Moreover, *T. superba* was also planted over vast areas, including DRC, and the known planting dates allowed for exact dating and confirmation of the annual character of tree rings in this species (see also Chapter 2). The formation of tree rings was already studied by Mariaux (1969), who used periodic woundings and dendrometers to monitor tree growth, but his study was limited to less than 20 trees younger than 20 years. Therefore, proper cross-dating and comparison with climate was not possible. Worbes et al. (2003) also used *T. superba* discs and wood cores from Cameroon yet without climate matching. In our study, tree rings of *T. superba* from old plantations (ca. 50 to 55 years old) and natural forests in the Mayombe Forest (southern hemisphere) and western Ivory Coast (northern hemisphere) were analyzed in combination with climate data to analyze the following hypotheses:

(1) Planted and natural *T. superba* trees in the Congolese Mayombe Forest reveal different growth patterns due to different sites and/or different responses to climate. Cross-dating can be used to distinguish if growth trends are common or not in planted and natural trees.

(2) The growth of *T. superba* is influenced by climate at three levels: local (precipitation), regional (SST anomalies) and global (ENSO events).

(3) The presence and strength of climate-growth relations depend on the location of the forest regions. The relation between climate and growth at the three levels is not necessarily similar in the Mayombe and Ivory Coast.

3.2 Material and Methods

3.2.1 Study sites

All study sites belong to the Guineo-Congolian regional centre of endemism (White 1983). The Ivorian study sites are classified as evergreen moist rainforest, but the Congolese study sites are situated within a drier semi-evergreen rainforest.

The three Congolese study sites (Luki, Monzi and Tshela, Fig. 3.1) are located at the southern border of the Mayombe Forest that covers the western parts of Gabon, the

Republic of Congo, DRC and Cabinda (Angola). Two study sites were chosen within the UNESCO Man and Biosphere Reserve of Luki (05°30' to 05°45' S and 13°07' to 13°15' E). The first study site (Luki) was a natural forest stand close to the climate station of the reserve and the second study site was located at a distance of 15 km in a plantation of *T. superba*, established between 1955 and 1957 in the village of Monzi. Plantations were installed on clear-felled areas, at planting distances of 8 x 12 m. After the installation, no structured management was carried out. Natural regeneration of *T. superba* and other species took place after a few years (see Chapter 2). A third study site was selected in a natural forest stand near Tshela, about 70 km to the north. All study sites were situated at altitudes < 300 m above sea level. The region is characterized by a dry season of approximately five months (May to September-October) and a short period with less precipitation during the rainy season (January – February). The proximity of the ocean, manifested by a strong nebulosity, buffers the intensity of both dry periods. Relative humidity remains more or less constant throughout the year (84% in the rainy season, 82% in the dry season). The average annual precipitation, based on precipitation data from 1959 to 1996 is 1168 mm, but some years are particularly dry (Fig. 3.1). For instance the annual precipitation in 1972 and 2002 was less than 800 mm and the lowest values were registered in 1954, 1978 and 1997 with annual precipitation values of respectively 657, 692 and 626 mm. Temperatures oscillate around 26 °C in the rainy season and drop to a minimum of 20 °C in the dry season. The soils of the Luki Reserve are classified as orthic Ferralsols, but Tshela is characterized by ferric Acrisols (FAO 2008). Most soils are argillaceous with a pH between 4 and 6 and a C/N between 4 and 9.

In western Ivory Coast (06°07' to 07°15' N, 07°30' to 08°15'W), the four study sites (Scio, Bin Houye, Goya and Danane, Fig. 3.1) are located in natural forests. The forest of Scio can be considered as primary forest whereas the forests of Goya, Bin Houye and Danane are secondary forests, often with cacao plantations in the understory. Unlike in DRC, study sites were widespread and sometimes more than 100 km apart. Moreover, no central climate station was available and data (including monthly precipitation and temperature) from six surrounding climate stations (Table 3.1, Fig. 3.1) were therefore averaged. Ivorian climate data were extracted from the KNMI explorer (van Oldenborgh and Burgers 2005). In this region, the dry season generally lasts for three months (December to February). In July and August, a period of less precipitation is observed. Relative humidity drops from approximately 88% during the rainy season to approximately 70% during the dry season. The average annual precipitation, based on precipitation data from 1959 to 1996, is 1650 mm. Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March (van Oldenborgh and Burgers 2005). Study sites were situated between 200 and 370 m above sea level. Soils have a pH between 4 and 7, a C/N of

8 to 12 and are classified as Ferralsols and Acrisols, i.e. typical acid soils of tropical lowlands (FAO 1986).

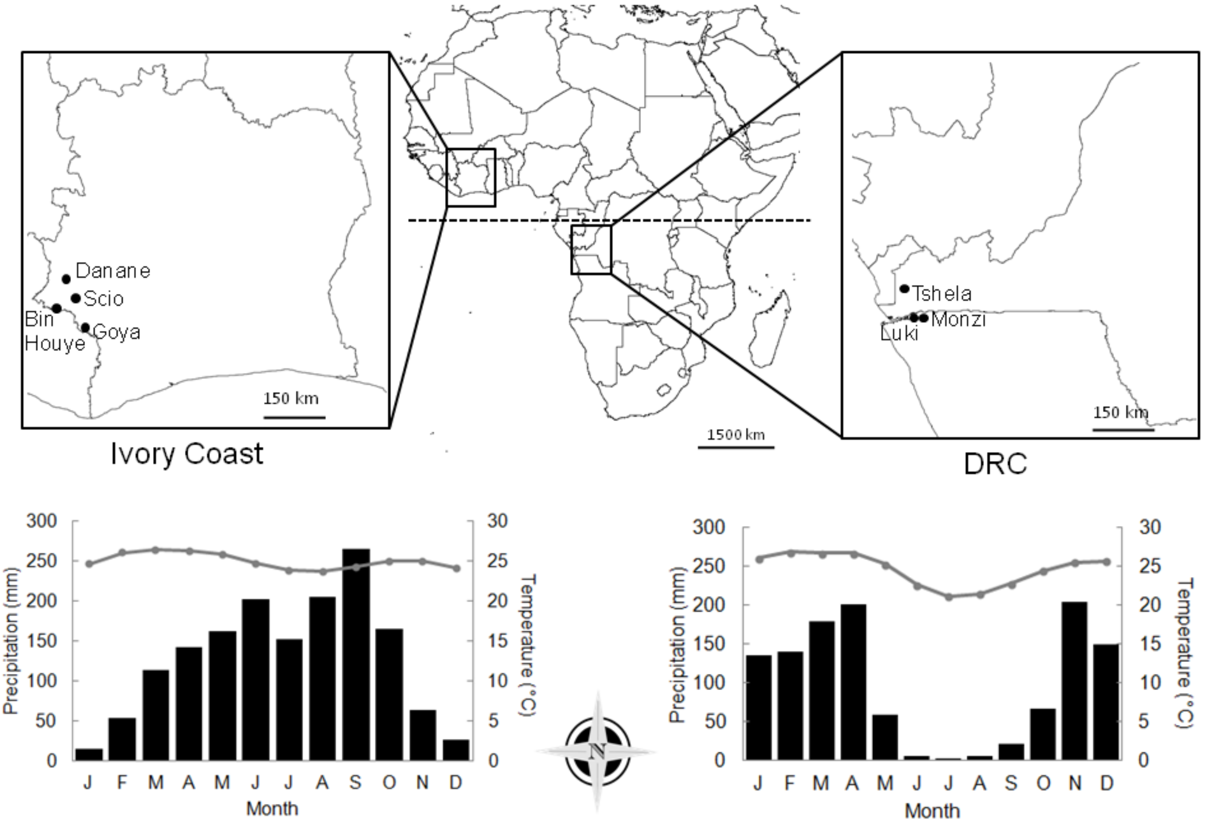


Fig 3.1. Geographical location of all study sites in Ivory Coast and the Mayombe Forest in the Democratic Republic of Congo (DRC) with a climate diagram for the Mayombe Forest (climate station of Luki, 1959-1996) and Ivory Coast (regional climate average from 6 climate stations, 1959-1996, extracted from the KNMI explorer (van Oldenborgh and Burgers 2005); for temperature data only two stations, Man and Gagnoa, provided data from 1959 to 1984). The dashed line represents the equator.

Table 3.1. Characteristics of climate stations around Ivorian study sites and the Mayombe (station, precipitation, period of observations, dry season (< 60 mm), distance to the closest study site). The common timespan in all stations is from 1959 to 1996.

Station	Region	Annual precipitation (mm)	Dry season	Distance to closest study site (km)
Daloa	Ivory Coast	1256	Nov-Feb	140 (Goya)
Guiglo		1644	Nov-Feb	52 (Scio)
Man		1607	Nov-Feb	58 (Danane)
Soubre		1401	Dec-Jan	110 (Goya)
Toulepleu		1668	Dec-Feb	25 (Bin Houye)
Nzerekore	Guinea	1838	Dec-Feb	100 (Danane)
Luki	Mayombe	1168	May-Sep	5 (natural forest of Luki)

3.2.2 Sampling strategy

A total of 41 stem discs was collected from natural forests in the Mayombe and western Ivory Coast (one stem disc per tree). In Monzi, two perpendicular wood cores were taken per tree, resulting in a total of 120 cores from 60 planted trees (Table 3.2). Cores were taken above the buttresses where possible. All samples were air-dried to prevent fungal infestation. Wood cores were frozen for two weeks to prevent insect infestation. Stem discs were too large for freezing and therefore only superficially disinfected before storage in the Tervuren Xylarium. All discs and cores were sanded with gradually increasing grid from 50 to 600 or 1200.

Table 3.2. Summary of the sampling campaigns in the Mayombe and Ivory Coast.

Study site	Region	Number of sampled trees	Date sampling
Luki	Mayombe	5	Oct-Nov 2005
Monzi		60	Aug 2007
Tshela		7	Jun 2008
Scio	Ivory Coast	8	Jan 2009
Goya		8	
Danane		6	
Bin Houye		7	

3.2.3 Tree ring analysis

Before measurement, all tree ring boundaries were marked with pencil under a stereomicroscope or magnifying glass. On stem discs, three radii were chosen and every tenth ring was followed along the circumference to check for ring anomalies. In case of anomalies (false rings and particularly wedging rings), every tree ring in this zone was followed separately. When unclear, the particular ring number(s) were archived to facilitate corrections during subsequent tree-ring analysis. Ring widths were measured to the nearest 0.01 mm using a stereo-microscope and a Lintab measuring device with TSAP-Win software (Rinn 2003).

The age of plantation trees was compared with the planting period if two conditions were fulfilled: at least one of the two wood cores included the pith and the trees were sampled within the fixed planting scheme of 8 x 12 m. Outside of this scheme, *T. superba* trees could be regenerated naturally or planted later. If the age corresponded with the planting period, tree rings were considered annual (Stahle 1999).

Temporal correspondence between the various tree ring series was checked by cross-dating (Douglass 1941). Cross-dating is a technique that ensures that each individual tree ring is assigned to the exact year of its formation. This is accomplished by matching patterns of wide and narrow rings between cores/radii from the same tree. Subsequently, the tree ring series of each tree are merged into an average tree ring series and then cross-dated with the other trees of the same site. Successful cross-dating of several trees indicates that there is a common external factor influencing the growth of these trees (Cook and Kairiukstis 1990; Worbes 1995). Those trees can then be averaged to a site chronology or even to a regional tree-ring chronology.

Two statistical parameters are taken into account to evaluate the success of cross-dating: the Pearson's correlation (r) and the t-value of Baillie-Pilcher (Baillie and Pilcher 1973). Another non-statistical parameter is *Gleichläufigkeit* (Eckstein and Bauch 1969) or percentage of parallel run (ppr), which reflects the percentage of oscillations in the same direction within the overlapping interval. Still, especially for tropical trees, visual control and expert knowledge of *Terminalia* wood anatomy and tree rings are indispensable. The work of Trouet et al. (2010) is referred to for a detailed explanation on the lower thresholds for ppr (≥ 60%) and t-values (≥ 2) in tropical trees compared to temperate regions. Autocorrelation (AC) was checked to filter possible age trends and standardize the tree ring series to enable dendroclimatological analysis (Fritts 1976). For site and regional chronologies, series were standardized using a one-sided moving average over five years (Baillie and Pilcher 1973). The mean sensitivity (MS) of these standardized chronologies reflects the sensitivity of tree growth to a common external factor (Fritts 1976). For each site chronology, the expressed population signal (EPS) was also calculated (Haneca et al. 2005; Wigley et al. 1984) to quantifying uncertainty due to decreasing sample replication. As such, the EPS indicates how well the finite-sample chronology matches the theoretical population chronology. A value of 0.85 was considered as a reasonable limit for a reliable chronology (Wigley et al. 1984).

3.2.4 Analysis of climate-growth relationships

A climatological year was considered as a sequence of a dry and a rainy season. As such, climatological years for the Mayombe Forest were delimited from May_{n-1} to May_n where n is the calendar year to which the tree ring is assigned. For western Ivory Coast, years were delimited from December_{n-1} to December_n. First, annual, seasonal (dry/rainy season) and monthly precipitation data were correlated with regional tree-ring chronologies. Depending on the resulting Pearson's correlations, months were grouped to test the influence of the early rainy season, transition from dry to rainy season, etc. Precipitation data were derived from the aforementioned climate stations (Table 3.1, Fig. 3.1). In DRC, the regional chronology (plantation and natural forest chronologies combined) was correlated with precipitation data of the Luki station. The regional tree-ring chronology for western Ivory Coast was correlated with the mean precipitation data of six surrounding climate stations. Both growth-precipitation relations were calculated over the common time span limited by the length of the regional chronologies and precipitation time series (1959-1996).

We conducted spatial correlation analyses to study the influence of SSTs on precipitation and tree growth in the two regions. Spatial correlation maps were generated using the KNMI explorer (van Oldenborgh and Burgers 2005, Trouet and van Oldenborgh 2013; http://climexp.knmi.nl) and were based on gridded 5°x5°monthly and seasonal SST fields (Hadley Centre HadSST3; Kennedy et al. 2011a, 2011b). Correlations were calculated over the period from 1959 onwards. These correlation maps give a clear view on which oceanic regions influence precipitation patterns and tree growth.

Furthermore, we used the SST indices for the Niño3.4 region (Trenberth and Stepaniak 2001) to study ENSO influence on regional precipitation patterns and tree growth. For this purpose, we calculated spatial correlation maps between the annual (July-June) Niño 3.4 index and gridded 1°x1°monthly and seasonal precipitation fields (CRU T.S3.0; Mitchell and Jones 2005). ENSO signals in the regional tree-ring chronologies were analyzed following the method described in Schöngart et al. (2004, 2006). Two sample tests between tree growth in ENSO years and other years were performed (Schöngart et al. 2004, 2006). In this analysis, ENSO years were defined by 5-month running means of SST anomalies in the region of 5 °N–5°S and 120°–170°W exceeding +0.4 °C for 6 or more consecutive months (El Niño years) or -0.4 °C for 6 or more consecutive months (La Niña years) (Trenberth 1997).

3.2.5 Phenological data

Historical phenological data were available for the Congolese Mayombe study site (Couralet 2010). From 1948 to 1957, phenological data on 3750 woody plants were collected in Biosphere Reserve of Luki. Patterns of defoliation, flowering, fruiting and dissemination of fruits were studied, also for *T. superba* (n = 184 trees). These data were compared to precipitation and tree-ring chronologies within the overlapping timespan. No phenological data were collected or available for western Ivory Coast.

3.3 Results

3.3.1 Tree-ring related wood anatomy, ring anomalies and the use of wood cores

Tree rings were distinct and measurements were possible in the Mayombe as well as in western Ivory Coast. Tree rings in *T. superba* are also annual: this was confirmed by nine plantation trees that had the pith included in one of the wood cores and were located within the planting schemes. Those nine trees had ages comparable to the planting period, with differences between tree-ring dated and known planting age of up to three years. This discrepancy can be attributed to the sampling height and a more or less continuously active cambium during the first years, resulting in ill-defined or non-detectable tree-rings (Mariaux 1969). The structure of juvenile rings is somewhat different of other tree rings in Ivory Coast as well as the Mayombe: smaller vessels, less parenchyma and lighter fibre tissues. However, the anatomical structures of tree rings differed between the two regions. In general, with exclusion of the first juvenile rings, tree rings in the Mayombe (Fig. 3.2a) have mostly (sparse) aliform parenchyma. Banded parenchyma is sparse and when it is present, it is located in the middle and/or at the end of the tree ring. Confluent parenchyma is regularly present, but connects only a few vessels. Marginal parenchyma is distinct (Fig. 2a), but is often only present in most recent rings. The sharp transition between light and dark tissues (flattened fibres) in particular substantially simplifies tree-ring delineation. In Ivory Coast (Fig. 3.2b), tree rings were more undulating than in the Mayombe and transitions in colour were not as sharp. Ivorian stem *T. superba* wood contained a lot of parenchyma. In addition to a small amount of aliform parenchyma, the majority of tree rings contained confluent parenchyma, extending over several vessels. In the middle and at the end of tree rings, narrow parenchyma bands can occur. Marginal parenchyma bands were generally discontinuous and often hard to distinguish from other bands of parenchyma. In some tree rings, the anatomical structure was even inversed: flattened fibres (dark tissue) and banded parenchyma were found in the earlywood of the tree ring. In summary, tree-ring delineations were more complex on Ivorian stem discs.

Marking tree ring boundaries was rather straightforward in young trees (< 30 years), from both regions. Occasionally, the first rings showed intra-annual density variations but they were not considered problematic on stem discs because they were not present on the whole circumference. After a period of fast growth with wide tree rings, ring width drops significantly in the most recent rings. This decrease usually occurs gradually and could be linked to the age trend. False rings and double rings were easy to detect but wedging rings formed the main problem in identifying annual tree rings in *T. superba*. Wood cores from the planted trees in the Mayombe offered the opportunity to quantify these ring anomalies. A tree-ring chronology of stem discs from the natural Mayombe forest was developed (see below) and subsequently used to test through cross-dating if tree-ring series from wood cores were accurate enough to construct a tree-ring chronology. More than 28% of the measured wood cores showed no false or wedging tree rings upon comparison with the natural forest chronology. Those wood cores formed the foundation of a plantation chronology that spans from 1959 to 2007. On average, per tree, 1 false ring (3%) occurred and 0.5 ring (1%) was at least partially missing. In the latter case, the tree ring was visible on one wood core of a tree but not on the other one. Analysis of the exact location of tree-ring anomalies shows that 45% of the anomalies were found between the age of 21 and 30 years (0.15 anomalies/ring). In sections over 30 years, the number of anomalies decreased to 21% or 0.11 anomalies/ring (31-40 years), thus the most recent formed rings were not necessarily more sensitive to anomalous rings. However, plantation trees were not older than 55 years and wedging rings also caused many problems in 9 stem discs > 100 years. Unfortunately, quantifying these wedging rings was less straightforward due to the low growth rates and therefore, low visibility.

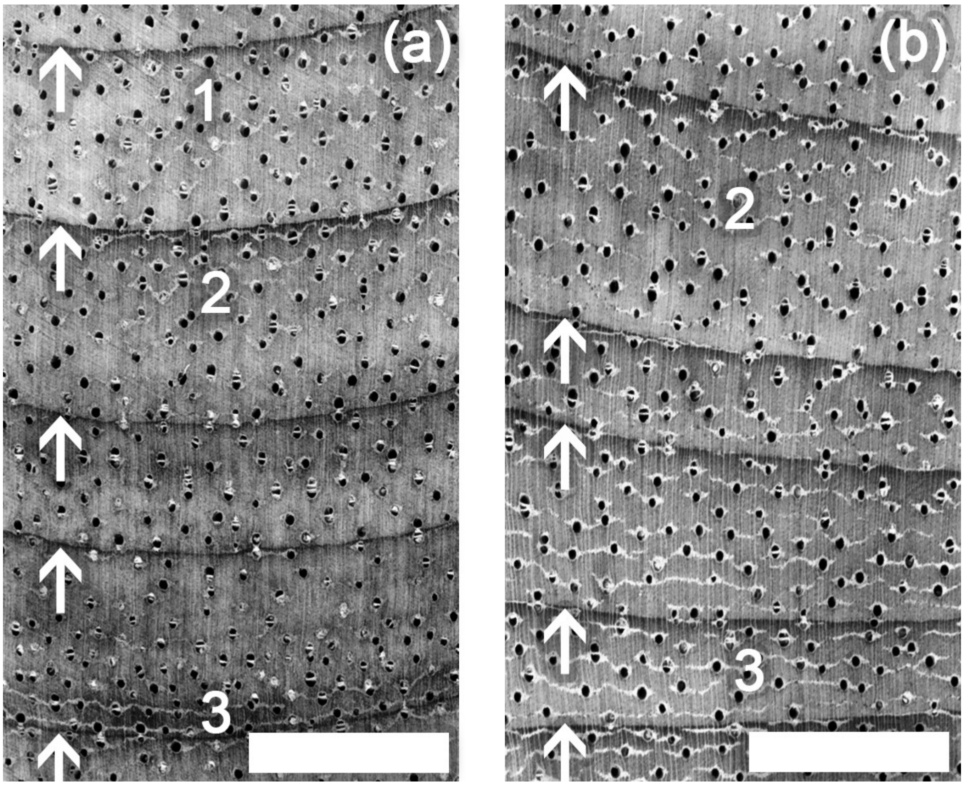


Fig 3.2. Transversal view on (a) Congolese *T. superba* tree rings with aliform (1) and confluent (2) parenchyma and (b) Ivorian tree rings with confluent parenchyma (2) and narrow bands of parenchyma (3). Tree-ring boundaries are marked. The white line represents 5 mm.

3.3.2 Growth patterns in natural and planted African forests

Cross-dating was successful at all sites in the Mayombe and Ivory Coast (Fig. 3.3) and site chronologies with a minimum of four contributing trees were developed for every site (Table 3.3). The t-value of the combination Luki – Tshela is not significant, but the ppr, inter series correlation and visual control confirm that a preliminary regional chronology covering the natural Mayombe forests can be constructed (Table 3.4, Fig. 3.4). The chronology of the plantation (Table 3.3, Fig. 3.4) was compared to this preliminary regional chronology, showing co-varying growth patterns ($r=0.89$; t-value=4.0; $p<0.001$). The regional chronology for the Mayombe thus includes all tree-ring series from the trees that were part of the site chronologies of Monzi, Luki and Tshela.

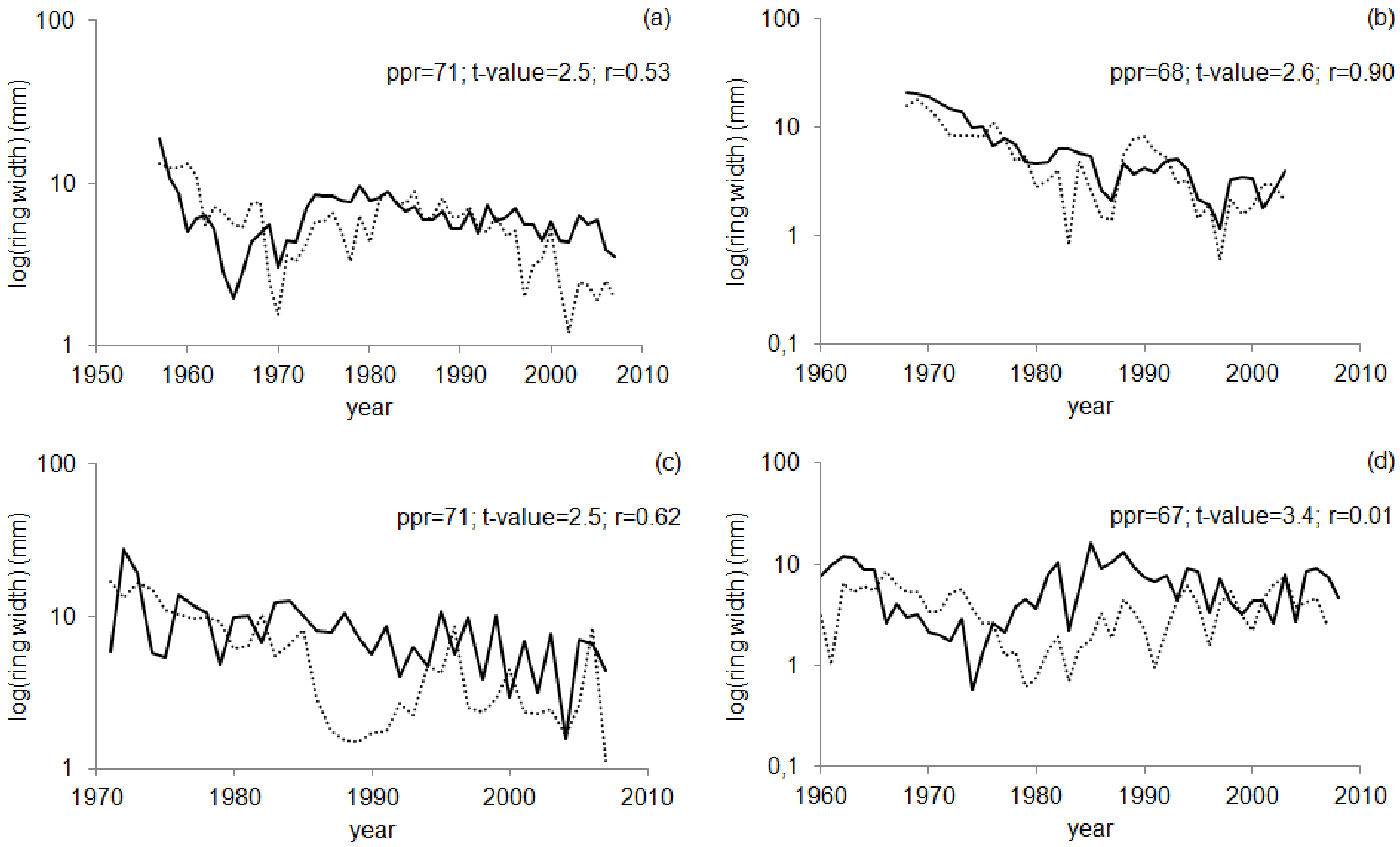


Fig 3.3. Selected examples of ring-width series with four pairs of trees from (a) the natural Mayombe forest, (b) the plantions of the Mayombe, (c) one sample site in Ivory Coast (Bin Houye), and (d) two sample sites (Bin Houye and Danane) in Ivory Coast. Solid and dotted lines represent the ring-width series of the two trees. The percentage of parallel run (ppr), t-value of Baillie-Pilcher (t-value) and the inter series correlation (r) are indicated in the graphs. The Y-axis is logarithmic for a better visualization because standardization was only applied on site and regional chronologies.

Table 3.3. Site and regional chronology characteristics of natural forests in Ivory Coast (IC) and the Mayombe (n samples, diameter, number of tree rings, mean growth, MS (mean sensitivity), AC (auto-correlation), time span, Pearson correlation, EPS (expressed population signal).

	Natural forest Ivory Coast	Plantations Mayombe	Natural forest Mayombe
Total n sampled trees	29	60	12
n of samples in chronology	22 (81%)	28 (47%)	11 (92%)
Mean diameter (cm)	56 ± 11	41 ± 12[a]	57 ± 15
Mean n of tree rings	46 ± 34	40 ± 6	47 ± 38
Time span chronology	113 (1895-2008)	49 (1959-2007)	36 (1973-2008)
Mean growth of chronology (mm)	4.53 ± 1.64	5.45 ± 2.60	7.19 ± 2.67
AC	0.64	0.91	0.84
MS after standardisation	0.26	0.16	0.16
Pearson r	0.14	0.36	0.33
EPS	0.79	0.94	0.84

In Ivory Coast, some sites show satisfactory results visually as well as for a minimum of two statistical parameters. Nevertheless, the relations are generally less strong and less significant than in the Mayombe (Table 3.4). Unlike in the Mayombe, not all trees from the Ivorian site chronologies were used to build the regional chronology (Table 3.3 and 3.4, Fig. 3.4). Instead, all individual Ivorian tree-ring chronologies were compared to each other and 22 trees that showed the strongest common signal, were extracted (e.g., Fig. 3.3c and d). Those 22 trees were used to construct the regional chronology for western Ivory Coast.

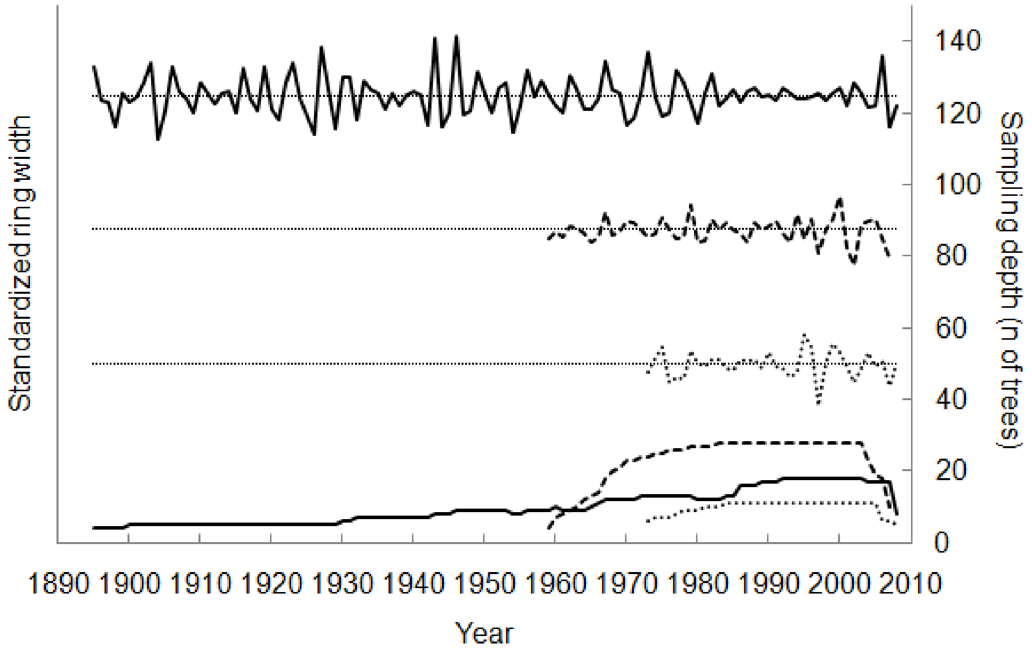


Fig 3.4. Standardized chronologies for natural forest (dotted line) and plantations (dashed line) in the Mayombe and the natural forests of Ivory Coast (full line). The lower part of this graph indicates the number of trees included in the chronologies (sampling depth).

Table 3.4. Ppr (percentage of parallel run), t-value Baillie-Pilcher and Pearson's correlation coefficient for cross-dating of local chronologies in the Mayombe and Ivory Coast. Overlap refers to the time period the two site chronologies have in common and n refers to the number of trees included in the site chronologies.

Sites	Region	Overlap (y)	n	ppr (%)	Pearson r	t-value Baillie-Pilcher
Tshela vs Luki	Mayombe	1981-2006	6 vs 5	61	0.51**	0.9
Tshela vs Monzi		1973-2007	6 vs 28	89	0.87***	5.6***
Luki vs Monzi		1981-2006	5 vs 28	63	0.76***	0.8
Bin Houye vs Danane	Ivory Coast	1972-2007	4 vs 6	62	0.21	1.0
Bin Houye vs Goya		1986-2008	4 vs 6	71	0.13	2.6*
Bin Houye vs Scio		1972-2008	4 vs 7	57	0.24	1.5
Danane vs Goya		1986-2007	6 vs 6	55	0.61**	1.7
Danane vs Scio		1966-2007	6 vs 7	63	0.45**	3.1**
Scio vs Goya		1986-2008	7 vs 6	62	0.09	2.3*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3 shows that the percentage of trees included in the stem disc-based chronologies is higher than in the wood core-based chronology. In the Mayombe, the mean growth of natural *T. superba* trees is remarkably higher than for plantation trees ($p < 0.01$). For comparable diameters, *T. superba* trees from the Mayombe grow faster ($p < 0.001$) than Ivorian trees. Plantation and natural forest chronologies from the Mayombe region showed high autocorrelations, indicating a clear age trend. The Ivorian chronology has a lower AC and therefore a higher MS. After standardization, AC was close to zero for all chronologies. All EPS values approach the threshold of 0.85.

Comparing the two regional chronologies, we found a weak long-distance relationship for the period 1959 to 2008 (ppr=55%; r=0.39; t=3.7). The ppr is low, but the Pearson correlation and t-value are significant ($p < 0.01$). A visual check confirms this correspondence and revealed a short discrepancy only during the 1990s (Fig. 3.5). Additionally, there exists a significant positive correlation between the precipitation from November to April in both regions ($r = 0.42$; $p < 0.01$).

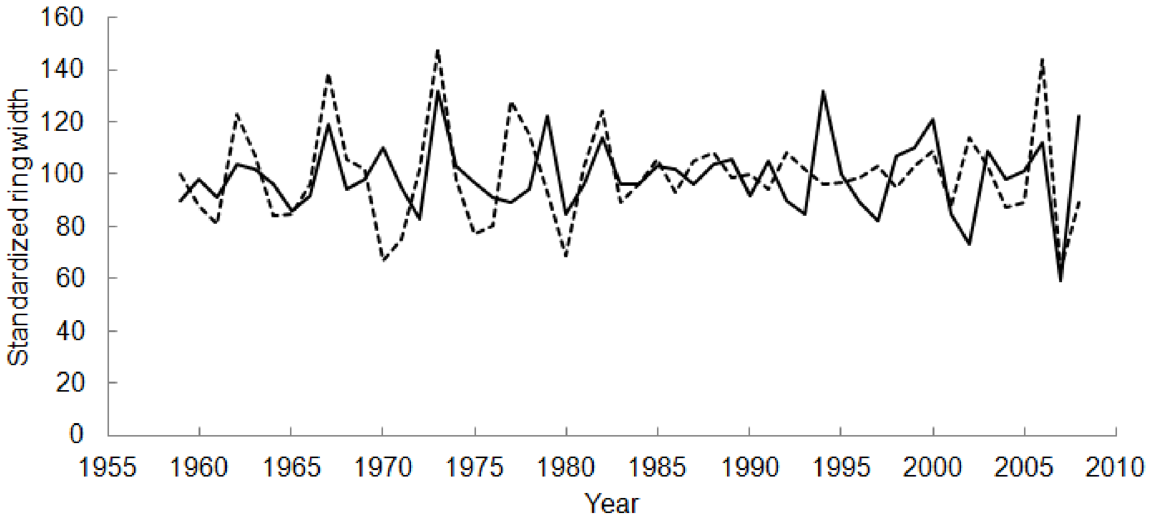


Fig 3.5. Standardized regional chronologies of the Mayombe (full line) and Ivory Coast (dashed line). Comparing both chronologies results in a t-value of 3.7 and a correlation of 0.39 (both $p < 0.01$).

3.3.3 Response of T. superba growth to interannual climate variability

At a local scale, Mayombe tree growth was primarily positively correlated with precipitation. However, a significantly ($p < 0.05$) positive correlation was found only for November, at the start of the rainy season and also the month with the maximum precipitation of the year (Fig. 3.6 and 3.7). Correlation values for Ivory Coast were much lower and no significant correlations were found.

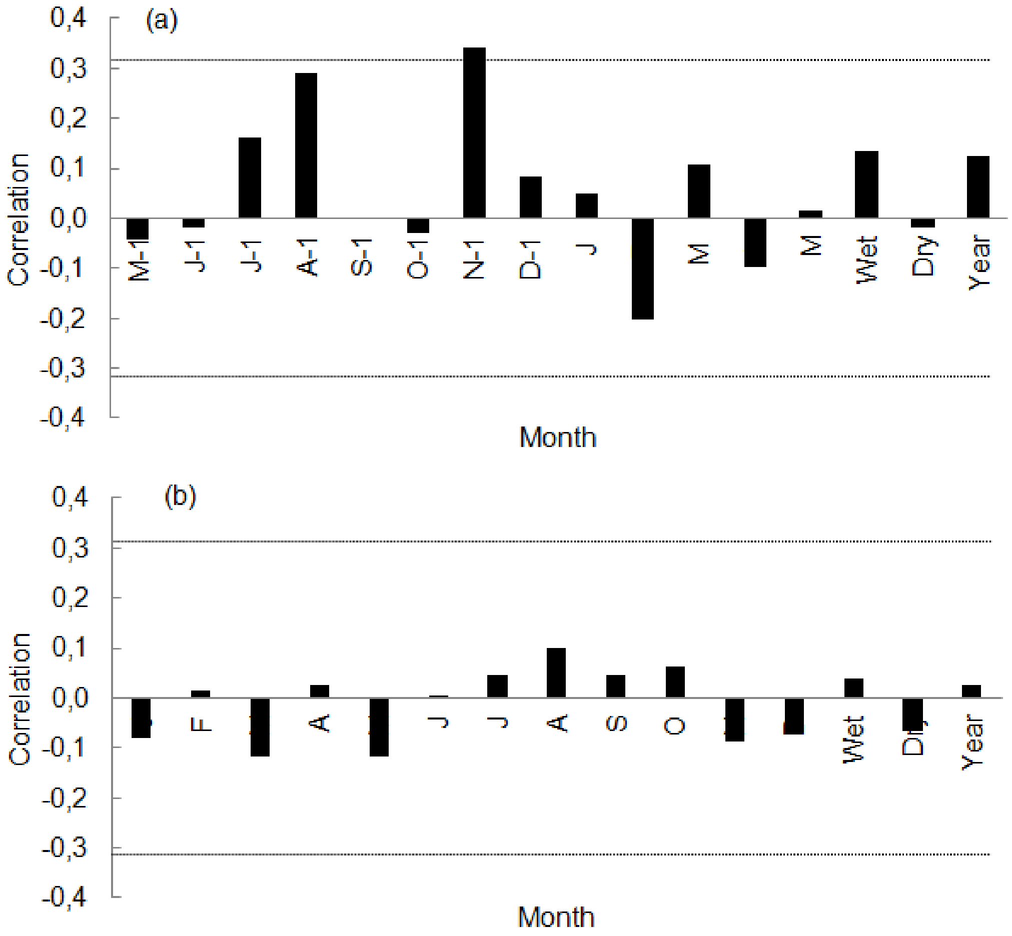


Fig 3.6. Correlations between (a) the Mayombe chronology, (b) the Ivorian chronology, and the monthly, seasonally and annual precipitation. The dotted lines indicate the $p < 0.05$ level.

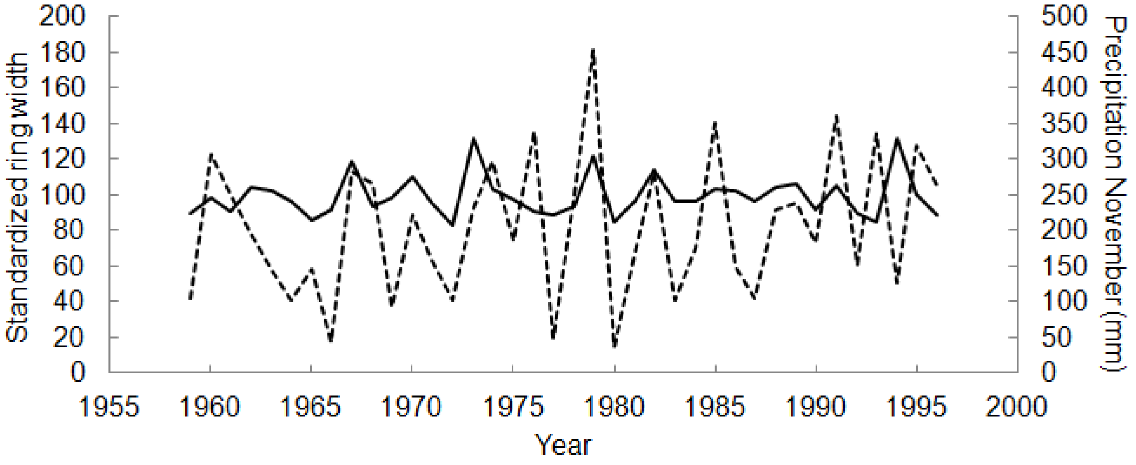


Fig 3.7. Correlation between the chronology of the Mayombe and November precipitation. The precipitation curve is a dashed line and the regional chronology is a full line.

At a regional scale, November precipitation in the Mayombe was used for correlation maps with SSTs and was positively influenced by SSTs of the Gulf of Guinea and mostly the coastal South Atlantic Ocean during the months of October-December (Fig. 3.8a). SSTs during this time of year were also positively correlated with our Mayombe tree-ring chronology in a part of the Gulf of Guinea and the South Atlantic Ocean (Fig. 3.8b).

At a global scale, early rainy season precipitation in both regions was influenced by ENSO, with negative ENSO (La Niña) years resulting in wetter than normal early rainy season conditions in the Mayombe region (Fig. 3.8c). As a result, tree growth in the Mayombe was significantly higher in La Niña years than in ‘normal’ years (Table 3.5). In Ivory Coast, no significant correlations were found between ENSO and precipitation on the sample sites. However, positive ENSO-years corresponded with higher precipitation in northern Ivory Coast (Fig. 3.8c), likely reflected by stronger tree growth during El Niño years (Table 3.5).

Table 3.5. Visualization of two sample test evaluating the influence of ENSO-events on tree growth. Ring-width indices during the ENSO-event and one year after the event were compared in the Mayombe region and western Ivory Coast (both from 1959 to 2008).

t-values	El Niño	Year (+1)	La Niña	Year (+1)
Mayombe	0.18	-0.32	2.41*	-0.94
Ivory Coast	2.04*	-1.00	0.72	-1.50

* $p < 0.05$

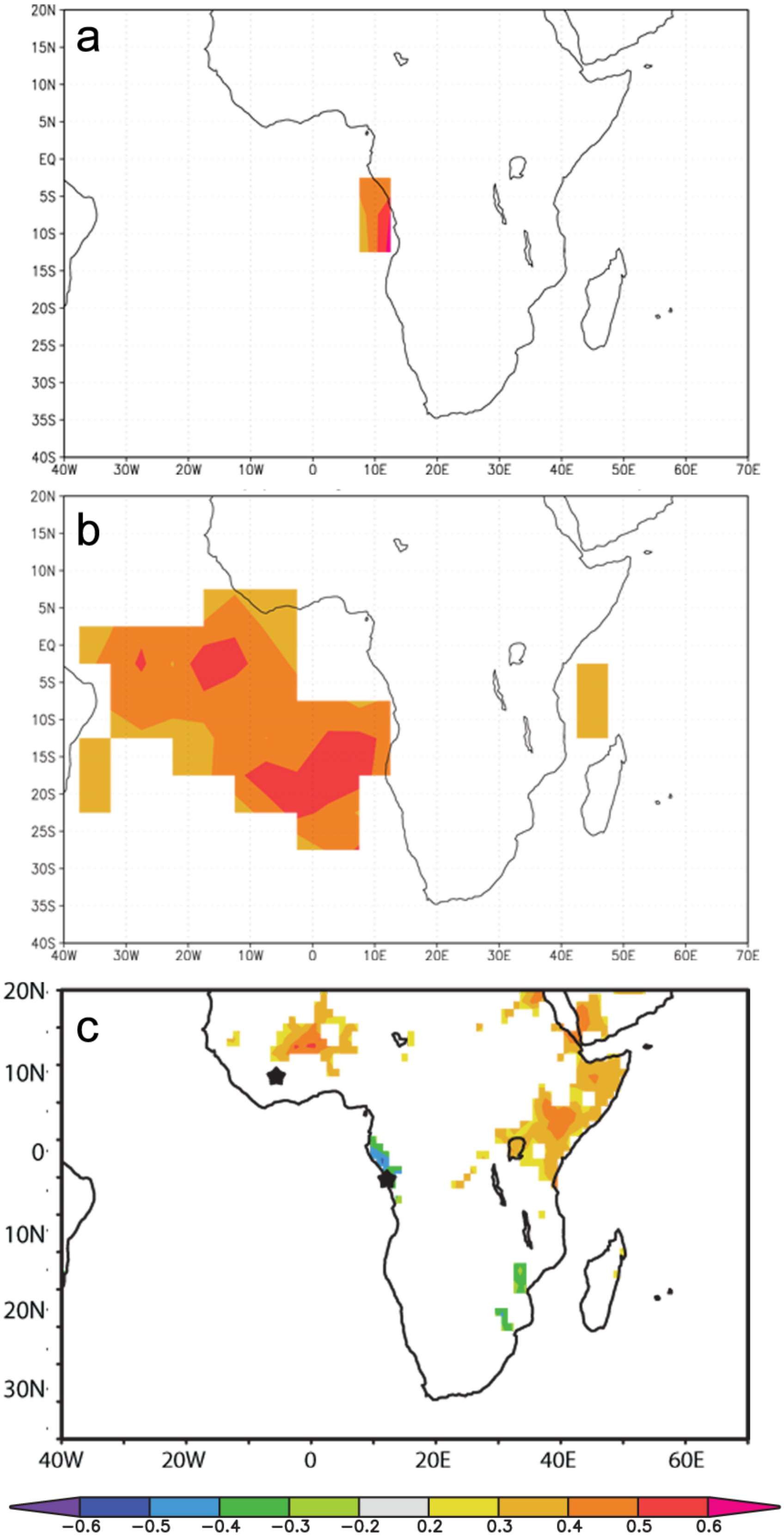


Fig 3.8. Correlation maps between (a) November precipitation, (b) tree growth, and gridded average SSTs for the months October-December, all for the Mayombe over the period 1959-1996. The correlation map (1959-2008) between the annual Niño 3.4 time-series and gridded October-November precipitation is shown in (c). The two study sites are indicated as black stars in (c).

3.4 Discussion

3.4.1 Tree-ring related wood anatomy, ring anomalies and the use of wood cores

Mariaux (1969) was the first to describe annual tree rings in *T. superba*. His description was based on young trees with a lot of juvenile wood. Mature tree rings appear to differ substantially. In trees older than 30 years, bands of parenchyma were less abundant and the marginal parenchyma (if present) was not always continuous. However, the large variations between years that Mariaux (1969) reported were also found in our study. In some years, there is a vessel-less area at the start of a growing season. Also, the normal anatomical structure within a ring can be inversed, as was the case in some Ivorian tree rings. Clearly, the anatomical tree-ring structure can differ in *T. superba* from different regions.

Tree rings were easier to detect in the Mayombe compared to Ivory Coast. This is potentially related to a difference in leaf shedding behaviour in the two regions and the generally drier conditions of the Mayombe. In the Mayombe, defoliation is simultaneous in the late dry season (up to 50% of *T. superba* trees lose their leaves in September (Couralet 2010)) and complete while in Guinea (adjacent to Ivory Coast), the leafless period occurs not simultaneously in every tree, is shorter in time and less complete (CTFT 1959). Personal observations confirm that defoliation in the DRC is complete in June-July for all trees of one whole plateau or valley while in Ivory Coast, it differs strongly between individual trees: trees with new leaves, leafless trees and trees that are still shedding leaves are found at the same site at the same time.

Problems to define tree rings were caused by the first unclear juvenile tree rings, false rings, double rings and especially ring wedging (Mariaux 1969). Worbes (2002) also classified *Terminalia* as a taxon that tends to form wedging rings. Ring wedging has been noted in many tropical tree species (e.g., Trouet et al. 2010, Tarhule and Hughes 2002), but the exact cause for this phenomenon is unknown. Our study confirms that wedging mostly occurs in the outer parts of the tree circumference, when the tree starts to grow slower due to its inherent growth trend and form buttresses (Worbes 2002). Buttresses become larger when tree diameters increase (see Chapter 2), and could also cause wedging. Worbes (2002) related ring wedging to trees that grew under poor light conditions and under competition. *T. superba*, abundantly present in fallows and forest gaps, mostly receives full light during its juvenile phase. Afterwards, when canopy closure occurs or trees of the climax forest reach their full height, competition for light could cause wedging, especially in the most recent tree rings. To answer Worbes' hypothesis on competition, more ecological data on *T. superba* and the accompanying tree species need to be collected within the sampled forests.

Because of the frequent occurrence of wedging rings and its interference with cross-dating, Worbes (2002), Trouet et al. (2006), and Brienen and Zuidema (2005) recommend the use of stem discs rather than wood cores for tropical tree ring analysis. Our study shows that the percentage of cross-dated samples in our wood-core based plantation chronology is significantly lower than in the stem disc-based chronology of the natural forest. However, there were three main reasons why plantation trees were excluded from the chronology: (1) trees had an eccentric center (the orientation of wood cores is difficult in this case), (2) wood cores were broken, resulting in invisible tree rings due to cracks, or (3) tree-ring series from opposing cores from the same tree did not cross-date. Tree-ring anomalies were the main cause for omitting tree ring series in the latter case. However, when a first chronology can be built from stem discs with accurate mapping and documenting of ring anomalies (especially wedging and false rings), tree-ring series of wood cores can be checked and implemented in or omitted from this existing chronology. In the tropics, Schöngart et al. (2006), Stahle et al. (1999) and Worbes (1999) also successfully analyzed tree growth using only wood cores and one or a few stem discs. Moreover, sampling wood cores is less destructive and substantially facilitates sample transport.

3.4.2 Growth patterns in natural and planted African forests

In the Luki Reserve (DRC), Couralet et al. (2010) found between-trees correlations for understory trees that were similar in magnitude to our results. The correlation strength in our study was also in accordance with the findings of Bräuning et al. (2009) and Brienen and Zuidema (2005), lower than those of Stahle et al. (1999) and Therrell et al. (2006), and higher than the correlations of Trouet et al. (2006, 2010). Auto-correlation is high compared to other tropical tree species (Bräuning et al. 2009; Couralet et al. 2010; Trouet et al. 2006, 2010) but not unusual because *T. superba* has a strong and known age trend, colonizing fallows with fast growth during the first years and strongly decreasing in growth after this juvenile phase.

Fifty-year old plantations and 40 to 50 years old natural forest of the same tree species in the Mayombe enable an original comparison of growth patterns in natural versus planted trees. Eshete and Stahl (1999) as well as Worbes (1999) used plantation trees but their time-series were too short for chronology development (< 25 years). In our study, the overlap between planted and natural trees is 36 years and planted and natural trees showed similar growth patterns. The higher autocorrelation in the plantations compared to natural forests could be related with a stronger age trend in a generally even-aged forest but even without standardization, cross-dating was successful. The studied plantation is a production forest that is not intensively managed, but nevertheless, the natural forests were more diverse with a more explicit competition for light and nutrients. The average growth as well as the initial growth (first 20 years) were lower in the plantation compared to the natural forest. Two extremely dry years (1956 and 1958) and the use of inferior planting material has been shown to explain the loss of plantation trees immediately after the installation (see Chapter 2) and have likely also influenced the growth of surviving trees.

In temperate regions, reference chronologies are available from a dense network of dendrochronological records and can be used for provenancing and dating wooden objects (Haneca et al. 2009). These chronologies can span more than 10 000 years (e.g., oak (Friedrich et al. 2004)). Such long time spans are difficult to accomplish in the tropics, but the development of a regional network of species-specific chronologies that include older trees is feasible. *T. superba* appears to be a suitable tree species for this goal, because it shows distinct tree rings, has a wide distribution range, and displays cross-dating potential throughout a large section of this range. The longest regional chronology here developed only spans 113 years, but the oldest sampled tree was 165 years in the Mayombe and 182 years in Goya (Ivory Coast) and nine trees in total in our dataset covered > 100 years. Unfortunately, the sample replication for such long tree ring chronologies was too low to incorporate the oldest trees in the regional chronologies. Our study shows that wood cores give an accurate indication of the number of tree rings and thus of the age of a tree and we suggest to first core trees before cutting for chronology development. With additional samples, it should be possible to reconstruct a regional chronology for *T. superba* with a length of up to 200 years, which would greatly increase the time span covered by instrumental climate records and thus allow for paleoclimatic analysis.

Our regional chronologies for the Mayombe and Ivory Coast were located more than 2600 km apart, overlapped in time for 50 years (1959-2008), and showed a weak synchronization. Fichtler et al. (2004) did not find a match between two sites in southern Africa that were 900 km apart and used spectral analysis of both master chronologies to reveal similar long-term oscillation patterns. Trouet et al. (2010) cross-dated chronologies from five Miombo woodland sites in Zambia over a distance of more than 1000 km and found long-distance growth correlations between some sites. To our knowledge, our study is the first to indicate long-distance growth correspondence in rainforests. One hypothesis for these synchronized growth variations could be the presence of a common growing season as Mariaux (1969) confirmed with dendrometer studies. On a limited number of trees, he found that tree growth in both the Mayombe and central Ivory Coast mainly occurred during October-December. Tree growth and November-April precipitation are not directly related in either of the regions, but both tree growth and November-April showed similar variability. Other relations between tree growth and climate are discussed in detail in the next paragraph.

3.4.3 Response of T. superba growth to interannual climate variability

In the Mayombe, early rainy season precipitation is an important driver of tree growth. This matches with the abovementioned dendrometer measurements in the Mayombe Forest that show the strongest growth during the onset of the rainy season (Mariaux 1969). A positive response to the first rains was also found in one understory species (*Aidia ochroleuca* (K. Schum.)) in the Mayombe (Couralet et al. 2010) and tropical forests in Bolivia (Brienen and Zuidema 2005) and Thailand (Pumijumnong et al. 1995). In Ivory Coast, there is no important influence of precipitation on tree growth.

Thus, no comparable relation appears to exist between tree growth and precipitation in the two regions, despite the long-distance relation between the two regional chronologies for growth on one hand and November-April precipitation on the other hand. Differences in response to climate could be related to climate sensitivity of the trees or the use of short precipitation time series. Regarding climate sensitivity, western Ivory Coast is located in a wetter region than the Mayombe. This could cause a stronger climate signal in the Mayombe following the principle of limiting factors (Fritts and Swetnam 1989). Also, trees near the margins of their climatic distribution have a higher climate-sensitivity (Cook and Kairiukstis 1990). The microclimate in the Congolese Mayombe still enables the growth of tropical trees while in fact, annual precipitation is too limited for their growth (optimal annual precipitation for *T. superba* is 1500 mm; Groulez and Wood 1985). In addition, our climate-growth relations were only tested over a rather short but common time span to enable comparison between the two regions (1959-1996). We correlated growth and precipitation from 1959 to 2006 with data from the Luki climate station (Mayombe) to illustrate the influence of longer climate series. In addition to a stronger relation with November precipitation ($r=0.42$; $p<0.01$), summed October-December precipitation also showed a strong positive relation with tree growth ($r=0.37$; $p<0.01$). So, more and stronger climate correlations in the Mayombe were found if the most recent precipitation data were included. This difference could not be tested in Ivory Coast (shorter precipitation time series, more stations with lacking data), but we hypothesize that stronger relations with precipitation in Ivory Coast could come out if longer precipitation time series, including the most recent years, were available. This is indirectly confirmed by the ENSO-study (see below), which was run for the two regions from 1959 to 2008, resulting in a significant relation between tree growth and ENSO climate indices in both regions.

Based on the local relation between climate and growth in the Mayombe, the regional influence of SSTs on tree growth and precipitation was analyzed with correlation maps, in order to provide a clear view on the influencing oceanic regions. The South Atlantic Ocean, including parts of the Gulf of Guinea, appears the most important driver for the Mayombe precipitation as well as tree growth. Balas et al. (2007) and Paeth and Friederichs (2004) also confirmed the influence of the Gulf of Guinea and the tropical Atlantic Ocean on precipitation in western Central Africa and indicated the ENSO mode as another important factor. In addition to precipitation, the SSTs of the Gulf of Guinea and the South Atlantic Ocean in October-December influenced tree growth in the Mayombe. This was also the case in Benin with significant correlations between tree growth and May-August SSTs from the Gulf of Guinea for four tree species ($p<0.05$): *Afzelia, Pterocarpus, Daniellia,* and *Isoberlinia* (Schöngart et al. 2006).

Finally, anomalous ENSO conditions were associated with growth effects in both Ivory Coast and the Mayombe, even though local precipitation patterns did not influence tree growth in both regions. So far, the effect of ENSO on African tree growth in two different hemispheres has not been encountered in literature. Because the influence of ENSO on precipitation occurred during the growing season, tree growth could be influenced by ENSO. Schöngart et al. (2006) only found an influence of ENSO on precipitation during the dry season and subsequently, no relationship with tree growth. In general, the Mayombe region appears to be more sensitive to climate variability than Ivory Coast, with higher October-November precipitation and higher growth clearly observed during La Niña years. In Ivory Coast, higher precipitation during El Niño years slightly northward of the sample sites was found during the growing season, probably resulting in higher growth during El Niño years. In literature, most studies in West and Central Africa are focused on the relation between precipitation and ENSO. Camberlin et al. (2001) found a negative correlation between ENSO and precipitation in August-November for Cameroon, Gabon, the Republic of Congo and coastal DRC, confirming the higher precipitation during La Niña years in the Mayombe, as did also Paeth and Friederichs (2004). For Ivory Coast, Paeth and Friederichs (2004) did not observe a consistent relationship for West Africa between ENSO and precipitation. However, we compared the actual zones of higher precipitation in October-November during El Niño years in Fig. 3.8c with the precipitation response map of Camberlin et al. (2001) (their Fig. 4), resulting in a response type with some dry months during El Niño years but with wet conditions in October-November. Still, this type of response in October-November is not as strong as the response in the Mayombe, both for precipitation as well as growth. Again, the principle of limiting factors (Fritts and Swetnam 1989) and the presence of *T. superba* trees near the margins of their climatic distribution (Cook and Kairiukstis 1990), could explain the higher climate-sensitivity in the Mayombe. Apart from the higher climate-sensitivity in the Mayombe, other site factors such as differences in the rooting system along with soil properties and the depth of the water table (Couralet et al. 2010; Fichtler et al. 2004), differences in tree phenology (Brienen and Zuidema 2005), and genetic differences (Gourlay 1995) could influence different climate-growth relationships in the Mayombe and Ivory Coast. Unfortunately, no data on these factors are available for comparative analysis.

From the abovementioned studies on precipitation and SSTs, it is evident that results are often linked to the methods used and the area and season studied. The diversity in results underlines the complexity of our study region in its response to seasonal and interannual SST changes and ENSO events. Furthermore, Camberlin et al. (2001) did not observe consistent relationships with any of the SST indices in some parts of Africa, suggesting that precipitation variability responds to other oceanic patterns, or only to local/regional atmospheric dynamics.

3.4.4 Conclusion and perspectives

Although planted and natural forests with *T. superba* have distinct differences in site conditions like structure and light competition, both forest types showed significantly similar growth patterns and responses to climate. Cambial growth probably occurs at the same time in planted and natural forests and is most likely influenced by the onset of the rainy season in the Mayombe. However, local precipitation does not appear to correlate with the Ivorian regional chronology. Regional climate variability was influenced by SST anomalies in the Mayombe whereas ENSO indices controlled climate variability over both hemispheres during the rainy season (October-November) with higher growth at the northern hemisphere sites during El Niño years and higher growth at the southern hemisphere sites during La Niña years. Generally, the presence and strength of climate-growth relations is more clear in the Mayombe than in Ivory Coast, which is probably related to more limiting precipitation, trees at the edge of their distribution and the availability of longer time-series of local precipitation.

So, if growth and local climate relations aren’t successful due to e.g. the length or quality of this precipitation data, comparison with large-scale climate factors as SSTs can indicate important influences on precipitation patterns and tree growth. Therefore, in tropical regions, where climate data are often scarce, comparison with these SSTs and derived ENSO indices offers interesting possibilities for future dendroclimatological studies in the tropics, even in equatorial Africa. Finally, cambial marking is also recommended to get a better understanding of climate-growth relations. Cambial marks provide information on the onset, ending and length of the growing season in both regions and therefore, can be related to differences in growth response to climate.

Chapter 4

Tree-ring analysis of an African long-lived pioneer species as a tool for sustainable forest management

Abstract

Improved sustainable forest management in the tropics is hampered by the limited availability of quantitative data, especially in tropical Africa. Important management parameters such as the minimum logging diameter (MLD), the associated biological rotation age (BRA) and the timing of silvicultural treatments are too often based on merchantable dimensions and state regulations instead of ecological data and tree growth. This study combines diameter, height and bootstrapped tree-ring curves of natural and planted trees of the long-lived pioneer species *Terminalia superba* Engl. & Diels. A growth-oriented MLD was calculated, and the need and timing of silvicultural treatments was estimated based on the analysis of growth releases and suppressions. Study sites were situated in the Congolese Mayombe forest and western Ivory Coast. Tree rings from 41 natural forest trees (stem disks) and 29 plantation trees (increment cores) were measured, along with diameter and height measurements. Planted and natural forests showed considerable differences in mean growth rate and growth curves. More than 50% of the trees nevertheless reached the canopy without growth releases or suppressions, confirming that *T. superba* does not require intensive management. The growth-oriented MLD not only differs considerably between sites but bootstrapping revealed large differences within forest regions/types. Furthermore, volume-based MLD and BRA are on average larger than basal area-based calculations. The modified monocyclic management system is suggested, especially for planted forests with light-demanding, fast-growing tree species. One small-scale thinning during the juvenile phase is recommended before a final harvest that includes all trees above the growth-oriented MLD. The introduction of sustainable management for *T. superba* therefore primarily depends on forest type and cannot be generalized at the species level.

Accepted for publication in Forest Ecology and Management

De Ridder M, Van den Bulcke J, Van Acker J, Beeckman H (2013). Tree-ring analysis of an African long-lived pioneer species as a tool for sustainable forest management. Forest Ecology and Management (revised version accepted, May 2013)

4.1 Introduction

Tropical forests hold about half of the world's terrestrial biomass (Pan et al. 2011). These forests need to be managed properly if they are to supply the necessary resources in addition to performing their social and ecological functions. These functions should be described and well-balanced in management plans. This is a complicated task, especially in the tropics, where complex forest structures (Whitmore 1990), increasing human pressure (Iloweka 2004), and a lack of systemic research are common. Moreover, every year millions of hectares of tropical forest are lost or seriously degraded. Although the amount of sustainably managed forest increased slightly worldwide between 2005 and 2010 and even tripled in Africa, these forests only account for less than 8% of the world's forests area (Blaser et al. 2011). Successful sustainable management depends on the collection of quantitative data. This study will focus on one of the main elements within the framework of sustainable management – sustained yield – in keeping with the principle that log removal should not exceed the capacity of the growing population to replace the removed tree volume (Sands 2005).

Timing of log removal should mostly be based on the biological rotation age (BRA) and the adjoined minimum logging diameter (MLD). Governments, scientists, and others define the MLD differently. Legally, the MLD is mostly defined as the minimum diameter cutting limit for tree species. This means that the MLD is not calculated, but fixed by national regulations and/or set at values that coincide with merchantable wood volumes (Schöngart 2008; Sist et al. 2003). From a scientific point of view, the MLD is calculated based on tree growth. For example, Junk et al. (2011) defined the MLD in the Amazonian floodplain forests as the diameter at the age of maximum current volume increment rates. This study follows Philip (1994) and Rondeux (1999), who define the optimum MLD as the diameter at the age of maximum mean volume or basal-area increment rates. This age of maximum mean increment rates corresponds with the BRA.

Both volume and basal-area based calculations depend on tree growth data, collected periodically in permanent sample plots (PSPs) or during one inventory with extraction of stem discs or increment cores for tree-ring analysis. Although tree rings are not always easy to distinguish in the tropics (Schweingruber 1988), they have proven to be a reliable management tool (Baker et al. 2005; Schöngart et al. 2007; Schöngart 2008). Because of the frequent occurrence of tree-ring anomalies, Brienen and Zuidema (2005) recommend the use of stem discs for tree-ring analysis. Sampling stem discs is not only destructive, it is also difficult, because logging in the tropics is not straightforward. This mostly results in small sample sizes with large variability in growth rate. Computer simulations such as bootstrapping (Brienen et al. 2006; Efron 1979; Rozendaal et al. 2010) are useful tools to counter such variability and make a more reliable estimate of the MLD.

The definition of sustainable forest management nevertheless involves more than the calculation of annual allowable cut and the calculation of the MLD (Sist et al. 2003). Silvicultural treatments often improve diameter/volume increments (Peña-Claros et al. 2008; Villegas et al. 2009), but the timing and number of these treatments is usually only based on experimental modelling and national regulations. Again, tree-ring data can be used to, e.g., calculate and study the presence and frequency of so-called growth releases and suppressions. The definition of these major changes in growth rates is based on the percentage of growth change, with thresholds for growth releases and suppressions (Brienen and Zuidema 2006; Nowacki and Abrams 1997). Those releases and suppressions mark critical moments in the trees' lifespan (Baker et al. 2005; Brienen and Zuidema 2006) when management could influence the growth of trees positively.

This study explores the use of combined growth data, which can be collected during forest inventories, and tree-ring analysis to formulate recommendations for sustainable management of West and Central African forests. The studied tree species is the long-lived pioneer *Terminalia superba* Engl. & Diels. This species has a vast natural distribution area, stretching from Sierra Leone to Angola (Groulez and Wood 1985). Due to its fast growth, straight stems, and high commercial heights (Groulez and Wood 1985), large plantations were installed in the Democratic Republic of Congo (DRC) beginning in 1948. *T. superba* is listed by the International Tropical Timber Organisation (ITTO) as one of the major tropical species traded and is used for, among other things, interior joinery, furniture, veneer, and plywood (Groulez and Wood1985). The presence of distinct annual tree rings in Central and West Africa (Chapter 3; Mariaux 1969) allows us to raise the following research questions:

(1) Is it possible to suggest silvicultural treatments based on tree-ring patterns of a long-lived pioneer species? If so, can the need and the timing of these treatments be determined based on the analysis of growth releases and suppressions?

(2) How do MLD and BRA vary within and between sample sites? Is it possible to define one MLD for all forest regions/types, similar to current regulations?

(3) Combining the results of the first two research questions, is there an important difference in the management of a planted or a natural forest? In other words, does the introduction of sustainable management with silvicultural treatments and a final harvest based on MLD/BRA depend on forest region/type or can it be generalised at the species level?

4.2 Material & methods

4.2.1 Study sites

All study sites belong to the Guineo-Congolian regional centre of endemism (White 1983). The Ivorian study sites are part of the evergreen moist rainforest. The Congolese study sites are situated within a drier semi-evergreen rainforest. A map with detailed information is available in chapter 3.

The three Congolese study sites are situated on the southern border of the Mayombe Forest, which covers the western parts of Gabon, the Republic of Congo, the DRC and Cabinda (Angola). Two study sites were chosen within the Luki Biosphere Reserve (05°30’ to 05°45’ S and 13°07’ to 13°15’ E). The first study site in Luki is a natural forest stand; the second is located in Monzi, 15 km away, in a *T. superba* plantation established between 1955 and 1957. Plantations were installed at planting distances of 8 x 12 m and no structured management was carried out (Chapters 1 and 2). A third study site was selected in a natural forest stand in Tshela, about 70 km to the north. All study sites were situated at altitudes below 300 m above sea level. The average annual precipitation, based on precipitation data from the Luki climate station from 1959 to 1996, is 1168 mm, but some years are particularly dry. The region is characterised by a dry season of four to five months (May to September–October) and a short period with less precipitation (January–February). The proximity of the ocean and the associated high relative humidity likely buffer the intensity of the dry season. Temperatures oscillate around 26 °C in the rainy season and drop to a minimum of 20 °C in the dry season. The soils of the Luki Reserve are classified as orthic Ferralsols, while Tshela is characterised by ferric Acrisols (FAO 2008). Most soils are argillaceous, with a pH of between 4 and 6 and a C/N of between 4 and 9.

In western Ivory Coast (06°07’ to 07°15’ N, 07°30’ to 08°15’W), four study sites are situated in natural forests (mostly secondary forests), some of them more than 100 km apart. Study sites were situated between 200 and 370 m above sea level. The average annual precipitation, based on precipitation data from six climate stations from 1959 to 1996, is 1650 mm. In this region, the dry season generally lasts for three months (December to February). In July and August, a period of less precipitation is observed. Relative humidity drops about 20 % in the dry season. Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March (Van Oldenborgh and Burgers 2005). Soils have a pH of between 4 and 7 and a C/N of 8 to 12, and are classified as Ferralsols and Acrisols, i.e., typical acid soils for tropical lowlands (FAO 1986).

4.2.2 Sampling and tree-ring analysis

Stem disks and increment cores were collected for tree-ring analysis. In natural forests, a total of 12 stem disks from the Mayombe and 29 stem disks from western Ivory Coast were sampled. Trees' stem height (until the first branch) and diameter were measured in the natural forests. In the plantations of the Mayombe, two perpendicular increment cores were taken per tree, but no stem height or diameter measurements are available. Tree rings were measured on 60 plantation trees. All samples were air dried to prevent fungal infestation, and increment cores were frozen for two weeks to prevent insect infestation. Stem discs were too large for freezing and therefore only superficially disinfected before storage in the Tervuren Xylarium. All disks and cores were sanded with grits increasing gradually from 50 to 600 or 1200.

The procedure for tree-ring measurements is described in detail in chapter 3. Ring widths were measured to the nearest 0.01 mm using a stereo-microscope and a Lintab measuring device with TSAP-Win software (Rinn 2003). Approximate age is therefore known for the sampled trees, in addition to diameter. For increment cores without pith, it is better to use the number of rings than approximate age. Missing pith was not corrected for, due to many samples with pith eccentricity and large variations in juvenile ring-widths. The time necessary to grow to the sampling height is not taken into account. Therefore, tree ages are slightly underestimated.

4.2.3 Analysis of growth changes

Basal-area growth rather than diameter growth was used to calculate growth events, as *T. superba* has a known age trend, especially in plantations (Chapter 3). Based on the tree-ring data, the percentage of growth change was calculated with Nowacki and Abrams's formula (1997):

$$GC_i=[(M_2-M_1)/M_1] \times 100 \qquad (4.1)$$

Where GC_i = percentage of growth change for year i, M_1 = the preceding 10-year mean basal-area growth (including the year of change) and M_2 = the subsequent 10-year mean basal-area growth. For example, for GC_{1979}: M_1 is the mean from 1970 to 1979, whereas the mean for M_2 is from 1980 to 1989. Brienen and Zuidema (2006) defined a growth release as a growth increase of more than 100%, and a growth suppression as a growth decrease of at least 50%. A growth release lasting for at least 5 years is regarded as sustained. Growth changes were calculated for individual trees and the mean growth curves for the forest regions/types. In classical dendrochronology, tree-ring series are synchronised by calendar date. To answer the current research questions, however, mean growth curves for each forest region/type were constructed by synchronising individual tree-ring series by age. The patterns of canopy accession presented by Brienen and Zuidema (2006) were used to classify all sample trees:

- ‘No (sustained) release’. Canopy accession occurred without major growth changes. A slight growth release (< 5 years) is allowed and this pattern is often found in trees where light since seedling stage was never limited.
- ‘One sustained release’. At least one growth release (> 5 years or preceded by a growth suppression) is distinguished, due to, e.g., a gap in the canopy.
- ‘One suppression’. Trees reach the canopy after one growth suppression. Usually, this type of tree has fast initial growth, followed by a strong growth decrease.
- ‘Multiple releases and suppressions’. Canopy accession takes place after several growth releases and suppressions. Successful growth into the canopy involves repeated growth shifts, probably due to canopy dynamics.

Canopy accession is secured because long-lived heliophilous species such as *T. superba* are known for their strong growth towards the light, and are usually part of the main canopy (pers. obs.). The proportion of trees belonging to each of these patterns is calculated for each forest region/type. Also the age, the year in which, and the diameter at which the growth releases/suppressions take place, is recorded. Precipitation (Chapter 3; Van Oldenborgh and Burgers 2005) in years with growth releases/suppressions is compared with precipitation in years without such major growth changes to check whether the influence of climate can be neglected, as stated by Nowacki and Abrams (1997), using the 10-year time spans for the calculation of growth releases/suppressions.

4.2.4 Minimum logging diameter (MLD) and biological rotation age (BRA)

The MLD represents the diameter at which maximum mean annual growth increment occurs (Philip 1994; Rondeux 1999). In this study, maximum annual increments of basal area and volume were calculated (Fig. 4.1) and the resulting MLDs were compared for the different forest regions/types.

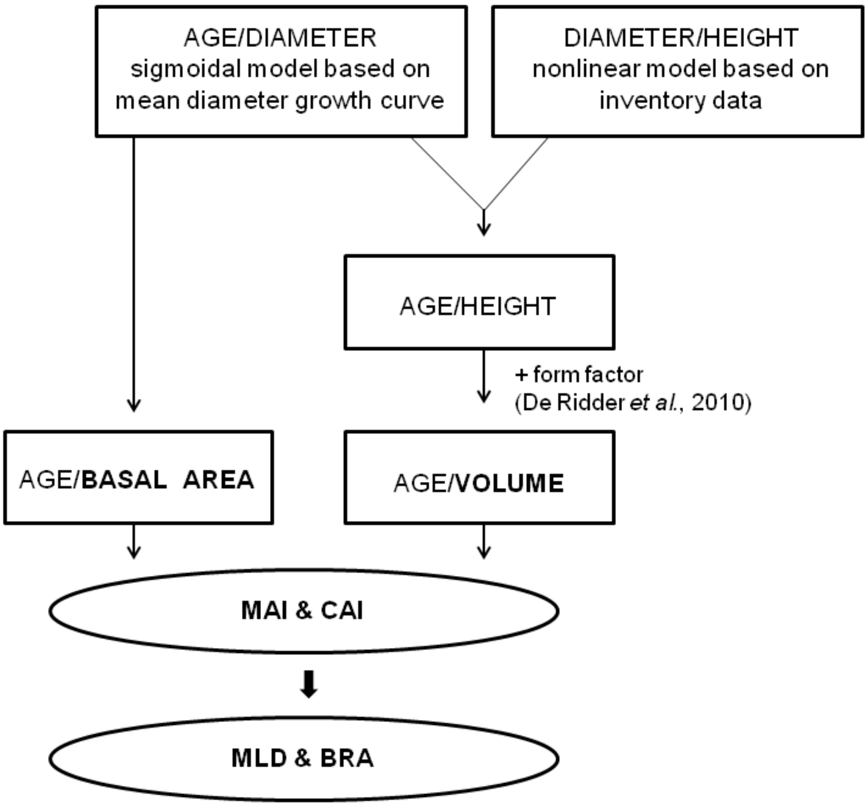


Fig 4.1. Flowchart illustrating the calculation of the minimum logging diameter (MLD) and the biological rotation age (BRA), based on maximum annual increments of basal area and volume. MAI; mean annual increment, CAI; current annual increment.

The general procedure described by Philip (1994), Rondeux (1999), and Schöngart (2008) was applied for the MLD based on maximum annual volume increments. A sigmoidal nonlinear regression was fitted to the mean diameter growth curve (age–diameter) of the Mayombe plantations as well as the natural forests of Ivory Coast and the Mayombe (Schöngart et al. 2007; Schöngart 2008; Verhulst 1838), whereas a nonlinear regression was fitted to the diameter–height data (Schöngart et al. 2007; Schöngart 2008). The volume at each age was then calculated as the product of basal area, stem height, and a fixed form factor, previously published in chapter 2. From the cumulative volume growth (CG_V), the current (CAI_V) and mean annual volume increment (MAI_V) were calculated (Philip 1994; Rondeux 1999):

$$CAI_V = CG_{V(t+1)} - CG_{V(t)} \quad (4.2)$$

$$MAI_V = CG_{V(t)} / t \quad (4.3)$$

An optimal volume production of the tree is found at the intersection of the CAI_V and MAI_V-curves, coinciding with the optimum MAI_V. The age at which the peak in MAI_V occurs corresponds with a specific diameter on the modelled mean diameter growth curve, i.e. the minimum diameter limit for optimal exploitation rates or the MLD. In addition to the optimal volume growth, CAIs and MAIs can also be calculated (Eqs. 4.2 and 4.3) for basal area (Philip 1994; Rondeux 1999).

Abovementioned procedure for calculation of MLD/BRA based on actual datasets, was repeated for bootstrapped growth curves. The bootstrap procedure as described in Brienen et al. (2006) was implemented in Matlab® (version R2011a). In total 1000 MLDs were calculated, each based on a set of simulated growth curves equal to the original amount of measured growth curves. Growth curves were simulated in 5 year intervals, as such including total autocorrelation. The mean growth curve of each forest region/type thus is simulated a 1000 times. MAIs and CAIs of volume and basal area were calculated on these simulated growth curves and histograms of MLD/BRA values are generated. The method of Brienen et al. (2006) was slightly modified by implementing continuous random sampling of the growth rate, in between the minimum and maximum growth rate found within a growth class, instead of using the measured values. Diameters were truncated at 60 cm for calculations of MLD/BRA in the natural and planted Mayombe trees. A maximum age of 40 year in the plantations and 50 years in all natural forests was used as older trees were rare and are given too much importance at higher ages, especially regarding the specific growth of the sampled trees.

4.3 Results

4.3.1 Growth characteristics of natural and planted T. superba

In both forest regions/types, tree ring analyses were successful (Chapter 3). A concise summary of the growth characteristics can be found in Table 4.1. All study regions had normally distributed diameters ($p > 0.05$). The diameter distribution of the natural forests approximately followed a negative exponential curve whereas the diameter distribution of plantations followed a more Gaussian curve, as expected for natural and planted forests.

Table 4.1. Growth characteristics of the natural forest in western Ivory Coast, the natural forest of the Mayombe, and the plantation in the Mayombe based on the original growth data.

	Natural forest Ivory Coast	Natural forest Mayombe	Plantation Mayombe
Number of samples with distinct tree rings	29	12	29
Mean diameter (cm)	56 ± 11	57 ± 15	41 ± 12[b]
Mean stem height (m)[c]	17 ± 8 (19)	23 ± 2 (7)	no data
Mean age (years)	55 ± 43[a]	47 ± 38	40 ± 6
Mean diameter growth (cm year^{-1})[d]	0.70 ± 0.27 (114)	1.32 ± 0.42 (50)	1.09 ± 0.52 (49)
Mean diameter growth first 25 years (cm year^{-1})	1.58 ± 0.41	1.61 ± 0.30	1.27 ± 0.34
Mean diameter growth first 40 years (cm year^{-1})	1.21 ± 0.31	1.24 ± 0.19	1.15 ± 0.16

[a] The number of tree rings was estimated for three stem disks with unclear, degraded or rotten rings around the pith

[b] The mean diameter was reconstructed from the increment cores.

[c] Between brackets is the number of sampled trees.

[d] This is the mean diameter growth derived from the mean diameter growth curve, of which the length in years is given between brackets.

Comparing the mean diameter growth of the three study regions, the natural forest Mayombe trees grow significantly faster than the plantation trees and the natural forest Ivorian trees ($p < 0.01$) (Table 4.1). However, until the age of approx. 25 years, tree growth appears high and similar in Ivory Coast and the natural Mayombe forest but significantly higher than in the plantation ($p < 0.01$) (Fig. 4.2). Mean diameter growth after 40 years is still lower in the plantations but the differences are no longer significant. Mean diameter growth curves of bootstrapped simulations are very similar to the original mean diameter growth curves in the Mayombe. Only in Ivory Coast, diameter growth seems slightly overestimated until 25 years but quite underestimated afterwards (Fig. 4.2).

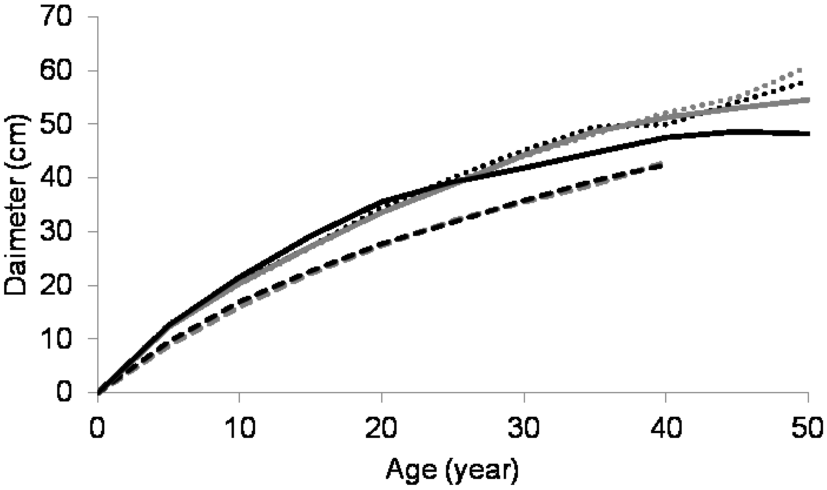


Fig 4.2. Mean diameter growth curves for the natural forest of Ivory Coast (solid line), the natural forest of the Mayombe (dotted line) and the plantation of the Mayombe (dashed line). The equivalent bootstrapped mean growth curves are shown in grey.

The individual diameter growth curves (Fig. 4.3) show that the variability in growth is high, especially in the Ivorian trees and in the Mayombe plantations. No difference is found between the two natural forests, based on the individual diameter growth curves. In the plantation, however, two separate groups are noticed (Fig. 4.3c): trees with diameters smaller or larger than 30 cm. The smaller diameters are significantly younger than the larger diameters (34 years versus 43 years, $p < 0.05$). Also, the larger trees grow significantly faster than the smaller trees ($p < 0.001$). Mean diameter growth and age show negative correlations for natural forests whereas positive correlations characterise the plantation (Table 4.2). The same is true for mean diameter growth and diameter relations.

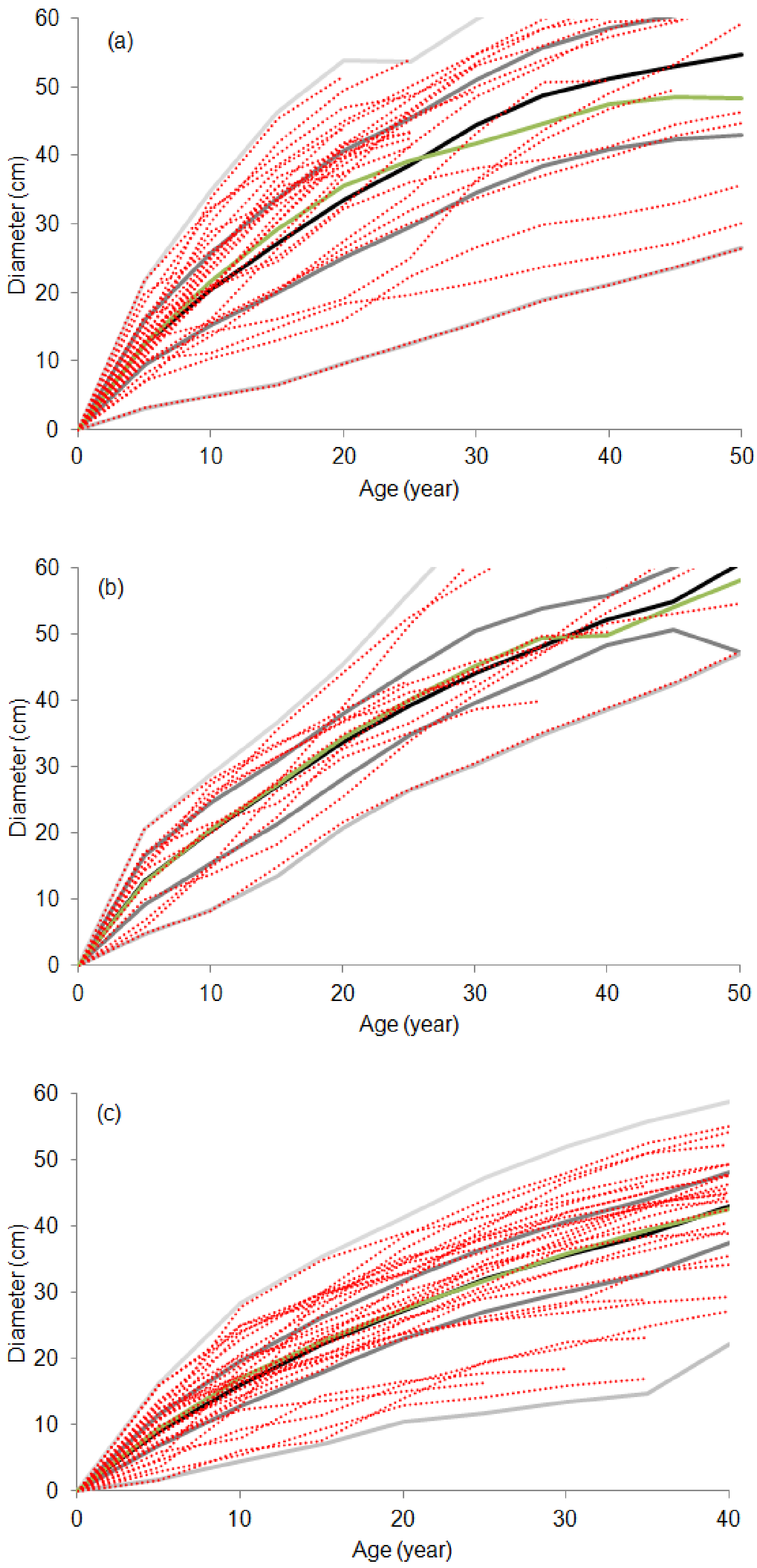


Fig 4.3. Individual diameter growth curves for the three study regions with (a) the natural forest in Ivory Coast, (b) the natural forest in the Mayombe, and (c) the plantation in the Mayombe. The dotted red lines are the original individual growth curves, the green solid line is the mean growth curve based on the these individual growth curves and the black line is the mean growth curve based on bootstrapped simulations. The two light grey lines delimit the range of all simulations and the two dark grey lines delimit the range of the mean growth curves based on a set of simulations equal to the amount of original individual growth curves available (1000 mean growth curves, each based on a subset of simulations).

Table 4.2. Correlations of age, diameter, height, and mean diameter growth. Mean diameter growth is defined as twice the mean tree-ring width of the tree-ring series. The number of samples included in the Pearson correlation is given between brackets.

	Natural forest Ivory Coast	Natural forest Mayombe	Plantation Mayombe
Diameter–height	-0.05 (19)	0.79*(7)	no data
Age–diameter	0.70*** (29)	0.34 (12)	0.77*** (29)
Age–mean diameter growth	-0.78*** (29)	-0.78** (12)	0.36 (29)
Diameter–mean diameter growth	-0.60*** (29)	-0.29 (12)	0.87*** (29)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4.3.2 Analysis of growth changes

At the individual tree level, the canopy accession pattern ‘no sustained release’ is found in more than 50% of all trees, independent of the forest region/type (Fig. 4.4). The second most important canopy accession patterns is ‘one sustained release’, found in 20 to 25% of the natural trees, whereas growth suppressions are more frequent in planted forests (ca. 20%). At the forest region/type level, no growth releases/suppressions were found in the mean basal-area growth curves.

Trees without growth releases/suppressions or one suppression reached the canopy (i.e., a diameter of 30 cm according to Clark and Clark 1999) on average after 18 years. Trees with one release or multiple releases and/or suppressions reached this diameter significantly later, after 25 to 30 years. Trees with the most abundant accession pattern (no sustained release) are significantly younger (40 compared to 54 years) and faster-growing (1.33 compared to 0.99 cm year^{-1}) than the trees with other accession patterns ($p < 0.05$). Trees with one suppression are older (44 years) and slower-growing (1.03 year^{-1}) than trees without major growth changes but only the difference in growth rate is significant.

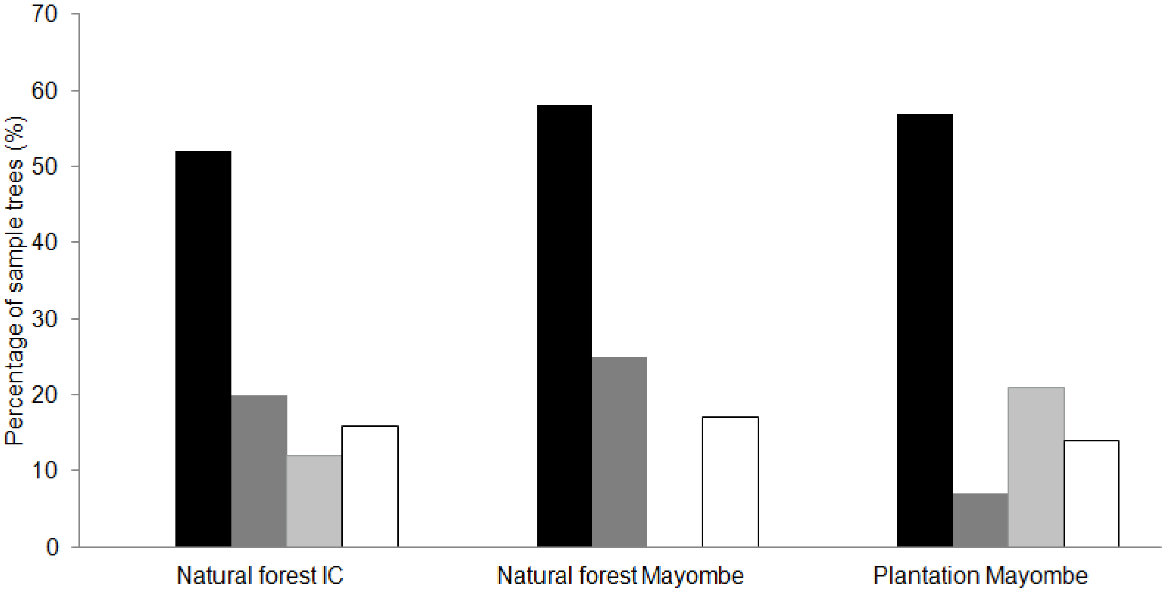


Fig 4.4. Percentage of accession patterns, based on basal-area increments. Black bars represent ‘no sustained releases’, dark grey bars represent ‘one sustained release’, light grey bars represent ‘one suppression’, and white bars represent ‘multiple releases and suppressions’.

Growth suppressions were not related to one principal diameter or age class (data not shown) when based on basal-area increments. In all three forest regions/types, growth releases occurred mostly between 10 and 20 year and between 10 and 30 cm (Fig. 4.5).

In the plantations, the longest growth releases were found in the 1970s and the longest growth suppressions from 1993 to 1997. In Ivorian natural forests, growth releases were longest during 1974-1986. Natural Mayombe trees did not have a sufficient number of growth releases and suppressions to distinguish peak periods for growth releases and suppressions.

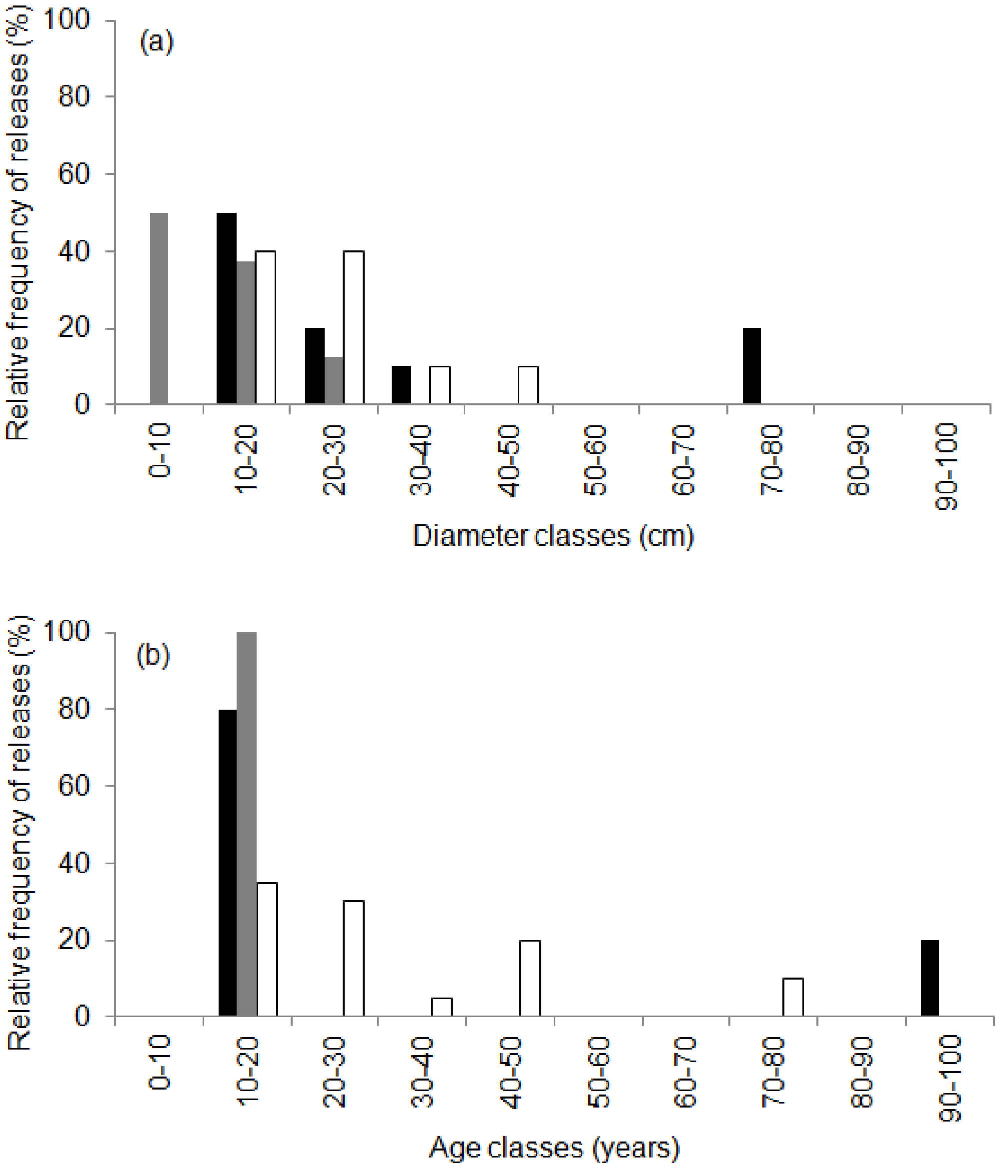


Fig 4.5. Relative number of growth releases (%) compared to the total number of trees/region: (a) for diameter classes, (b) for age classes based on basal-area increments, in the three forest regions/types. Black bars represent the natural Mayombe forest, grey bars the plantation in the Mayombe, and white bars the natural forest in Ivory Coast.

4.3.3 Minimum logging diameter (MLD) and biological rotation age (BRA)

Diameter and stem height of Ivorian trees showed no relation (Table 4.2) and could not be modelled. Therefore, in Ivory Coast, the volume based MLD was not calculated. For the natural and planted forests of the Mayombe such a regression was possible ($R^2 \geq 0.37$, $p < 0.01$). For the plantations without height measurements, the diameter-height regression from a large plantation inventory of *T. superba* was used (Chapter 2).

Based on actual and simulated growth curves, the optimum MAI_V and MAI_{BA} of the Mayombe plantations is lower than in natural forests (Fig. 4.6) and this optimum is reached about 15 years later in plantations (data not shown). The actual MLDs of plantations and natural forests in the Mayombe appear similar but the distributions of simulated MLDs show considerable differences (Fig. 4.7): the actual MLD for natural forests is located in the left part of the distribution whereas the actual MLD for the plantations is located near the maximum of the distribution. In general, the MLD and BRA of natural forests associated with the optimum MAI_{BA} result in lower values than those associated with the optimum MAI_V. Ivorian trees had the lowest MLDs and shortest BRAs, based on basal area calculations. In the latter case, the calculated MLD differed clearly from the distribution of MLDs.

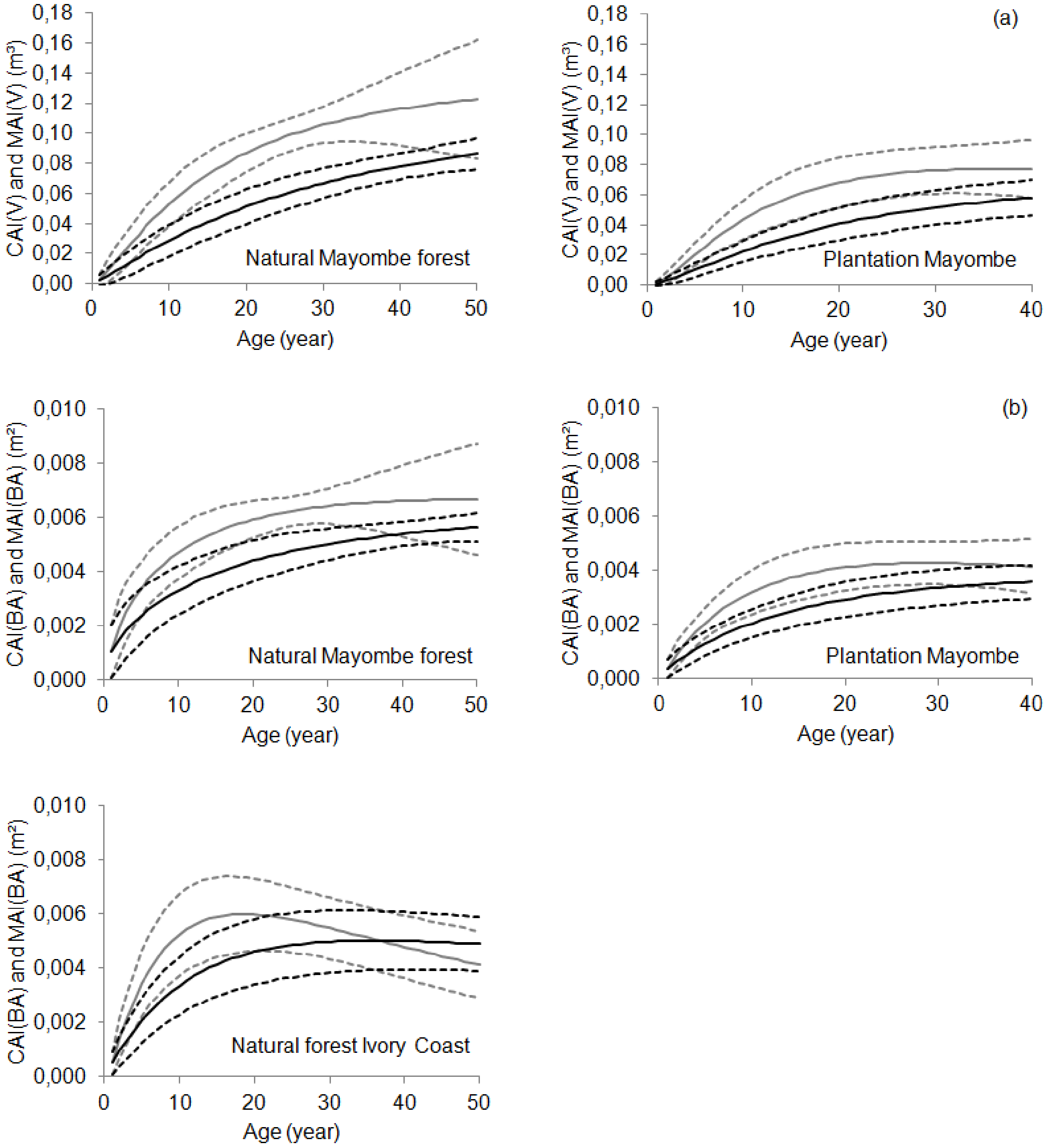


Fig 4.6. Current (CAI: grey line) and mean (MAI: black line) annual increments of bootstrapped data and 95% confidence intervals (dashed lines) for the three forest types/regions. Based on (a) volume, graphs were calculated for natural and planted Mayombe forests. Based on (b) basal area, graphs were calculated for natural Mayombe forest, planted Mayombe forest, and Ivorian natural forest.

The actual MLD of natural Mayombe trees based on volume is found beyond the actual dataset but extrapolations are small. The actual BRA of natural and planted forests of the Mayombe is also found at ages higher than 40 or 50 years but all values are part of the distribution of simulated BRAs. Histograms of the BRAs are not shown in Fig. 4.7 because the distributions are similar to those of the MLDs.

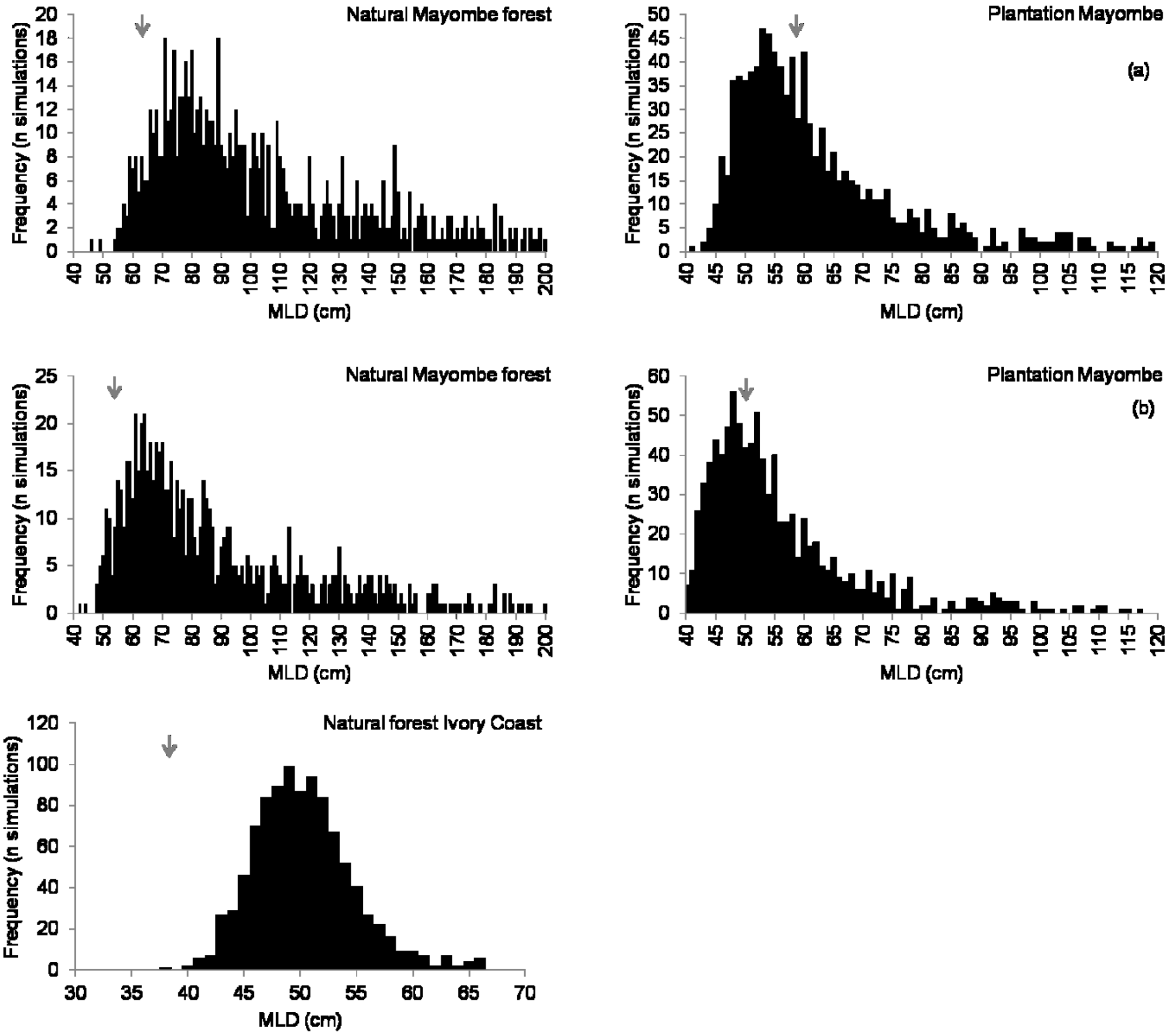


Fig 4.7. Histograms of minimum logging diameters (MLDs) based on (a) volume and (b) basal area. The arrow indicates the value of the MLDs based on the original sample dataset.

Some simulations of growth curves did not lead to a logical MLD/BRA (values < 10 cm or years and values > 200 cm or years). The percentage of inconclusive simulations was about 25% in natural Mayombe forests and about 7% in planted Mayombe forests. All simulations lead to logical MLDs/BRAs in Ivory Coast.

4.4 Discussion

4.4.1 Analysis of temporal growth patterns

Pioneer species such as *T. superba* often have a known and strong age trend, especially in planted forests (Chapter 3). Ring widths are subjected to a decrease over time, even when approximately the same cross-sectional area of wood is added (Stan and Daniels 2010). Because of this size-related trend, the M_1 values were relatively larger for smaller diameter trees when ring widths as opposed to basal-area increments were used. Stan and Daniels

(2010) concluded that the calculation of growth releases/suppressions with basal-area increments was more appropriate for sites with large inter- and intra-species variability in tree size, similar to the variability in our forest regions/types.

Generally, at tree level, the canopy accession pattern of ‘no sustained release’ is most abundant and can be linked to the light-demanding and fast-growing character of the tree species (Brienen and Zuidema 2006). More than half of the planted and natural *T. superba* trees reached the canopy without suppressions or releases, suggesting that competition for light was not a significant problem. In closed moist forests with (non-pioneer) shade-tolerant species, releases are mostly recorded (Simkin and Baker 2008). Our study found growth releases mostly take place during the juvenile phase, as did Brienen and Zuidema (2006). They suggested two causes that could also apply for *Terminalia* trees: larger temporal shifts in light levels for trees in the understorey; or, and more likely, weaker responses by large trees to increased light levels. Next, Brienen and Zuidema (2006) also found suppressions in larger trees that could be provoked by, e.g., liana manifestation or forking, two common phenomena observed for *T. superba* trees. Trees with multiple growth releases and/or suppressions were also found, however, so canopy accession patterns differ not only between but also within species, as is reported by Baker and Bunyavejchewin (2006) and Brienen and Zuidema (2006).

Brienen and Zuidema (2006) suggested that trees without major growth changes reached the canopy in the shortest time, and those with multiple releases and suppressions needed the most time. This was true for *T. superba*. Trees that reach the canopy without showing growth releases/suppressions are younger and faster-growing than the trees with other accession patterns. Although trees with growth suppressions reached the canopy after a similar period, they still grew significantly slower than the trees without distinct growth changes. This phenomenon could be linked to the ‘juvenile selection effect’ that Rozendaal et al. (2010) discuss. They define this effect as the higher chance of fast-growing (juvenile) trees to reach the canopy compared with slow-growing (juvenile) trees.

Growth releases and suppressions based on basal-area growth were also calculated for the three mean basal-area growth curves. This reveals that major growth changes only took place on a small scale, not at the site level. Finally, the influence of precipitation on growth releases/suppressions was analysed and no significant relations were found. The methodology of Nowacki and Abrams (1997), who used large timeframes to rule out the influence of climate, appears to be suitable for *T. superba*.

The lower diameter growth rate in the plantations is remarkable, even if we compare with the bootstrapped mean growth curves (data not shown). Based on the sample trees, the correlations between mean diameter growth and age/diameter show opposite signs for planted and natural forests (Table 4.2). This is probably caused by the ‘reversed’ patterns of diameter growth rates over time: plantation trees grow slowly during the juvenile phase and have a higher growth rate later on (Table 4.1), whereas natural forest trees grow quickly during the juvenile phase and slower at older age. Still, not all planted trees had similar growth patterns: evidence is given that fast- and slow-growing trees could be distinguished with a diameter threshold set at 30 cm. This diameter is also known as the diameter at which trees enter the canopy (Clark and Clark 1999). Although the smaller diameters are significantly younger than the larger diameters, they probably did not regenerate in one specific year below the older trees because the age distribution of the plantations is unimodal Gaussian shape (data not shown). These younger trees clearly tolerated some shade from the larger, older trees. Most likely, planting processes as well as regeneration from old seed trees/replanting played an important role in the stand structure of the plantations. Regeneration under crown cover is rarely met in (long-lived) pioneer species, but Alvarez-Buylla and Martinez-Ramos (1992) also found such natural regeneration of *Cecropia obtusifolia* Bertol., a neotropical pioneer tree.

4.4.2 Evaluation of the minimum logging diameter (MLD) and biological rotation age (BRA)

One of the most important parameters within the concept of sustained yield is the MLD, a cutting limit that can be calculated based on dendrochronological analysis of tree growth. Although the MLD can also be determined by basal-area increments (Bogino and Villalba 2008; Dorado et al. 1997; Verzino et al. 1999), studies in the tropics mainly focus on a volume-based MLD (Leoni et al. 2011; Nebel et al. 2001; Schöngart et al. 2007; Schöngart 2008). Two fundamental conditions for this volume-based MLD are height measurements and the existence of a significant age–diameter and diameter–height relation, as described by Schöngart (2008). Although Metcalf et al. (2009) concluded that size and age were not always associated by using a single parameter, the age–diameter relation was positive in most studies, e.g., Worbes et al. (2003), Baker et al. (2005) and da Fonseca et al. (2009). Our study confirms this positive correlation in the different forest regions/types. However, diameter and height only correlated strongly for the Mayombe plantation and natural forest trees, similar to the results of Leoni et al. (2011) and Worbes et al. (2003).

The use of volume-based CAI and MAI is thus limited by the aforementioned conditions. Height measurements for standing trees are especially prone to large measurement errors (Chave et al. 2004; Rondeux 1999). There is no need for these measurements if the optimal CAI and MAI of the basal area are used. Basal-area growth was derived from the sigmoidal regression, enabling the calculation of the MLD and BRA for the natural forest in Ivory Coast. The use of a rather limited set of growth curves, however, induces rather large uncertainty on the calculated MLD/BRA, both volume and basal-area based. Therefore, Brienen et al. (2006) developed an original bootstrapping method which was validated on tropical growth curves.

Whereas distributions of MLD/BRA are narrow in Ivory Coast and larger in the plantations in the Mayombe, the variation in both values is very large in the natural Mayombe forest, probably due to small sample size (only 12 trees). The sample trees of the different forest regions/types seem nevertheless to be representative for the Mayombe: the generated MLD/BRA histograms show that the mean calculated MLD/BRA is situated within the distribution of simulated MLD/BRA values. Also, there is a high correspondence between the measured and simulated mean growth curve. This correspondence was less clear for Ivory Coast. The 28 trees appear not to be representative for the population and seemingly underestimate the MLD/BRA. Clearly, the influence of growth speed on the MLD calculations is considerable. More individual growth curves are needed at higher age to be able to conclusively decide on the average growth pattern in Ivory Coast.

Generally, the MLDs/BRAs of basal-area based simulations are lower than for volume-based simulations but only small differences are observed in the shape of the distribution of MLDs/BRAs between basal-area and volume-based simulations. Bootstrapping of growth curves as such is useful in tropical forests where sampling is not straightforward and growth variations are usually large. Although the actual MLDs based on a limited dataset can look similar (cf. natural and planted Mayombe forests), the distribution of possible MLDs is quite different for both forest types. Such a mathematical technique however is based on a set of biological principles and depends on the sample trees included and the data limits imposed. Bootstrapping was applied here taking into account certain diameter and age limits. Including the oldest/largest trees, which are actually quite rare too, considerably changes the mean growth curves and the fitted sigmoidal functions that are used to calculate the MAI curves. Also, not all simulations lead to a logical MLD or BRA value, as such pinpointing at the limits of the actual measured tree-ring dataset. Sufficient sampling and thorough knowledge of the actual dataset are essential to cautiously interpret bootstrap results.

The relatively low MLDs and BRAs in Ivory Coast, compared to the natural Mayombe forest, are possibly related to the slightly higher diameter growth during the first two decennia (Fig. 3.2) combined with a less representative data set. The plantations also probably recovered partly after slow growth during the juvenile phase (Table 4.1, mean diameter growth rates after 25 and 40 years) because BRA is higher but still at a diameter that does not significantly differ from the MLD for natural Mayombe forest. The growth-oriented MLD/BRA is therefore not only site specific: it can also vary considerably within sites and depends on the growth variable used (volume or basal area). This is in line with the work of Schulze et al. (2008), reporting that a static MLD is not reconcilable with different specific life histories, local population structures, and stem densities.

Nowadays, legal MLD values are static, rather high and often result in increased exploitation (Sist et al. 2003). MLDs are mostly determined by law, whereas BRAs appear less strict. In

Liberia and Ghana, the MLD for *T. superba* has been fixed at 70 cm; in Ivory Coast, Gabon, and DRC, at 60 cm. The rotation that is often applied in plantations is 40 years, but under optimum conditions it can be as short as 20–25 years (Kimpouni 2009). The fixed MLD of 60 cm is part of the simulated range of MLDs for the natural Mayombe forest, although it is located in the left tail of the distribution (Fig. 4.7). Most of the simulated MLDs for planted Mayombe trees and natural trees in Ivory Coast are smaller than 60 cm, so the legally fixed MLD probably does not lead to overexploitation. The suggested BRA of 40 (Kimpouni 2009) to 60 years (Humblet 1946) seems also valid for Ivory Coast and planted Mayombe trees compared with the histograms. Only in the natural forests of the Mayombe it is recommended to use slightly higher BRAs than those suggested (left tail of the distribution).

Finally, the MLD and the associated BRA should also take into account the tree physiology (Sist et al. 2003): the BRA should be larger than the fructification ages of *T. superba*. If trees are being cut earlier, regeneration is hampered. In the Mayombe, fructification takes place from year 23 onwards. In Ivory Coast, fructification is mentioned from the age of 15 years (Ngueho-Yemele 2004). In all forest regions/types, MAI_V and MAI_{BA} culminate later, thus causing no regeneration problems. Whether MLD/BRA based on volume or basal area is a better choice, with or without bootstrapping, is hard to decide based on this study alone. Based on the calculation of a growth-oriented MLD and knowledge on the forest structure (growth changes), long-term management planning is documented and founded on scientific data.

4.4.3 Timing and type of silvicultural management

The importance of forest management and the positive influence on growth has previously been demonstrated in Amazonian rainforests (Peña-Claros et al. 2008; Schulze et al. 2008). Long-term growth data are indispensable for such sustainable management plans (Therrell et al. 2007). Not only does tree-ring analysis uncover the behaviour of a long-lived pioneer species, it is especially important to determine the need for and the timing of silvicultural treatments. So far, growth releases/suppressions were not really related to management planning. Brienen and Zuidema (2006) used the growth releases/suppressions in the tropics to evaluate varying growth patterns and age, whereas Baker et al. (2005) used large-scale growth releases/suppressions to study the long-term disturbance history of forests.

Defining one management strategy for natural and planted forests in two distant regions is rather complex because large variations in mean growth rates and growth curves exist between individual trees as well as between different regions/forest types. Still, long-distance relations in growth were found (Chapter 3), and, independent of forest type/site, more than half of all planted and natural trees reached the canopy without real growth events.

The theoretical approach for silvicultural treatments in natural and planted forests in the Mayombe and Ivory Coast appears similar. Intensive treatments are not necessary because many trees already reach the canopy at young ages without major growth changes. If treatment is considered, it is preferably recommended in plantations (as production forests) and during the juvenile phase of tree growth because of the 'juvenile selection effect', which has been confirmed using growth releases/suppressions. Slow-growing juvenile trees risk remaining slow-growing throughout their lifespans, hampering canopy accession. Two silvicultural treatments can be performed at the same time: removal of lianas, and thinning. In the Mayombe, lianas were a considerable problem in plantations and cutting them could not only avoid forked stems but could also lower the calculated MLD and the associated BRA; a similar effect was mentioned by Nebel et al. (2001). Furthermore, the removal of lianas could reduce the competition for soil water and soil nutrients (Villegas et al. 2009), protect the neighbouring trees, and protect loggers (Putz et al. 2008). Additionally, small-scale thinning of faster-growing trees during the juvenile phase stimulates juvenile growth of slower-growing trees and generates valuable wood volumes for local uses. Herault et al. (2010) confirms that trees with low inherent diameter growth rates benefit the most from gaps, e.g., by thinning. Brienen and Zuidema (2006) as well as Herault et al. (2010) observed that large trees become less dependent on gaps: they intercept more light due to their canopy position. The number of growth releases/suppressions per decade/diameter class also decreases in larger *T. superba* trees. Small-scale thinnings are recommended, as they are completed before the fructification age and regeneration should not be endangered.

There are also other (practical) reasons that support the management of planted *T. superba* forests. First, planted forests are easier to access while trees are still young. Also, the age of trees is generally known, and shows little variation (even-aged forests), enabling foresters to distinguish slow- and fast-growing trees by simply measuring diameters. In natural forests, slower-growing juvenile trees are hard to distinguish from faster-growing juvenile trees because of large variations in growth rates (uneven-aged forests). Small diameters can represent young as well as old trees, and the growth characteristics of other species in natural forests in West and Central Africa are mostly unknown; this makes management planning a lot more laborious.

Thus, even without knowledge on the growth-oriented MLD, it is possible to plan silvicultural treatments based on tree-ring analysis, especially in planted forests. We found different MLDs in different forest regions/types. The Schöngart's modified monocyclic system (2008) for fast-growing, light-demanding tree species could be used in planted forests, with one thinning and a final harvest. This final harvest could remove all trees above the calculated MLD, creating gaps for natural regeneration (Schöngart 2008). In the natural forests under study, monocyclic systems can be applied for *T. superba* with a MLD/BRA specified per forest region. The structure of natural forests is complex, however, with a wide variety of species and growth patterns, and requires further research.

4.4.4 Conclusion and perspectives

Tree-ring analysis is a valuable tool for management of natural and planted tropical forests. Growth releases/suppressions based on individual growth curves indicated that *T. superba* does not need intensive management. Only one small-scale thinning needs to be performed in production forests to increase the growth of slower-growing juvenile trees. Actual MLD/BRA values vary considerably among sample sites. Within sites, the range of bootstrapped MLDs varies from 20 cm in the natural Ivorian forest up to 150 cm in natural Mayombe forests. The BRA ranges from 40 years in natural Ivorian forest and 100 years in plantations to more than 200 years in natural Mayombe forest. Based on these results, the introduction of sustainable management can be mainly specified by forest type instead of species level.

Inventories of permanent sample plots (PSP) combined with tree-ring study offer scientists and forest managers the complete picture. Although PSPs are scarce in tropical Africa (Verbeeck et al. 2011), a multitude of variables could be measured periodically, suggesting or evaluating the implementation of silvicultural treatments that promote sustainable management (Herault et al. 2010; Peña-Claros et al. 2008; Schulze et al. 2008). Tree-ring analysis obviously tells the story of successful trees that survived the seedling stage. Further studies should focus on the germination and mortality rates of seedlings, and their relationship to environmental factors. Regeneration studies are recommended along with enrichment plantings to ameliorate post-logging recovery, which is still poorly documented.

Chapter 5

High-resolution proxies for wood density variations in *Terminalia superba* Engl. & Diels

Abstract

Density is a crucial variable in forest and wood science and is evaluated by a multitude of methods. Direct gravimetrical methods are mostly destructive and time-consuming. Therefore, faster and semi- to non-destructive indirect methods were developed. In this study, profiles of wood density variations with a resolution of approx. 50 µm are derived from one-dimensional resistance drillings, two-dimensional neutron scans and three-dimensional neutron and X-ray scans. All methods were applied on *Terminalia superba* Engl. & Diels, an African pioneer species which sometimes exhibits false heartwood. The use of X-ray tomography combined with a reference material permits direct estimates of wood density. These X-ray derived densities overestimated gravimetrically determined densities non-significantly and showed a very high correlation (linear regression, $R^2=0.995$). When comparing X-ray densities with the attenuation coefficients of neutron scans and the amplitude of drilling resistance, a significant linear relation is found with the neutron attenuation coefficient ($R^2=0.986$) yet a weak relation with drilling resistance ($R^2=0.243$). When density patterns are compared, all three methods are capable of revealing the same trends. Differences are mainly due to the orientation of tree rings and the different characteristics of the indirect methods. High resolution X-ray computed tomography is a very promising technique for the research on increment cores and will be explored further on other temperate and tropical species. Further study on false heartwood is necessary to reveal the causes of density variations and to see how the resistance drillings can be further refined.

Published in Annals of Botany

De Ridder M, Van den Bulcke J, Vansteenkiste D, Van Loo D, Dierick M, Masschaele B, De Witte Y, Mannes D, Lehmann E, Beeckman H, Van Hoorebeke L, Van Acker J (2011). High-resolution proxies for wood density variations in *Terminalia superba* Engl. & Diels. Annals of Botany 107:293-302

5.1 Introduction

Density is one of the most important variables in forest and wood science since it is as well crucial for understanding tree structures and functions as it is relevant for timber properties and energy content of the material. A lot of density variations within a tree can be ascribed to the anatomical structure of wood, e.g. characteristics of vessels and fibers (Roque and Filho 2007) while wood density also serves as an indicator of wood quality due to its strong positive correlation with e.g. mechanical strength properties (Nepveu 1976). Furthermore, reliable models on biomass and carbon content include density measurements (Chave et al. 2005).

The most common, direct method for estimating wood density consists of a gravimetrical procedure in which wood samples with clearly defined dimensions are weighed and measured with a vernier caliper (Kollmann 1951). In this study, sampling with a Pressler borer resulted in increment cores that were easy to weigh. Their volume, however, was hard to determine due to irregular sample shapes. As such the gravimetrical assessment of wood density is a time-consuming and destructive procedure because increment cores are to be split in small, irregularly shaped pieces. Each subsample has to be weighed and its volume needs to be measured accurately by water displacement methods or via specialized techniques such as gas pycnometry. Moreover, gravimetry is only suitable for low-resolution assessments of wood density variations (mm-scale).

Next to this direct method, numerous indirect methods to estimate wood density exist. Most of those densitometrical methods are based on high-resolution imaging of differences in attenuation of non-visible (short wavelength) radiation by the objects that are studied. In the following overview, methods were ranked by the dimension of their outputs: one-, two- or three-dimensional information.

Typical one-dimensional estimates for density are obtained from tree ring series where tree-ring widths are related to density variations (Alvarado et al. 2010), from resistance drillings (Rinn 1996), the measurement of cell wall thickness on a microscopic level with a transmission light microscope (Decoux et al. 2004) and high-frequency densitometry, which measures relative density variations along wood surfaces using the dielectric properties of wood (Schinker et al. 2003).

Two-dimensional estimates of wood density are typically extracted from radiographies: X-ray (Bergsten et al. 2001; Moya and Filho 2009) and gamma-ray (Macedo et al. 2002) as ionizing radiation techniques, neutron imaging (Lehmann et al. 2001; Mannes et al. 2007), color video camera imaging (Clauson and Wilson 1991), magnetic resonance imaging (Müller et al. 2002) and microwave polarimetry (Kästner and Niemz 2004). However, the two last mentioned methods focus on changes in moisture content for rot detection and the detection of cavities instead of density. Other two-dimensional density estimates can be generated by thermograms (e.g. infrared thermography) (Wyckhuyse and Maldague 2001) and acoustics methods (Bucur 2005; Martinis et al. 2004). Yet again, those two techniques are rather related with decay diagnosis.

Density studies in three dimensions are possible with X-ray (Entacher and Petutschnigg 2007; Freyburger et al. 2009; Skog and Oja 2009), gamma-ray (Macedo et al. 2002) and neutron tomography (Frei et al. 2009). Acoustic reconstruction can also be scaled from 2D up to 3D by performing measurements at different heights. Nevertheless, the reconstruction is based on 2D images that are interpolated over considerable distances (intervals of 50 cm) (Bucur 2005), gaining rather low-resolution information on the dispersal of decay.

From the abovementioned methods, the use of ionizing radiation probably has the longest tradition in the field of research on wood density (Bucur 2005; Lehmann et al. 2001; Lenz et al. 1976; Lindgren 1991; Polge and Nicholls 1972) and the highest resolution, up to sub-micron level (Trtik et al. 2007; Van den Bulcke et al. 2009). Both X-ray and neutron imaging are applied in this study, but the equipment is expensive and bound to the laboratory. Especially the number of neutron imaging beam lines is very low. Therefore, the results of these lab methods are compared to resistance drillings, which are obtained with a fast, low cost, semi-destructive technique that is employable in the field. In addition, all three techniques are compared to standard gravimetrical analysis.

The studied tree species is *Terminalia superba* Engl. & Diels (commercial name: limba), a pioneer species, characterized by large buttresses and typically found in secondary forests and fallows (Groulez and Wood 1985). Limba has a very large distribution area (from Sierra Leone to Angola) and is one of the major veneer timber species exported by African timber producers (Lamprecht 1989). Nevertheless, this tree species also has some characteristics that alter its popularity: the formation of a darker heart in some cases (false heartwood, in this case the so-called *limba noir*) and heart rot in older trees. From a commercial and ecological point of view, the assessment of a tree and its characteristics before harvesting is important, especially in the tropics, in order to limit the impact on the forest. We consider limba as a model species where precise information on density fluctuations in the trunk might be relevant to judge the presence of either unwanted heartrot or sought-after heartwood figures. During this study, density in limba trees and increment cores was estimated in order to answer to the following questions: Do microdensitometrical profiles assessed by means of high-resolution CT-scanning correspond with gravimetrically obtained data? Do neutron and X-ray densitometrical scans produce similar microdensity patterns? Are drilling resistance measurements reliable as a quick estimate of these density variations? Can density variations be related to the presence of false heartwood in limba trees?

5.2 Material and methods

5.2.1 Study site

In Western Ivory Coast (6 - 7° N and 7 - 8° W), 11 trees of *T. superba* were sampled at three natural forest sites. The forest of Scio (6 trees) can be classified as a primary forest while the forests of Bin Houye (3 trees) and Goya (2 trees) are young secondary forests, often with cacao plantations in the understory. All three forest types are classified under the Guineo-Congolian regional center of endemism by (White 1983) known as evergreen moist rainforest. Sampling sites were located between 200 and 300 m above sea level. Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March. Mean annual rainfall is approximately 1800 mm; during the dry season from November to February/March, monthly rainfall does not exceed 100 mm (Van Oldenborgh and Burgers 2005). Sampling took place in January 2009, during the dry season. According to (FAO 1986), soils are classified as Ferralsols and Acrisols, i.e. typical acid soils of tropical lowlands.

5.2.2 Materials

From every sampled tree, one or more stem disks were collected and eight radii were marked, equally distributed over the circumference of the stem disk. From the 11 trees, 15 radii on 14 stem disks were selected for detailed density measurements. The selected set includes a large distribution of circumferences and ages, and is representative of trees with and without false heartwood. Tree characteristics are summarized in Table 5.1. All disks were air-dried in the laboratory until they reached a moisture content between 12 % and 15 % as measured with a capacitance moisture meter (Exotek Humitest MC-100S). In this study, wood density is therefore defined as air-dry weight over air-dried volume.

Table 5.1. Characteristics of the 15 stem disks used in this study

Tree code[b]	Circumference stem disks (m)	Number of rings
B3R2	1.26	16
B5R1	1.67	17
B7.1R4	2.02	41
B7.2R7[a]	1.69	37
B7.3R7[a]	1.36	31
G2R3	1.54	24
G8R1	1.37	25
S1R5[a]	2.29	> 100
S2.2R5[a]	2.13	> 100
S2.3R1[a]	1.76	± 100
S2.3R8[a]	1.76	± 100
S4R6[a]	2.22	> 100
S6R5[a]	2.04	64
S7R3[a]	2.04	± 100
S8R1	1.80	40

[a] Trees with false heartwood and/or wood rot.
[b] Tree code: S = Scio; G = Goya; B = Bin Houye; R = radius; X.1 = stem disk taken just above the buttresses; X.2 = stem disk taken halfway the stem; X.3 = stem disk taken just under the crown. The number after the forest site indicates the number of the sampled tree, the number after R the sampled radius.

5.2.3 Drilling resistance measurements

Drilling resistance was measured on air-dried disks (one year after exploitation) with an IML Resi B-400 resistograph. With this tool, the drilling resistance at the front end of a thin drilling needle (maximum length of 40 cm, diameter of 3 mm) is registered along a trajectory from bark to pith at a resolution of 40 µm. The resistance value is expressed as a percentage, a relative measure of power consumption when the needle penetrates the wood (Rinn 1996).

5.2.4 Neutron and X-ray scanning

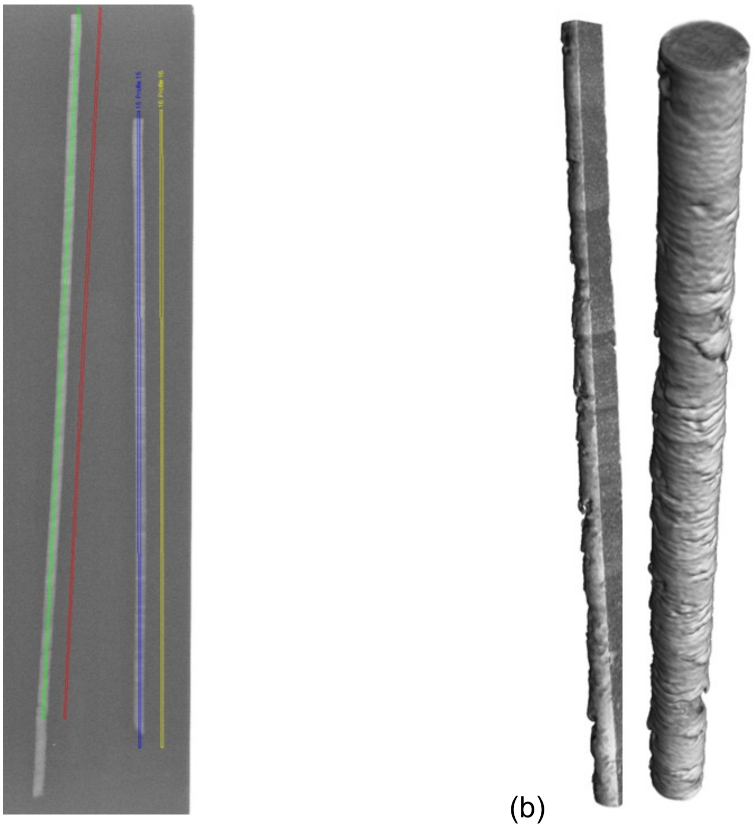
For neutron and X-ray imaging, 15 increment cores with a diameter of 5 mm were extracted from the stem disks with a Pressler corer (Table 5.1). Cores were taken maximum 3 cm away from the resistance drilling. The cores were fixed (but not glued) between two profiled boards to prevent warping. These cores had the same moisture content as the stem disks. No further preparation of the cores was required for neutron and X-ray scans. Extractives were not removed as the difference between bright sapwood and false heartwood was ascribed to their presence (Bauch et al. 1982) and could be the factor to distinguish white from false heartwood.

Neutron imaging

Two-dimensional radiographies of all increment cores were taken at the neutron imaging beamline NEUTRA at the spallation neutron source SINQ of the Paul Scherrer Institute (PSI, Villigen, Switzerland). For general information on the principles of neutron scanning and details on the sampling parameters, reference is made to the work of Mannes et al. (2007). The increment cores were wrapped in aluminium foil and attached to neutron-sensitive imaging plates that function as detectors. After exposure to the neutron beam, information on the imaging plates was read out and digitized with a dedicated image-plate-reader (Fujifilm BAS-2500) at a resolution of 50 µm per pixel. The resulting images (Fig. 5.1a), showing grey levels of neutron beam intensities, were analysed with the AIDA software. Within a rectangular frame of 1 mm width and the length of the increment core (drawn in AIDA) the attenuation coefficients (Σ) from bark to pith are calculated as follows (neglecting possible spatial variation of the intensity):

$$\Sigma = \ln (I_0/I) / D \, (\mathrm{cm}^{-1}) \qquad (5.1)$$

where I_0 is the incident intensity of the neutron beam (grey levels outside the sample), I is the weakened intensity of the neutron beam (grey levels inside the sample) and D is the sample thickness (cm). The grey levels outside the sample were obtained by copying the same rectangular frame to the area outside the sample.



(a) (b)

Fig 5.1. Example of (a) a 2D and (b) a 3D neutron scan. At the left, two increment cores on a neutron-sensitive imaging plate were scanned in 2D. The green and blue rectangular boxes represent I whereas the red and yellow boxes represent I_0 (Eq. 5.1). At the right, you see the 3D reconstruction of an increment core and a slice throughout this core made with Octopus software.

A selection of increment cores was also visualized in 3D with neutron tomography (Fig. 5.1b). Subsamples of six increment cores, with a maximum height of 8.8 cm, were scanned tomographically with a neutron sensitive CCD detector at a resolution of 86 µm. The data was reconstructed with the Octopus software package (Vlassenbroeck et al. 2007) and uploaded in MATLAB® for subsequent image analysis. Straightforward segmentation of air and wood allowed calculation of mean attenuation coefficients for each slice. The edges of the samples were excluded from analysis. Both 2D and 3D neutron scans were examined and compared to the results of 3D X-ray scans.

X-ray imaging

The CT scanner used in this study was built at the Ghent University Centre for X-ray Tomography (UGCT, http://www.ugct.ugent.be). To obtain a resolution of 50 µm, all cores were scanned with a closed microfocus X-ray tube reaching a spot size of approximately 30 µm. Increment cores were mounted in a custom-made holder made of a reference material with known density (Fig. 5.2). This material was chosen as its atomic composition and density approach the composition and density of wood cell walls (1.56 g cm^{-3}) (Kollmann 1951). By using this material and including the average grey level of air (zero density), grey values of reconstructed increment cores can be directly converted to densities.

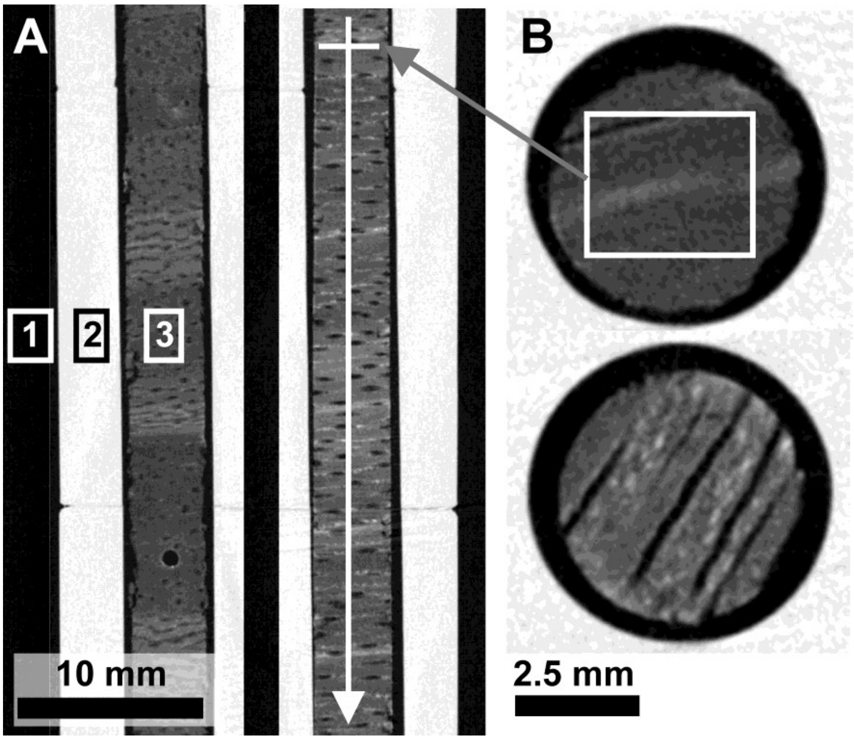


Fig 5.2. (a) X-ray scan of the reference material and increment cores: sectioning longitudinally through the holder (2) with 2 increment cores of limba sectioned in different directions (3) and air (1) with indication of the travel direction of the frame used for average density calculation. (b) Cross-section through 2 cores, with the rectangular frame shown as overlay on the upper core.

Calibration of grey levels into densities was done by applying the following formula:

$$D_i = D_{holder} * (G_i - G_{air}) / (G_{holder} - G_{air}) \qquad (5.2)$$

where D_i = absolute density value of voxel i (g cm^{-3}), D_{holder} is the absolute density value of the reference material (1.45 g cm^{-3}), G_i is the grey level of voxel I, G_{air} is the grey level of air and G_{holder} is the grey level of the reference material. A voxel is a volumetric pixel, representing a volume on a regular grid in a three dimensional space.

A fast and automated CT-scanning protocol was developed at UGCT (unpublished) for high-throughput 3D-analysis of microdensitometry on increment cores. Helical X-ray scanning reduces the time required to perform a full 3D-scan and volume reconstruction in comparison to classical tomography. The maximum length that could be scanned in one operation was 16.3 cm. Therefore, some increment cores were split up and the parts were scanned separately. Broken increment cores were orientated correctly and recomposed with glue. Split or broken parts were stitched manually. After scanning and reconstruction, a rectangular window was placed in tangentially oriented slices (i.e. LT-slices, see Fig. 5.2) and the average grey level within this window was calculated. In addition, the average grey levels of air and of the reference material were also calculated. The average X-ray density of the wood within the window was then transformed to an absolute density value using Eq. 5.2. This results in a 1D-microdensitometric profile based on a 3D X-ray scan of the increment core.

5.2.5 Gravimetric method

Twenty-one reference samples with a maximum length of 1.6 cm were extracted from three increment cores and their gravimetrical density, air-dried weight divided by air-dried volume, was determined. These reference samples were selected based on the largest possible range of densities observed in the microdensitometrical profiles and with respect to their location within the increment core.

The air-dry weight was determined with a laboratory balance (readability of 0.0001 g). The air-dried volume of the reference samples is determined with a sliding caliper as a first approximation (volume of a cylinder) and on 3D X-ray scans of the samples with a resolution of 25 µm (cone beam). For this volume measurement, reference samples were again mounted in a holder made of the chosen reference material to determine the density profile at the same time. These small cylindrical samples were extracted from the reconstructed dataset manually and air and wood were segmented based on greyscale thresholding. The volume of each cylindrical sample was then calculated on a binarized and mathematically filled version of the sample.

5.2.6 Data analysis

On the reference samples, mean density values from the X-ray scans are compared with the gravimetric results (ANOVA, SPSS 16.0). The results of this analysis also allow evaluating the reference material. Linear regressions between the gravimetric densities, mean X-ray derived densities, mean neutron attenuation coefficients and mean drilling resistance values are tested in SPSS 16.0. Next, the complete profiles are transformed with MATLAB® (simple linear interpolation) to a resolution of 50 µm, i.e. to the resolution of the density profiles obtained with the X-ray scans. Neutron scans also had this resolution but resistance measurements had a resolution of 40 µm. The correlation between the different indirect methods is analyzed with TSAP-Win Scientific™ 4.64, a program for the measurement and analysis of tree ring data. Within the module 'Cross-date', the different profiles are shifted until they reach the best fit based on the t-value of Baillie-Pilcher (TV_BP) and the cross-correlation (% CC). In general, significant values for these two statistical parameters are fixed at 3.0 for TV_BP and 60 for % CC (Rinn 2003). Complementary visual control is indispensable and can overrule the statistical results. For all samples, the presence and location of false heartwood is known. The density values inside and outside the border of this false heartwood have been examined for trends and the location of peak densities and tree ring borders has been determined.

5.3 Results

5.3.1 Gravimetric method versus indirect methods

Gravimetric densities and densities resulting from the X-ray scans on 21 reference samples have a normal distribution, are homoscedastic ($p < 0.05$), and do not differ significantly ($p = 0.31$). The linear relation between gravimetrical (X-ray volume based) and X-ray derived density is positive and highly significant, $R^2 = 0.995$ ($p < 0.01$). Densities derived from X-ray scans overestimate the gravimetric density by 9 % on average, based on manually segmented volumes in X-ray images (Fig. 5.3), whereas this is only 6 % for volumes determined with a sliding caliper. Highly significant positive relations ($p < 0.01$) are also found between the gravimetric density and the attenuation coefficients of 2D neutron scans, $R^2 = 0.986$. Only drilling resistance is not directly related to the gravimetric density for the reference samples, $R^2 = 0.243$.

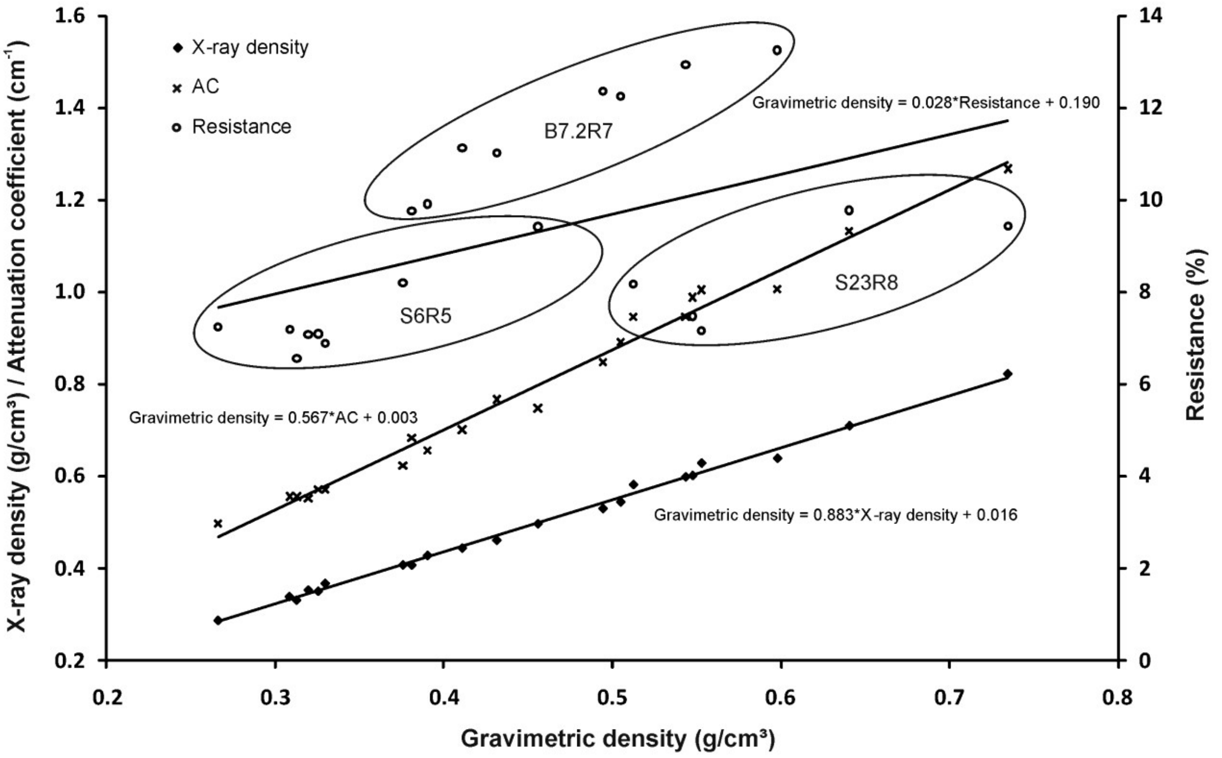


Fig 5.3. Gravimetric density (g cm^{-3}) and the relation with mean density of X-ray scans (g cm^{-3}), mean 2D attenuation coefficients of neutron scans (cm^{-1}) and mean resistance (%) of drillings on 21 reference samples. The relation between gravimetric and X-ray density is linear, the same holds for gravimetric density and neutron attenuation, but the relation between drill resistance and gravimetric density is rather weak.

The mean X-ray derived density (mean of all increment cores) is 0.55 ± 0.07 g cm^{-3}, which is in agreement with the air-dry density mentioned in the wood density database of the World Agroforestry Centre (0.48 to 0.65 g cm^{-3}) (www.worldagroforestrycentre.org).

5.3.2 Attenuation coefficients based on 2D or 3D neutron imaging

Visual control (Fig. 5.4) of the fits by TSAP-Win reveals similar trends inside the 2D and 3D based profiles of attenuation coefficients of all six samples, except for S2.2R5 and S2.3R8. This is also reflected by the lower cross-correlation obtained for these two samples (Table 5.2).

Table 5.2. Cross-correlation (% CC) and t-value of Baillie-Pilcher (TV_BP) for the profiles of attenuation coefficients based on 2D and 3D neutron scans (both profiles have the same length, max. 8.8 cm). Significant values ($p > 0.05$) are marked with an asterisk

Tree code	% CC	TV_BP
G2R3	78*	7.2*
S2.2R5[a]	44	7.2*
S2.3R8[a]	12	7.3*
S4R6[a]	88*	16.7*
S6R5[a]	89*	4.1*
S8R1	79*	3.0*

[a] Trees with false heartwood and/or wood rot.

Mean attenuation coefficients for all six profiles based on 3D scans were 19 % (S2.2R5) to 74 % (S2.3R8) higher than those of 2D based profiles. Profiles based on 3D scans also show less fluctuation.

A potential disadvantage is the shift within 2D and 3D based profiles. Fig. 5.4 reveals coincident peaks at the start of the 3D profile but shifts to the right -from 20 cm on- compared to the 2D based profile.

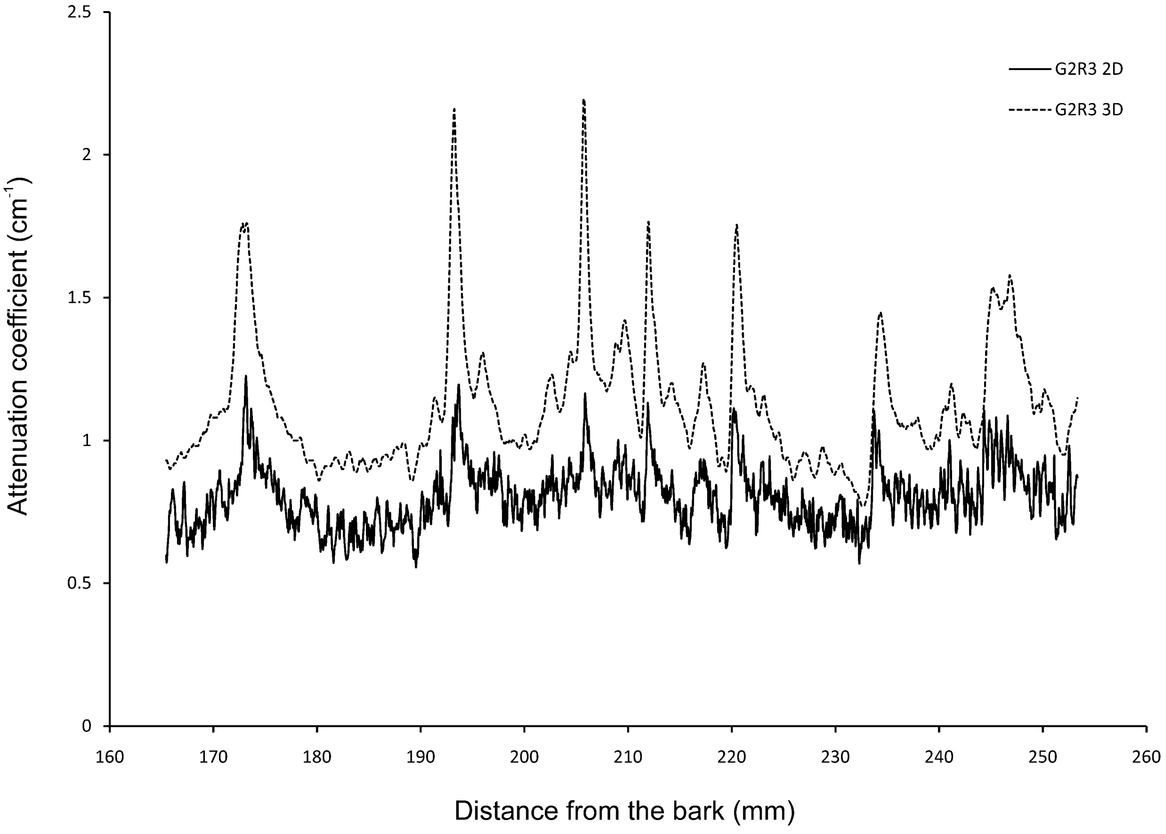


Fig 5.4. Overlay of a 3D and a 2D based profile of attenuation coefficients (cm^{-1}) for G2R3. The solid line represents a profile based on 2D scans; the dotted line is based on 3D scans. The 3D profiles show less fluctuations.

5.3.3 *Comparison of estimated density profiles with X-ray scans, neutron scans and drilling resistance*

Although the statistical parameters used to assess similarity between X-ray densities and 2D attenuation coefficients are not always significant (Table 5.3, Fig. 5.5), 13 out of 15 samples were visually matched. Only two cores were rejected: G2R3 because of an irregular shift between peak densities and peak attenuation coefficients and G8R1 because of a diagonal crack that causes a large gap between densities and attenuation coefficients which could not be stitched manually. However, 3D attenuation coefficients and X-ray densities all showed sufficient statistical and/or visual agreements.

X-ray density and resistance drilling profiles correspond rather well, apart from the shift in peaks along some drilling profiles. After visual and statistical control, only B3R2, G2R3 and G8R1 were insufficiently matching.

Table 5.3. TSAP parameters of X-ray, neutron and resistance drilling profiles

	X-ray - neutron		X-ray - resistance		neutron - resistance	
	% CC	TV_BP	% CC	TV_BP	% CC	TV_BP
B3R2	52*	3.0	32**	2.0**	2**	8.5
B5R1	73	3.2	42*	6.2	54**	11.2
B7.1R4	83	3.0	85	17.6	76	16.0
B7.2R7[a]	76	3.1	71	4.4	67	8.1
B7.3R7[a]	72	2.3*	66	7.0	60	6.0
G2R3	41**	1.7**	-3	1.4**	-6**	5.6
G8R1	47**	2.0**	18	13.1	32**	5.7
S1R5[a]	46*	2.1*	22*	1.6*	15*	4.1
S2.2R5[a]	68	4.3	48**	4.6	47*	10.5
S2.3R1[a]	65	4.6	62	2.9*	50*	5.2
S2.3R8[a]	59*	4.0	22*	7.5	29**	9.2
S4R6[a]	69	5.1	24*	8.1	27**	8.1
S6R5[a]	78	2.7*	71	9.6	65	7.3
S7R3[a]	76	3.6	55*	3.4	53**	9.3
S8R1	70	2.5*	63	6.0	62	7.6

* values too low according to TSAP measures but visually OK

** values too low according to TSAP measures and visually not OK

While t-values are significant for all comparisons between attenuation profiles of 2D scans and resistance drillings, only 5 out of 15 samples are significantly cross-correlated. After visual control, half of the samples showed an acceptable agreement between resistance drillings and 2D neutron scans. When comparing the 3D scans of subsamples with the corresponding section cut from the drilling resistance profile, a similar pattern is observed: all t-values are significant while only 2 out of 6 samples (S6R5 and S8R1) are significantly cross-correlated (visual control revealed no other options).

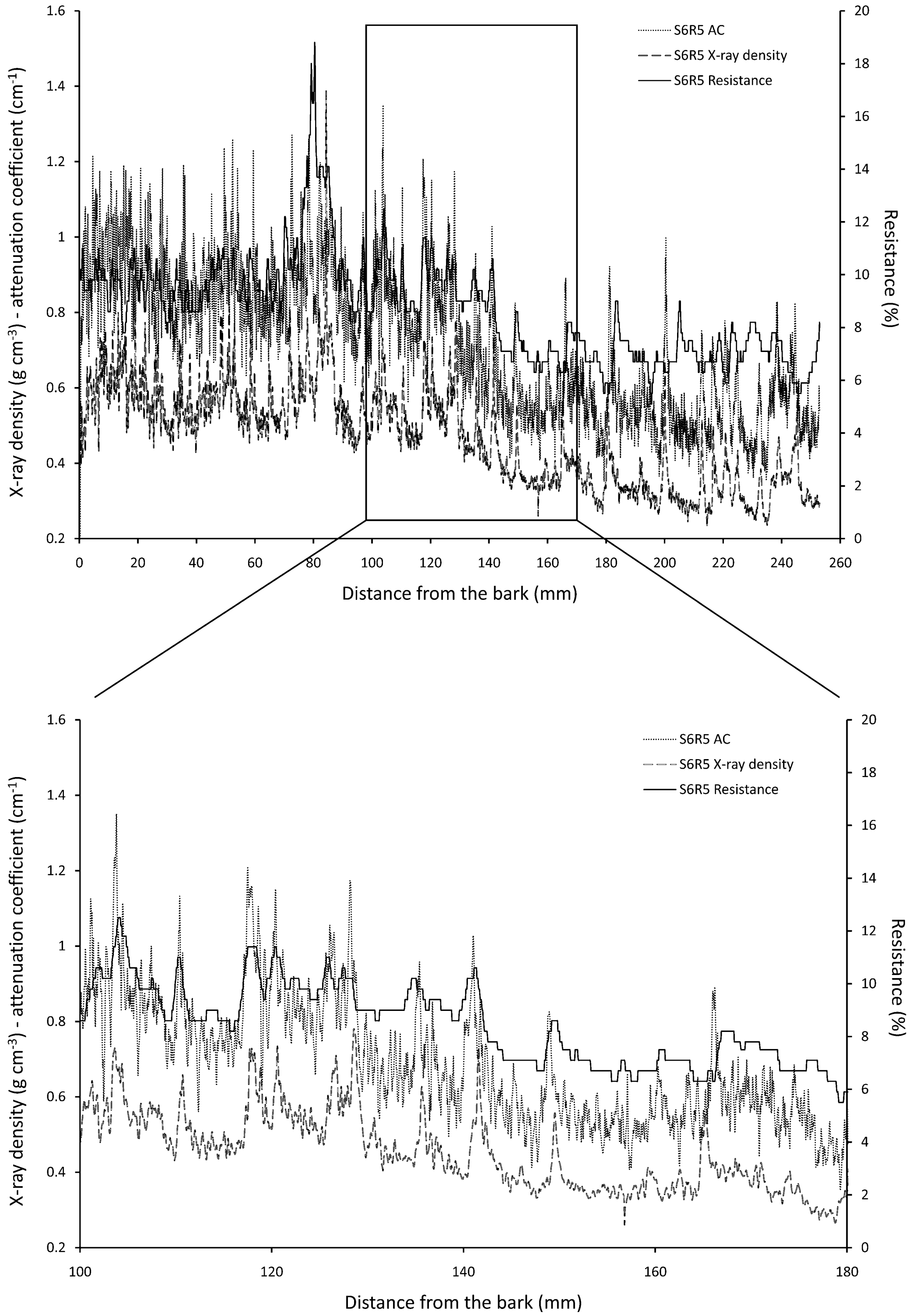


Fig. 5.5. Overlay of X-ray densities (g cm^{-3}), neutron attenuation coefficients (cm^{-1}) and resistance drillings (%) on a false heartwood (S6R5) sample. The box is expanded to visualise details as the shift in peaks of the different methods (from 15 cm onwards, larger shifts become visible). The large peak at 8 cm indicates the boundary between white and dark limba wood.

5.4 Discussion

Microdensitometric analysis of increment cores is a valuable method resulting in important information related to, among others, tree physiology, wood anatomy as well as wood technology. Three techniques were investigated in this chapter and compared to classical gravimetry of smaller subsamples with a large range of densities.

5.4.1 Gravimetric method versus indirect methods

The results in this chapter confirm the high correlation between X-ray density and gravimetrical density (Fig. 5.3), yet gravimetrical density is overestimated by approximately 9 %. Possibly this is due to the composition of the reference material not being 100 % comparable to that of wood as reported in literature (due to the presence of mineral compounds in wood; limba has prismatic Ca crystal inclusions) and the gravimetrical density being measured on supposedly perfect cylinders whereas the X-ray derived density is measured on the central part of the cylinder, avoiding the edges and preventing the incorporation of mixed air-wood voxels. Application of a linear correction factor, similar to what is described in Mothe et al. (1998), based on the gravimetrically determined densities can eliminate the difference. The necessity of a good reference material is clearly stated in literature. In the past, many microdensitometrical studies were performed with classical radiography using film and cellulose acetate wedges for calibration (Koga and Zhang 2004; Martinez-Meier et al. 2008; Moya and Filho 2009; Nock et al. 2009; Polge and Nicholls 1972). Polge and Nicholls (1972) were probably the first to focus on the nonlinear relationship between the optical density of an image on film and the actual density of a specimen. A better calibration method with superior reference materials to improve the accuracy of density measurements was suggested (Lenz et al. 1976; Lindgren 1991, Macedo et al. 2002). Bergsten et al. (2001) found that variations from different machine runs (Woodtrax scanner) were small but could possibly be avoided by using a standard sample with known density. Freyburger et al. (2009) also used a calibration and a validation set of air-dry samples covering a large range of densities, showing a strong linear relationship between wood density and Hounsfield numbers ($R^2 > 0.99$). Although density was not determined exactly, the combination of small cylindrical reference samples of the same species covering a large density range (ca. 0.3 to 0.8 g cm^{-3}) and embedded in a reference material indicates that the protocol described in this chapter is promising for research on increment cores.

The results of neutron imaging are also in accordance with literature (Fig. 5.3). Neutron attenuation coefficients for spruce (Keunecke et al. 2010; Mannes et al. 2007) have proven to correlate well with X-ray wood density ($R^2 = 0.92$) yet no comparison was made with gravimetrical densities. They conclude that neutron imaging is a good alternative to standard

X-ray methods based on films and nonlinear correction and calibrations with a step wedge. In a later experiment, oven-dry gravimetrical density and oven-dry measured attenuation coefficients resulted in an $R^2 = 0.99$ based on four tropical species (Mannes et al. 2009). Attenuation coefficients and oven-dry density of beech and spruce were again closely related: $R^2 = 0.97$, without scattering correction, which is also the case in this chapter since imaging plates were used. Better results are obtainable when using CCD detectors and scattering correction.

Resistance drillings were validated in the past with gravimetric density results and showed moderate to good correlations, depending on the species (Isik and Li 2003; Lima et al. 2007). For dry wood, the drilling resistance correlates with the gross density (Rinn 1996). The results of this study show only a low correlation between gravimetrical density and drilling resistance. This could be due to the generally smaller density variations observed in tropical woods, compared to temperate species. The graph in Fig. 5.3 however shows an interesting finding: the tree cores of which the 21 reference samples were taken are lumped in three separate point clouds. Clearly, drilling resistance depends on more than only density; moisture is one of the factors that play an important role as well (Eckstein and Sass 1994). Samples from the youngest tree (B7.2R7; no false heartwood) have the highest drilling resistance values and average gravimetric density whereas the oldest tree (S23R8; small surface of false heartwood) shows the highest densities and low resistance values. Rot might have played an important role here. The tree of intermediate age (S6R5; false heartwood) has a low density and low drilling resistance. As the results are not unequivocal, further research is necessary but X-ray density might be an important indicator for false heartwood, albeit also age related.

5.4.2 Comparison of estimated density profiles with X-ray scans, neutron scans and drilling resistance

When comparing profiles acquired with the three techniques (Fig. 5.4 and Table 5.3), X-ray and neutron scans show similar patterns with rather distinct peaks. Mannes et al. (2007) found that neutron profiles for spruce appear less noisy and more clearly than the X-ray densitometrical profile, but this is not very distinct here. The two types of curves differed slightly in specific parts and some of the amplitudes of the neutron gradient appear higher than those from the X-ray data, which is also the case with the profiles of limba. It is possible that, in these areas of the sample, different components are crucial for the attenuation of neutrons and X-rays, as they have different interaction probabilities, in particular for hydrogen; neutron imaging is more sensitive to hydrogen than X-ray imaging (Lehmann et al. 2001).

The resistance drilling profiles are less sensitive in comparison with the other techniques. The lag in peak drilling resistance from bark to pith has to be noticed, especially from 170 mm on. Several effects can cause this lag and the lesser accuracy in general. Eckstein and Sass (1994) mention the built-up phase of the needle penetrating the wood. They also observed an increasing trend in drilling resistance from bark to pith due to the properties of the technique and warn that the needle can deflect during the measurement. Chantre and Rozenberg (1997) gave weights to the profiles that were proportional to the distance from the pith. This was due to the decreasing accuracy with the distance from the bark, however it is difficult to discern between a measurement error due to needle bending and a change in drilling resistance of the wood.

5.4.3 Density variations in limba

X-ray density and neutron attenuation coefficients increase from pith to bark in 13 of the 15 samples, which is typical of heliophilous tree species. This increase has also been reported in literature on South American tree species (Montes et al. 2007; Moya and Filho 2009), whereas Nock et al. (2009) showed radial gradients for six tropical species from Thailand that increased with ca. 70% from pith to bark in a shade-intolerant species but decreased with ca. 13 % in a shade-tolerant species. According to Montes et al. (2007), the difference in density between the pith and bark is larger where trees grow faster. They explained this phenomenon by a shift in resources from height growth to structural reinforcement of the trunk as the trees reach the canopy. It can also be expected that wood density is significantly determined by the age of the tree, the climatic conditions and the management regimes (Moya and Filho 2009), yet no density trends are considered in relation to age or growing speed in this study. The lower density for limba at young age could be caused by juvenile wood, as explained by Nepveu (1976) who focused on the important influence of age on the density of *Terminalia ivorensis* A. Chev. in Ivory Coast and the fact that the first 15 years are characterized by juvenile wood with lower densities. Yet wood degradation might be another explanation. The strong decrease in density in trees with false heartwood is striking. Bauch et al. (1982) found heavy incrustations in vessels, fibres and ray parenchyma of false heartwood of *Terminalia*. However, tyloses were very infrequent in false heartwood. Extractives could also affect density, but Mannes et al. (2009) did not find a large influence of extractives as the influence of elements other than carbon, oxygen and hydrogen, seemed insignificant during neutron imaging. They suggest that the extractive content influences the attenuation coefficient only as far as it affects the density. Bergsten et al. (2001) found that the true density of pine is affected by extractives but not the density of spruce. Within the false heartwood, a zone was identified as wetwood associated with bacterial activity. This wetwood (high moisture content) is supposed to increase the density, attenuation coefficients and resistance values (Eckstein and Sass 1994; Mannes et al. 2009). Nevertheless, several increment cores with false heartwood showed sudden peaks followed by a rather abrupt decrease in density, attenuation coefficients and drilling resistance, e.g. for S1R5, S2.2R5, S2.3R1, S4R6 and S6R5. One possible explanation is the destruction of the wooden structure by bacteria and/or other wood destroying organisms that can cause density losses (Klaassen 2008). Eckstein and Sass (1994) observed the same phenomenon in temperate trees (beech, ash) and related this to wood rot; before the profile drops down into the decomposed area, a peak indicates compartmentalization. This peak is interpreted as a defense mechanism of the tree against fungal / bacterial attack. Future research could further focus on this phenomenon, analyzing microscopic slides for bacteria and fungi. Still, in the first place, those microscopic slices could be used to further document causes for differences in density from pith to bark. In chapter 3, e.g., we described how juvenile rings have smaller vessels, less parenchyma and lighter fibre tissue than rings of mature wood. This could have consequences for density but quantitative data are lacking because the resolution of the scans was not sufficient for wood anatomical analysis. Methods like serial sectioning are strongly recommended to document the current gap between density variations and variations in wood anatomy at a microscopic scale, especially in the tropics. Zanne et al. (2010) did not find clear relationships between vessel parameters and density variations in more than 3000 angiosperm species but at an intra-annual scale, Moya and Tomazelo-Filho (2007) found relations between cell wall thickness, vessel percentage and wood density. Therefore, at least vessel and fiber properties should be combined in wood anatomical studies to uncover their relation with density variations.

5.4.4 General performance comparison

Obviously, the X-ray approach is the preferable technique for obtaining high resolution information on density with a relative high speed and easy access to the equipment. With helical X-ray scanning in combination with a reference material, it is possible to approximate the actual density of the wood material. Tomographical imaging is still time-consuming, but compared to the classical use of film and with the advantage of high throughput scanning, the time for the almost automatic retrieval of a densitometric profile for up to 8 increment cores of each maximum 16.3 cm is limited to 2.5-3 hours, with total operator-time being limited to less than 30 minutes (depending on sample imperfections). As such, very accurate results can be obtained and the cores can be scanned at a relatively high resolution of 20 µm in three dimensions without additional sample preparation. Orientation of the samples is still of concern, although tilt is already partially overcome in the reconstruction software. While 2D based neutron attenuation coefficient profiles were reconstructed from a 1 mm wide frame, 3D based profiles were reconstructed from a larger circular surface for every two-dimensional slice. This way, errors due to a weak alignment of the measurement frame with the plane of the tree rings are more dispersed in the resulting profiles. Mannes et al. (2007)

drew profiles on the scans perpendicular to the tree rings but encountered the same problem near the pith of the samples. Polge and Nicholls (1972) found that a ring boundary inclination of 10° in a 5 mm thick sample leads to a blurred profile. Bergsten et al. (2001) found that fiber orientation played an important role, which makes mounting of the samples very important. Both fiber and ring orientation are known to cause poor matching between measured density profiles and visually assessed wood structural variations. Until now, most studies dealing with rather long increment cores for X-ray microdensitometry (e.g., Koga and Zhang 2004; Martinez-Meier et al. 2008; Moya and Filho 2007) did not mention this problem. Bergsten et al. (2001) proposed a method to integrate fiber orientation but fails in correcting for sample mounting and varying thickness of samples in 2D scans (see further). Only recently, a method was developed to correct errors in 3D scans caused by local changes in ring and fiber orientation (Van den Bulcke et al., under review). Fortunately, the wood of *T. superba* is known for its straight grain (Groulez and Wood 1985), as confirmed by random controls of ring and fiber angles on 3D scans, thus limiting variations in density caused by varying fiber angles. Variations in tree-ring angles occur but also remain limited in *T. superba.* Future measurements will integrate these sources of error automatically by applying the procedure described in Van den Bulcke et al. (under review).

Advantageously, microdensity values determined with 3D tomographic methods are not subject to the effects of variations in sample thickness (due to sample shape irregularities) which inherently cause errors when using 1D or 2D imaging techniques. For instance, in classical radiography of 5 mm cylindrical cores, it has been shown that the ‘depth’ of 5 mm only exists in the central pixel at every radial position along the core (Polge and Nicholls 1972). Sample thickness variations have also to be accounted for in 2D X-rays of thin cross-sectional strips (Mothe et al. 1998). By contrast, the grey value of a voxel measured by X-ray CT does not integrate information over a certain depth or thickness, but it represents the relative amount of matter versus void present in that unit volume. The same is valid for 3D neutron tomography. Results indicate that the profiles show less fluctuations due to the larger area per slice that was integrated compared to the densitometric profile extracted from a window on a 2D radiograph (Fig. 5.4). However, this larger reduction of noise offers only a small advantage over the X-ray CT-scanning method as 3D neutron scans are more time-expensive (approx. 5 to 6 h for a 360° scan) and because the latter remains problematic due to neutron beam instability and artifacts. Furthermore, neutron imaging requires using small samples - if not, more extensive scattering corrections are needed - and is available only at a few large-scale research facilities. Nevertheless, resolutions can still be enhanced by improved detector systems, the use of cold neutrons, etc. In essence, both techniques are complementary for research purposes regarding their different sensitivity and the fact that differences can be captured in the contrast of some selected features (Osterloh et al. 2008). Resistance drillings reveal trends within the density patterns and are as such useful, but these profiles do not deliver quick estimates of absolute density. Further study on false heartwood in *T. superba* is necessary to reveal the causes of density variations and to see how the resistance drillings can be further refined.

High resolution X-ray computed tomography is a very promising technique for the research on increment cores and will be explored further on other temperate and tropical species. In addition to the assessment of microdensitometric profiles, the proposed X-ray CT-scanning method also opens possibilities for quantitative analysis of wood anatomy (Fonti et al. 2009; Van den Bulcke et al. 2009), expanding the possibilities for dendroclimatology.

Chapter 6

The influence of density variations in *Terminalia superba* Engl. & Diels on carbon stock quantification

Abstract

Carbon stocks receive increasing attention but data and long-term measurements are lacking, especially for tropical Africa. Therefore, biomass models are constructed merely relying on diameter measurements only. It is, however, recommended to include wood density for more reliable biomass estimates. Especially the development of a method to estimate density variations accurately would reduce the uncertainty on biomass estimates. In this study, detailed density measurements were performed on a long-lived pioneer species in Ivory Coast, *Terminalia superba* Engl. & Diels, to investigate pith-to-bark density variations. An important objective is to calculate the annual carbon stock increments based on tree-ring analysis, inventory data and annual density values. Density from pith to bark was measured on 15 air-dried increment cores using helical X-ray CT. Density was significantly influenced by age, radial position and the presence of juvenile wood. The calculation of carbon stocks was possible for one tree and revealed that cumulative carbon stocks are mostly overestimated if fixed density values are used. Also, mean annual carbon stock increments with fixed density values culminate earlier than mean annual carbon stock increments with annual density values. For a subsample of nine trees that were bootstrapped, relative cumulative carbon stocks (without height data) were again overestimated if fixed density values were used. Curves of relative mean annual carbon stock increments suggest that the age of culmination of mean annual increments is similar for annual or fixed density values. For more conclusive results on the role of annual density values, the methods developed in this chapter need to be applied on a larger sample of trees that have tree-ring series and density profiles at several measured heights along the stem. Additionally, a field method was tested to check if density and density variations could be assessed *in situ*. Drilling resistance measurements were performed on fresh and air-dry stem disks with a portable device, a resistograph. Average wet and air-dry drill values correlated positively with average density values, resp. $r=0.65$ ($p<0.01$) and $r=0.63$ ($p<0.05$) but variations in density were less clearly reflected in drilling resistance profiles. The resistograph can be used to estimate average densities but fails to estimate density variations in the field.

To be submitted

De Ridder M, Van den Bulcke J, Beeckman H, Van Acker J. The influence of density variations in *Terminalia superba* Engl. & Diels on aboveground biomass quantification.

6.1 Introduction

Carbon stocks receive increasing attention within the Kyoto Protocol and related programs like Clean Development Mechanisms (CDMs) and Reducing Emissions from Deforestation and Forest Degradation (REDD+). Aboveground biomass (AGB) of trees is the largest carbon pool and most directly impacted by deforestation and degradation (Gibbs et al. 2007). Ciais et al. (2011) report a lack of long term measurements in Africa although these forests are among the most pristine on the earth, with considerable carbon storage potential (Lewis et al. 2009). Moreover, most existing models overestimate the African carbon stocks (Bombelli et al. 2009). Especially the Congo Basin is under sampled, with only few data on AGB measurements (Djomo et al. 2010; Ebuy et al. 2011) and without connections to global monitoring networks (Verbeeck et al. 2011).

The most accurate AGB estimates are obtained from inventories and destructive sampling, which is a rather laborious task in developing countries (Brown 2002). AGB measurements are transformed into models and the debate on the use of specific or pantropical models is ongoing (Ciais et al. 2011). The pantropical models constructed by Chave et al. (2005) give results comparable with site specific models, certainly if not only diameter but also height and density are included as variables (Djomo et al. 2010; Ebuy et al. 2011; Henry et al. 2010; Nogueira et al. 2008a). Chave et al. (2004) recommend including density as it decreases the uncertainty of estimates. Density is included in the models as an average value per tree or even per species, neglecting density variations within or between the trees.

Gourlet-Fleury et al. (2011) and Williamson and Wiemann (2010a) define density as a fundamental trait related to the life-history strategies of tree species. Variations in density are the driving force of spatial patterns of AGB in the Amazon. Baker et al. (2004) and Nock et al. (2009) observed that mean density varies with age and stem size. Baker et al. (2004) found a radial gradient with increasing densities towards the periphery in early successional species. Moreover, juvenile wood was lighter than mature wood in both dry and moist forests (Bauch and Dünisch 2000; Chaturvedi et al. 2012). Current AGB estimates also do not take into account hollow trees, in some cases significantly present (Nogueira et al. 2008b).

Standard density estimates are obtained by destructive sampling and the water displacement method for volume measurements (Maniatis et al. 2011). Although several studies use this method on stem disks or parts of stem disks (e.g., Henry et al. (2010), Nelson et al. (1999), Nogueira et al. (2008b)) or increment cores (Chaturvedi et al. 2010; Chave et al. 2006; Djomo et al. 2010), many models rely on average density values from databases and literature (e.g., Baker et al. (2004), Chave et al. (2004), Gourlet-Fleury et al. (2011), Feldpausch et al. (2012)), neglecting the impact of age, stem size, juvenile wood and hollow trees. The use of X-ray densitometry (Alvarado et al. 2010; Moya and Filho 2009; Nock et al.

2009) and more recently customized protocols for X-ray tomography of increment cores (Chapter 5) were developed to permit fast and accurate estimates of pith-to-bark density at high resolution. Nevertheless, these methods require expensive equipment and cannot be used under field conditions. A field method that is already successfully tested for indirect measures of density in temperate forests, is the use of drilling resistance, where a needle penetrates the wood at a constant speed and the resistance is registered (Rinn 1996). Drilling resistance measurements were also tested in chapter 5 but the relation with average density and density variations was quite opposed to previous studies (Isik and Li 2003; Lima et al. 2007). For that reason and because of the lack of field methods for density measurement in the tropics, other detailed ways of comparison will be explored here. In this study, density variations of the tree species *Terminalia superba* Engl. & Diels are analyzed in Ivory Coast using both the X-ray methodology as elaborated in chapter 5 and drillings of resistance. *T. superba* is a light-demanding, long-living pioneer species with a large distribution area from Sierra Leone up to Angola (CTFT 1959; Groulez and Wood 1985). The impact of juvenile wood, false heartwood or hollow spaces are often present (Bauch et al. 1982) and their influence is quantified. Following research questions arise:

1. Are density variations in *T. superba* significantly influenced by age, diameter, horizontal/vertical position within the tree, juvenile wood and the presence of false heartwood? Subsequently, is tree ring analysis useful to study variations in density?
2. How are carbon stocks influenced by density variations?
3. Can drilling resistance in the field be used as accurate estimates of density variations from pith to bark?

6.2 Material and methods

6.2.1 Study sites

All study sites are situated in natural evergreen moist rainforests that belong to the Guineo-Congolian regional centre of endemism (White 1983). Full site description is given in chapter 3. In western Ivory Coast (06°07’ to 07°15’ N, 07°30’ to 08°15’ W), four study sites were selected. The forest of Scio can be considered as primary forest whereas the forests of Goya, Bin Houye and Danane are secondary forests. In this region, the dry season generally lasts from December to February (van Oldenborgh and Burgers 2005). In July and August, a period of less precipitation is observed. The average annual precipitation is 1650 mm (1959-1996). Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March (van Oldenborgh and Burgers 2005). Study sites were situated between 200 and 370 m above sea level. Soils have a pH between 4 and 7, a C/N of

8 to 12 and are classified as Ferralsols and Acrisols, i.e. typical acid soils of tropical lowlands (FAO 1986).

6.2.2 Material

Eleven trees, representing a large range of stem sizes and ages, with and without cavities or false heartwood, were selected for sampling (Fig. 6.1). From each tree, at least one stem disk was collected above buttresses. For two trees, several stem disks were taken, to compare density variation in height.

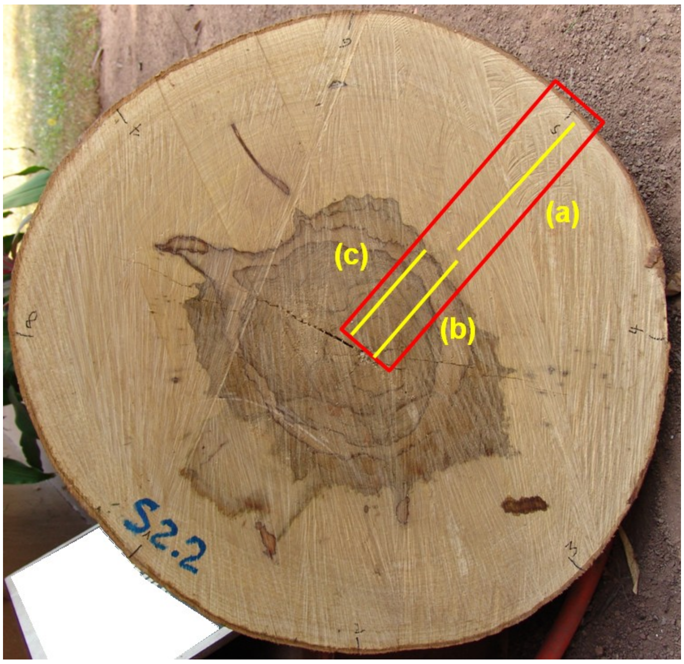


Fig 6.1. An example of one sampled stem disk (S2.2R5). The red box indicates the sampled radius. Three yellow lines delimit (a) mature wood, (b) juvenile wood (distinction between juvenile and mature wood, see Fig. 6.3) and (c) false heartwood (darker color).

6.2.3 Measurements

In this study, density is defined as the air-dry weight over the air-dried volume (Chapter 5). Density was measured using helical X-ray CT and also estimated by drilling resistance. Density and drilling resistance values averaged over an entire profile are compared. Density and drilling resistance profiles are also averaged every 5 mm from pith to bark. On the one hand, average values already smooth the data by removing high-frequency variations (e.g., Fig. 5.5) that could blur common trends in density and resistance. On the other hand, data volume decreases considerably and facilitates calculations in spreadsheets. Trends are analyzed by calculation of linear regressions between the density and drilling resistance profile of every sample and by visual assessment of the graphs. All values were normalized by subtracting the average value and dividing with the standard deviation to enable comparison. The standardized regression coefficient *beta* (Y = a + *beta* X) is given to illustrate radial variations from pith to bark. Y stands for the 5 mm average values of resistance or density, X for the distance from the pith (mm).

Drilling resistance. Drilling resistance measurements were first performed on freshly cut stem disks (Fig. 6.2). The moisture content (MC) was measured at 10 different points of each stem disk with a capacitance moisture meter (Exotek Humitest MC-100S), ensuring a MC higher than 50 % (above fibre saturation point). Afterwards, disks were air-dried for one year and drilling resistance measurements were repeated. Drilling resistance was measured with an IML Resi B-400 resistograph. The drilling resistance at the front end of a thin drilling needle (maximum length of 40 cm, diameter of 3 mm) is registered along a trajectory from bark to pith at a resolution of 40 µm (Rinn 1996). Drilling resistance was measured along eight radii from pith to bark equally spread around the circumference of the disks, starting from the north side and following the counterclockwise direction. The stem disk's surface was reconstructed in 2D using inverse distance weighing interpolation.

Fig 6.2. Drilling resistance measurements: in the field (left) and on freshly cut stem disks (right).

X-ray scans. Fifteen increment cores were extracted from 14 air-dried stem disks for helical X-ray CT. Increment cores and drilling resistance measurements were located maximum 3 cm apart in a vertical direction. Cores were fixed temporarily between two boards to prevent warping during storage. No further preparation was necessary for scanning. Increment cores were mounted in a custom-made holder made of a reference material with a density close to the cell wall density of wood. By using this material and the average grey level of air (zero density), grey values of reconstructed increment cores can be directly converted to densities. All samples were scanned with the X-ray CT scanner built at the UGCT (University Ghent, Centre for X-ray Tomography; http://www.ugct.ugent.be). More information on the scanner and the helical scanning protocol can be found in chapter 5. After scanning and reconstruction, a 1-D microdensitometric profile is extracted based on a 3-D volume of the increment core (resolution of 50 µm).

Tree ring analysis. All stem disks and increment cores were measured during previous tree-ring analyses (Chapter 3). Tree-ring analysis is used to determine the age of trees and study density variations as a function of age. This way, annual changes in carbon storage can also be calculated. In most cases, the juvenile growth spurt is clearly visible and a double linear regression was used to separate juvenile from mature wood (Fig. 6.3).

Tree ring data were plotted as a function of age and two linear regressions were fitted to these data. The border between juvenile and mature wood was defined as the point with the highest combined determination coefficient of both linear regressions. Based on the number of rings at this border (also indicated by the arrow in Fig. 6.3), the corresponding diameter was derived from the growth curves and furthermore, density and drilling resistance values for this interval could be extracted to compare with mature wood values (average value and trends).

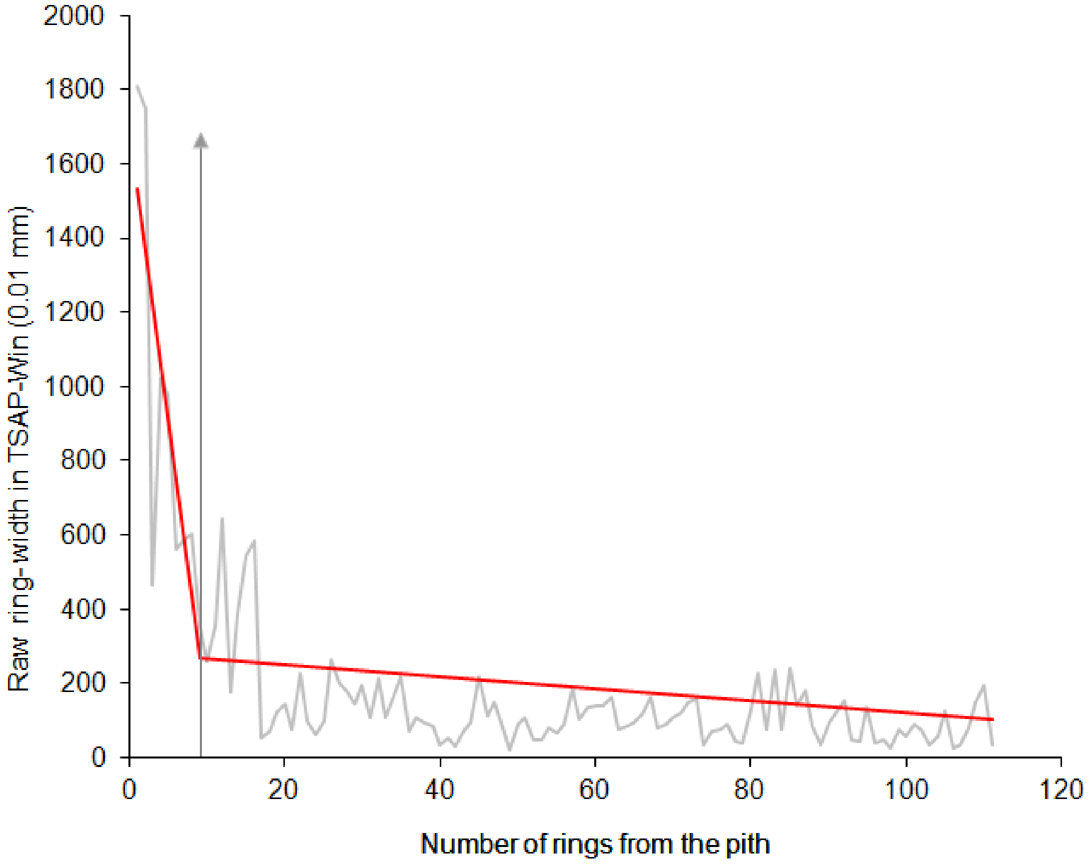


Fig 6.3. An example of the double linear regression used to distinguish juvenile and mature wood of the sample tree with the name S2.3R1. The two lines represent two linear regressions. The Y axis indicates raw ring-widths as they are measured in TSAP-Win, the program used for tree-ring analysis (see Chapter 3). The arrow indicates the line that you can move to see how the determination coefficient R² changes when the tree gets older. Changes in R² are visible for the separate as well as the combined linear regressions.

Annual carbon stocks. Carbon storage was calculated for sample tree S2, the only tree of which tree-ring series and density profiles in the middle and the top of the stem (just before the first large branch) were available, along with diameter and corresponding height at breast height, in the middle and at the top of the merchantable stem. The carbon stored in the black cone between 2 and 12 m height in Fig. 6.4 could not be calculated annually because no tree-ring series are available for S2.1. Carbon stock of this part is estimated as a cone with radius 10.5 cm, height 10 m and density 0.510 g cm^{-3}, the average density during the juvenile phase. Next, annual carbon storage was calculated as conical volumes for diameters up to 43 cm (e.g., dark grey cone in Fig. 6.3) and multiplied with the annual density value. The stem height increased linearly and is supposed constant at 24 m (diameter of 43 cm). Tapered cones were used from this diameter onwards (e.g., light grey tapered cone in Fig. 6.4). The cumulative carbon stock is modelled with the sigmoidal curve of Schöngart et al. (2011) and mean annual increments of carbon stock (MAI_c) were derived. Finally, the resulting carbon storage accumulation and MAI_c are compared with commonly used mean densities.

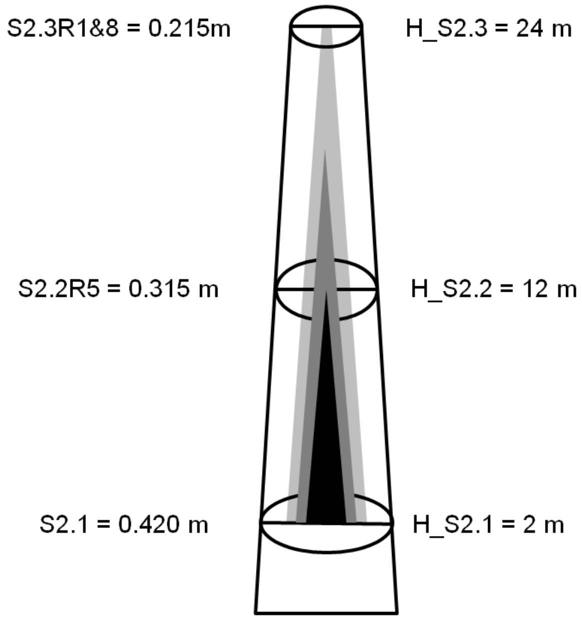


Fig 6.4. Sample tree S2 has three measured heights (H_S2.1, H_S2.2, H_S2.3) and radii (S2.1, S2.2R5, S2.3R1&8). The black cone represents the carbon stored between 2 and 12 m whereas carbon stock is subsequently calculated as annual conical volumes (dark grey cone) or tapered conical volumes (light grey tapered cone).

Finally, the carbon stock of this one tree will also be calculated using the models from chapter 2: equations 2.1 (classical volume formula), 2.2 to 2.5 (pantropical models) and 2.7 (the volume model for *T. superba* plantations in the Mayombe). The cumulative carbon stocks and annual increments were graphically compared.

The other sample trees had no or only one height measurement per tree and there is no consistent diameter-height relation in this region (Chapter 4). Annual diameter growth was converted into annual basal-area growth, multiplied with annual density values and bootstrapping was applied using the methods of Brienen and Zuidema (2006) and chapter 4. The resulting average cumulative 'basal area x density' is modeled in the same way as sample tree S2, and the optimum $MAI_{BA\ x\ dens}$ represents a measure for carbon without height measurements. Different age and diameter limits were simulated with the bootstrap method and results were compared.

6.3 Results

6.3.1 Density variations

An overview is given of length and number of rings of the scans in Table 6.1, along with the average density values: the average of the complete profile from bark to pith, the average density of the juvenile and the mature part and the average density of the part with false heartwood. In one case, two radii of one stem disk were sampled, showing similar average densities. Stem disks were taken at different heights for two trees (B7 and S2.2) with the highest average density at the top of the trees.

Table 6.1. Characteristics of the sample trees and average density values for the microdensitometric profiles (general, juvenile and mature wood, false heartwood).

Sample	Length scan (cm)	Age scan (n rings)	Average density (g cm^{-3})	Juvenile wood density (g cm^{-3})	Mature wood density (g cm^{-3})	False heartwood density (g cm^{-3})
B3R2	19.5	16	0.588 ± 0.079	0.536 ± 0.064	0.613 ± 0.072	
B5R1	28	17	0.516 ± 0.095	0.456 ± 0.080	0.574 ± 0.070	
B71R4	33.5	41	0.513 ± 0.141	0.469 ± 0.104	0.736 ± 0.071	0.405 ± 0.060
B72R7	20	35	0.499 ± 0.101	0.467 ± 0.084	0.531 ± 0.105	0.471 ± 0.079
B73R7[a]	21	31	0.562 ± 0.111	0.524 ± 0.110	0.626 ± 0.077	0.314 ± 0.235
G2R3	27	24	0.485 ± 0.057	0.483 ± 0.060	0.486 ± 0.054	
G8R1	15.5	20	0.590 ± 0.101	0.570 ± 0.093	0.692 ± 0.072	
S1R5	26	58	0.569 ± 0.092			
S22R5	31	100	0.597 ± 0.134	0.449 ± 0.084	0.664 ± 0.092	0.463 ± 0.098
S23R1	21	100	0.651 ± 0.147	0.551 ± 0.098	0.687 ± 0.145	0.602 ± 0.161
S23R8	21	100	0.668 ± 0.117	0.590 ± 0.092	0.722 ± 0.102	0.566 ± 0.090
S4R6	26	100	0.712 ± 0.127	0.604 ± 0.068	0.756 ± 0.119	0.619 ± 0.079
S6R5[b]	25.5	59	0.469 ± 0.133			0.381 ± 0.095
S7R3	30	100	0.578 ± 0.102			0.541 ± 0.090
S8R1	34	35	0.518 ± 0.106	0.428 ± 0.064	0.581 ± 0.082	

[a] The first ring is not completely included in the juvenile wood part (the scan did not reach the pith so the first part of the first ring is missing in the scan).
[b] Estimated age because not all tree rings were present or clear.

The length of the scan, in general equal to the radius of the tree, is negatively but not significantly correlated with the average density ($r = -0.26$). A significant positive relation was found between the number of rings of the scan and the average density ($r = 0.67$; $p < 0.01$). This significant relation was also observed for mature wood ($r = 0.61$; $p < 0.05$) but not for juvenile wood ($r = 0.43$).

The density of juvenile wood is always significantly lower than mature wood, respectively 0.507 and 0.639 g cm^{-3} ($p < 0.001$). Density at 1/3 from the bark, suggested by Williamson and Wiemann (2010b) to generate quick estimates of the average density, was significantly higher than the average density along the profile ($p < 0.05$). The average density of trees with false heartwood (0.578 g cm^{-3}) is not significantly higher than the average density of trees without false heartwood (0.539 g cm^{-3}). Juvenile wood of both types of trees had similar densities (resp. 0.495 and 0.515 g cm^{-3}). Naturally, the average density of four samples with cavities in the center was significantly higher than the average density of the other samples (resp. 0.650 and 0.538 g cm^{-3}; $p < 0.05$).

86% of the density profiles (13 out of 15) have significant linear regressions for density along the length of the scan (Table 6.2) ($p < 0.05$). Profile S1R5 showed very high densities around the pith. This linear regression is also significant if the measurements of the first cm from the pith and cavities are discarded. In the case of G2R3, a polynomial regression fits better than a linear regression with a negative regression coefficient. Apart from this negative regression coefficient, the regression coefficient of the other linear regressions is positive and fluctuates around 0.009 ± 0.005 showing that density increases from pith to bark. On average, the density increases 30% from pith to bark (Table 6.2).

Regression coefficients are lower in the juvenile (*beta*=0.006 ± 0.009) than in the mature part (*beta*=0.011 ± 0.021) but differences are not significant and standard deviations are high. Considering density variations as a function of age, density also increases linearly and significant with age (average *beta*=0.058 ± 0.048), except for three samples, S1R5, G2R3 and B3R2 (Table 6.2).

Table 6.2. Standardized regression coefficients (*beta*) of density variations as a function of radius and age.

Sample	*beta* $_{\text{radius}}$	*beta* $_{\text{age}}$	% density increase pith to bark
B3R2	0,011*	0,064	11
B5R1	0,009***	0,164***	32
B71R4	0,009***	0,079***	50
B72R7	0,010***	0,080***	38
B73R7	0,011***	0,064***	26
G2R3	-0,002	-0,031	-2
G8R1	0,017*	0,078***	27
S1R5	< 0,001	< 0,001	11
S22R5	0,010***	0,034***	45
S23R1	0,012***	na	33
S23R8	0,011***	na	26
S4R6	0,007***	0,015**	25
S6R5	0,012***	0,061***	50
S7R3	0,009***	0,055***	36
S8R1	0,008***	0,088***	40

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, na = no data available

6.3.2 Annual variation in carbon stocks

Carbon stocks were estimated accurately for sample tree S2. The MAI_c culminates after 77 years whereas the volume-based MAI already reached a maximum at 59 years. This is also the case for the MAI_c maxima that are based on one fixed density value for all years (Fig. 6.5), the common method for deriving carbon stocks. The cumulative carbon stock based on the mean density of S2.2R5 (0.669 g cm^{-3}) looks quite similar but naturally, the maximum MAI_c is also reached at 59 years. Differences in cumulative carbon stock and maximum MAI_c become larger as the mean density used becomes more general.

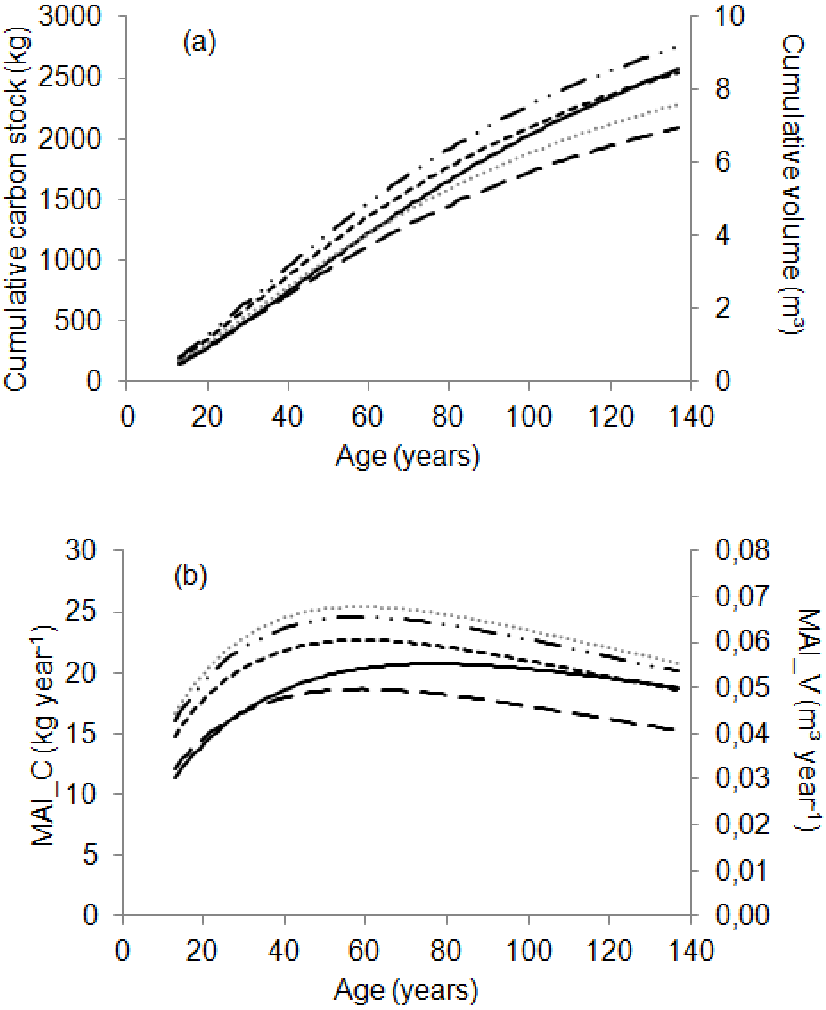


Fig 6.5. Carbon stock of tree S2: (a) cumulative carbon stock and volume over time, and (b) mean annual increment of volume (MAI_V) and carbon stock (MAI_C). Grey dotted curves represent volume calculations, black curves represent carbon stock calculations. The solid black curve was calculated with annual densities whereas the other black curves used a fixed density for all years: 0.669 g cm^{-3} (mean density of S2.2R5; small dashes), 0.725 g cm^{-3} (mean density of the first 5 cm of S2.2R5 starting from the bark; dashes and dots), 0.550 g cm^{-3} (mean density of all 15 increment cores; longer dashes).

Then, we compared the detailed carbon measurements of sample tree S2 with several models (Fig. 6.6) and observed that deviations in carbon stock estimates were highest for pantropical models (Eq. 2.2 to 2.5), followed by the volume model for plantations (Eq. 2.7) and the classical volume equation (Eq. 2.1).

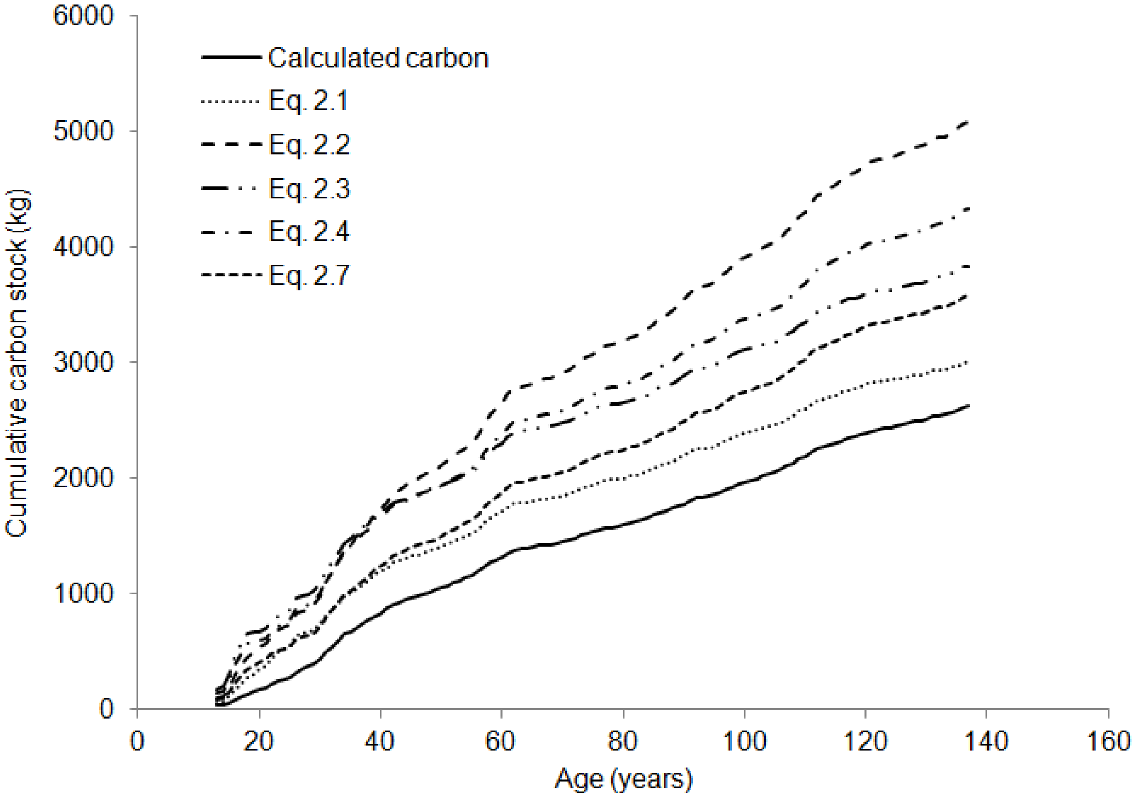


Fig 6.6. Cumulative carbon stocks for sample tree S2 calculated with detailed height, diameter and density measurements (solid line) and estimated by three pantropical equations (Eq. 2.2 to 2.4 from chapter 2), one species-specific volume model (Eq. 2.7) and the classical volume formula (Eq. 2.1). Eq. 2.5 resulted in a similar curve as Eq. 2.4 and is left out.

A dataset of nine trees was available for bootstrapping using both 5-year-average basal area data and density data. The mean bootstrapped curve of $MAI_{BA\ x\ density}$ culminates after 33 years, only one year before the culmination of the mean bootstrapped curve of MAI_{BA} at 34 years (Fig. 6.7). The age at which MAI culminates does not differ significantly if fixed density values were used: 31 years for mean density values per tree and 34 years for mean density values of the first 5 cm from the bark of each tree. Cumulative stocks of BA x density were overestimated by using mean density values and overestimations become larger as trees become older. Moreover, even larger differences in cumulative carbon stock could appear because tree height and growth through time is not incorporated for the moment.

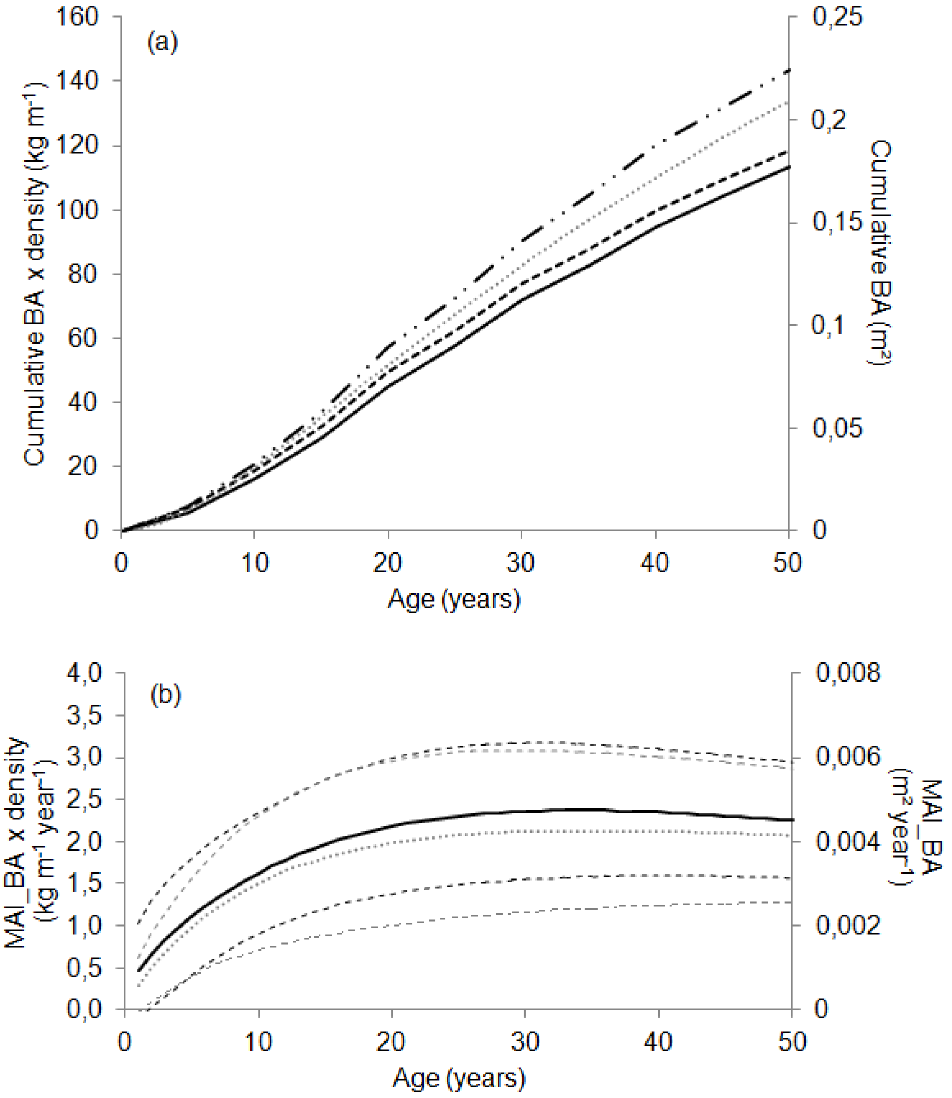


Fig 6.7. Relative measure of AGB/carbon stocks by multiplying basal area and density: (a) cumulative stock of basal area and basal area x density over time, and (b) mean annual increment of basal area ($\mathrm{MAI}_{\mathrm{BA}}$) and the product of basal area and density ($\mathrm{MAI}_{\mathrm{BA\ x\ density}}$). Grey dotted curves represent basal area based calculations, black curves represent basal area x density based calculations. The solid black curve was calculated with annual densities whereas the other black curves used a fixed density for all years: small dashes for mean density values per tree, dashes and dots for mean density values per tree of the first 5 cm starting from the bark.

Limits for bootstrap simulations were fixed at 50 years without diameter limit, representing the main range of ages within the dataset of nine trees. However, results change if, e.g., a diameter limit of 60 cm is chosen (Fig. 6.8). Then $\mathrm{MAI}_{\mathrm{BA\ x\ density}}$ culminates after 22 years, more than 10 years before the maximum $\mathrm{MAI}_{\mathrm{BA\ x\ density}}$ without diameter limit (Fig. 6.8a). There is also a clear difference in age at maximum $\mathrm{MAI}_{\mathrm{BA\ x\ density}}$ (Fig. 6.8b): the distribution of simulated ages shifts to the right if a diameter limit is imposed.

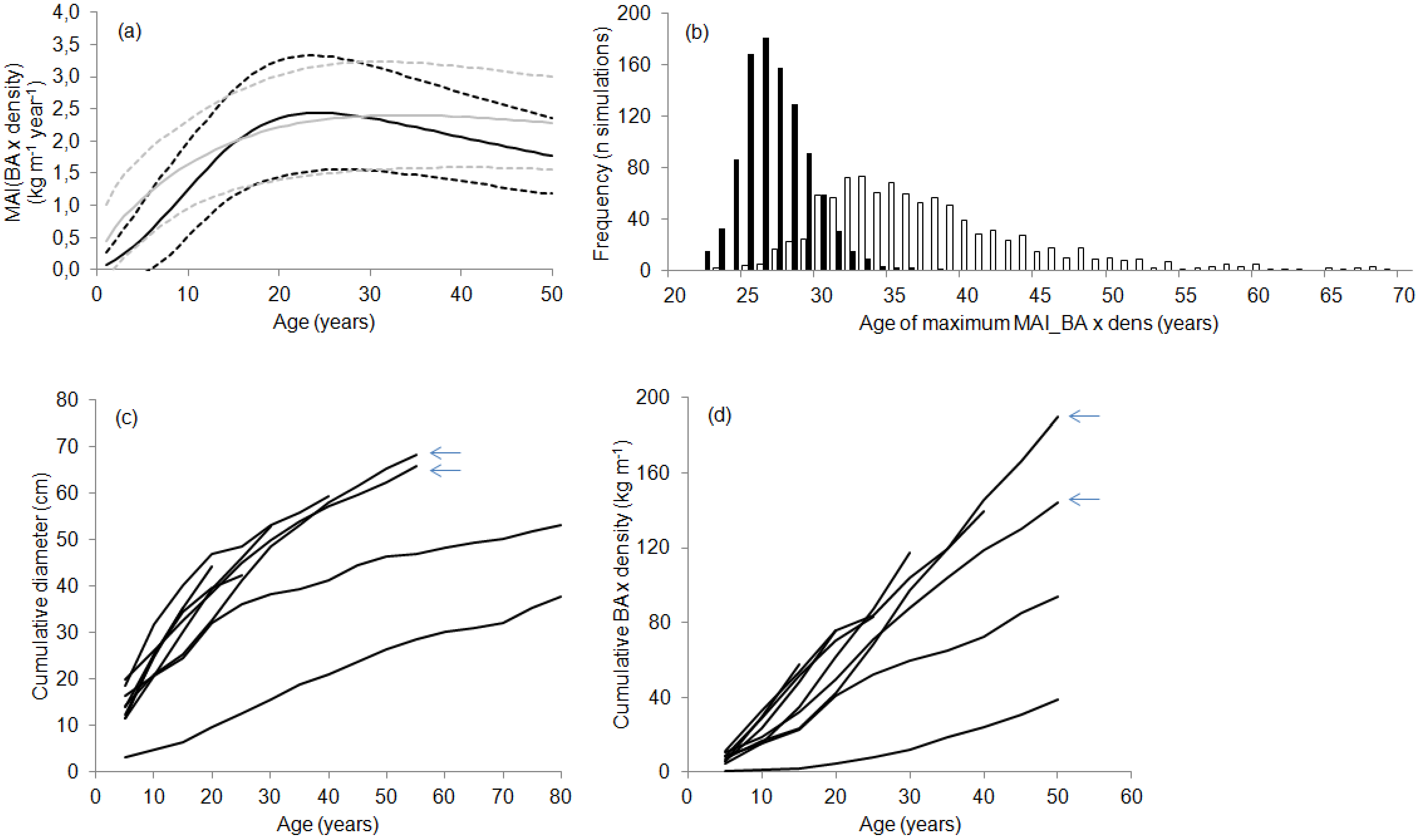


Fig 6.8. Influence of diameter limits for bootstrapping: (a) mean annual increments (MAI) of basal area x density with a diameter limit of 60 cm (black curves) or without diameter limit (grey curves), (b) distribution of the age of maximum MAI with a diameter limit of 60 cm (black boxes) or without diameter limit (white boxes), (c) diameter curves of the nine sample trees, and (d) curves of BA x density of the nine sample trees. In (c) and (d), the two arrows indicate the trees with a diameter > 60 cm.

6.3.3 Density estimations with drilling resistance measurements

Average densities from pith to bark and average juvenile wood densities are significantly correlated with both average air-dry and average wet drilling resistance from pith to bark (Fig. 6.9). Average density of mature wood is only significantly correlated with average air-dry drilling resistance. No significant correlation was found between average air-dry or wet drilling resistance and false heartwood densities. If we compare the averages of wet and air-dry drilling resistance, significant correlations are observed between pith-to-bark average wet and air-dry drilling resistance and also for their juvenile and false heartwood parts, not for the mature wood.

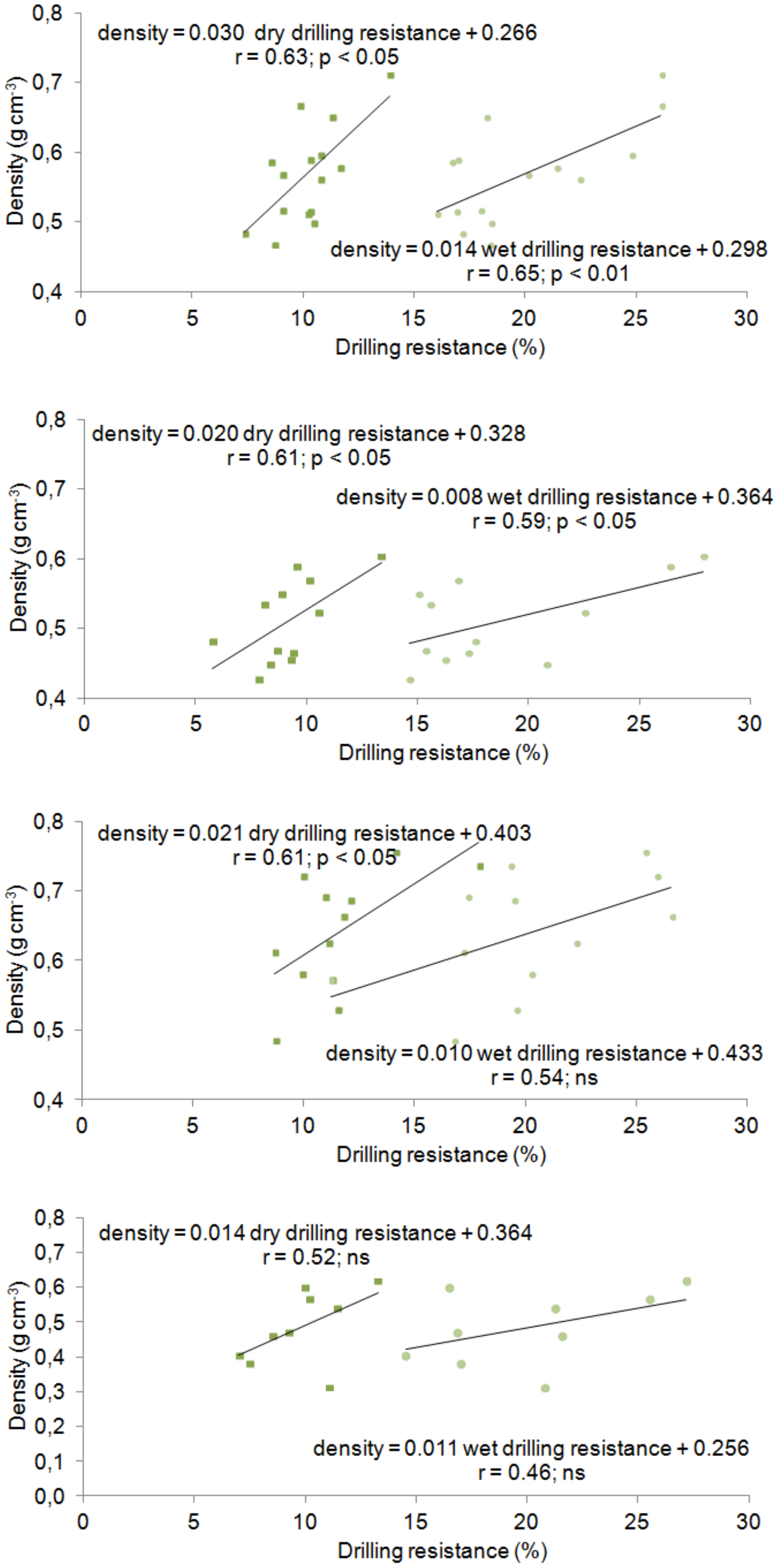


Fig 6.9. Linear regressions between average densities and average dry and wet drilling resistance (from above to below): from pith to bark and in juvenile, mature and false heartwood.

Differences between drilling resistance profiles on fresh water-saturated wood and air-dried wood are obvious. From pith to bark (but also in juvenile, mature and false heartwood, results not shown), significant linear regressions between density and drilling resistance profiles were more frequently noted for air-dry drilling resistance profiles (73%) than for wet drilling resistance profiles (60%) (Table 6.3). However, not all drilling resistance profiles with similar *beta* values and a significant correlation with density profiles are good predictors of radial density variations. Significant correlations at the 0.05 level were not reflected in the graphs so these drilling resistance profiles were not considered as good estimates for density variations. Further, one significant correlation between density and dry drilling resistance profiles (S2.2R5, Fig. 6.10) and two significant correlations between density and wet drilling resistance profiles (S6R5 and S2.2R5) revealed different radial patterns during visual assessment and were rejected for density estimation. Thus, successful air-dry drilling resistance measurements decreased to 60 % whereas successful wet drilling resistance measurements dropped to only 33 %.

Table 6.3. Overview of the relation between density and drilling resistance profiles from pith to bark (trend analysis). The standardized regression coefficients (*beta*) are given, along with the correlation coefficients (r) for each linear regression between density and dry or wet drilling resistance. Correlation at the 0.05 level and correlations in italic were rejected for density estimation based on visual assessment.

	standardized regression coefficient *beta*			r (linear regression)	
	Density	Dry drilling	Wet drilling	density-dry drilling	density-wet drilling
G2R3	0,002	-0,011	0,005	0,03	0,51***
S6R5	-0,012	-0,010	-0,008	0,9***	*0,71****
S7R3	-0,009	-0,006	-0,004	0,61***	0,21
B71R4	-0,009	-0,008	-0,008	0,92***	0,74***
S4R6	-0,007	0,000	0,004	0,09	0,15
S1R5	0,000	0,017	0,019	0,01	0,02
S22R5	-0,010	-0,006	-0,003	*0,71****	*0,48****
S8R1	-0,008	-0,008	-0,008	0,74***	0,74***
S23R1	-0,012	-0,008	-0,007	0,75***	0,64***
B5R1	-0,009	-0,009	-0,004	0,69***	0,28*
B72R7	-0,010	-0,014	-0,012	0,87***	0,5**
S23R8	-0,011	-0,013	0,005	0,35*	0,29
G8R1	-0,017	-0,016	-0,007	0,55**	0,12
B73R7	-0,011	-0,006	-0,003	0,68***	0,23
B3R2	-0,011	-0,007	-0,007	0,24	0,34*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

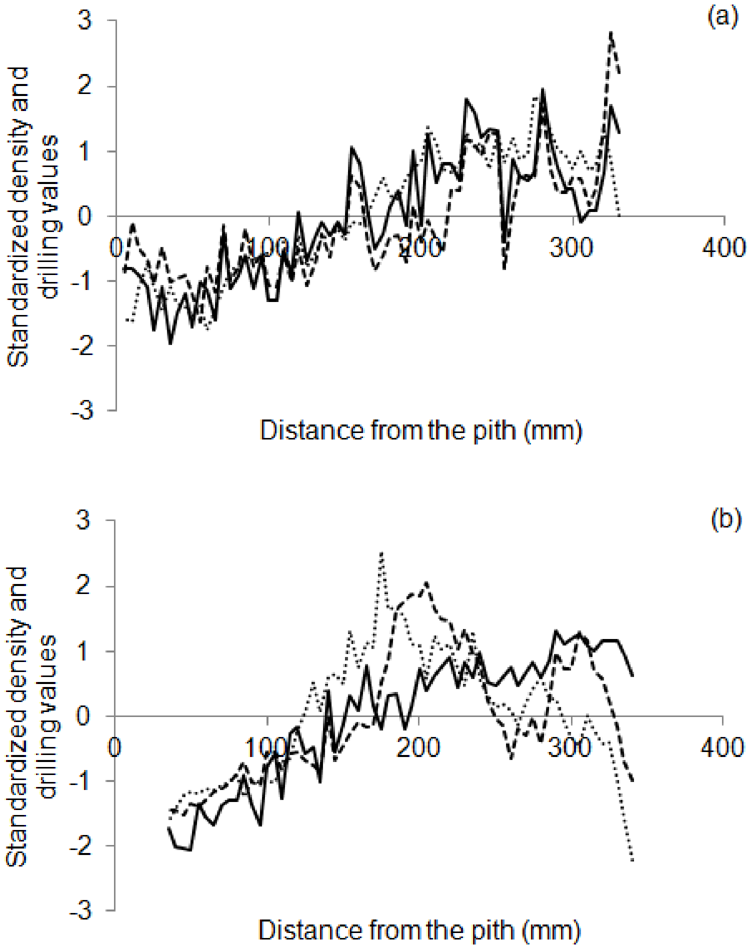


Fig 6.10. Density profile (solid line) and air-dry (dashed line) and wet (dotted line) drilling resistance profile. Both samples have profiles with similar regression coefficients and/or highly significant correlations between density and drilling resistance profiles. However, both air-dry and wet drilling resistance profiles reflect density variations in (a) S8R1 whereas the drilling resistance profiles in (b) S2.2R5 do not.

Several trees have similar drilling resistance and density profiles from pith to bark so we hypothesized that this similarity is also valid for the other radii of, e.g., B7.1R4 and S8R1 (Fig. 6.10). Thus, we reconstructed the stem disk's surface based on the eight drilling resistance profiles (Fig. 6.11). This 2D image of interpolated drilling resistance profiles is considered as a relative measure of radial density variations. The rather uniform radial drilling resistance patterns in Fig. 6.11 support the hypothesis that density is quite uniform over different radii of one stem disk as it was also the case for the two radii of stem disk S2.3 (Table 6.2). Although the success of drilling resistance measurements is not high, there are almost no trees without any correspondence regarding significant correlations or similar regression coefficients for density and drilling resistance profiles. Samples S2.3R8, S4R6 and S1R5 are the only samples without any relationship with density profiles. S2.2R5 only showed similarities between drilling resistance and density profiles for the false heartwood part.

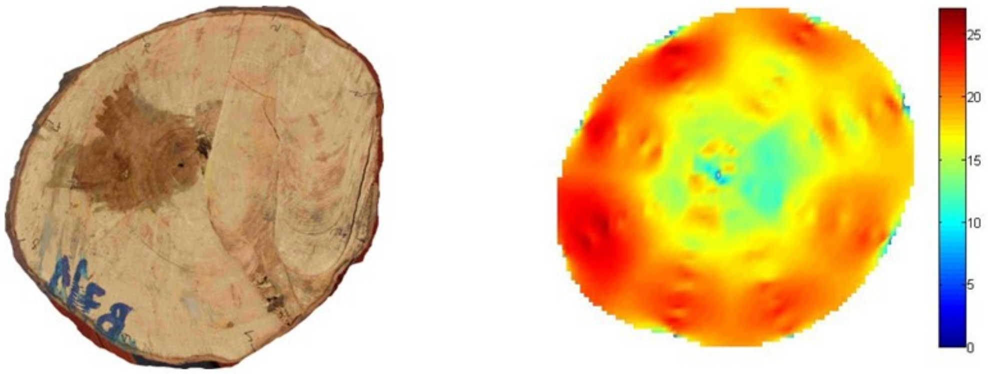


Fig 6.11. Example of stem disk B7.1: picture at the left and 2D reconstruction based on eight wet drilling resistance profiles on the right. The color bar represents percentages of drilling resistance with blue values for low and red values for higher drilling resistance.

6.4 Discussion

6.4.1 Density variations

The influence of diameter on density should be interpreted with caution. In our case, the length of the scans does not cover the full diameter but generally corresponds with the radius of the tree. However, no relation was found between radius and average density values, as was also reported by Baker et al. (2004), Basuki et al. (2009), Williamson and Wiemann (2010a), Williamson et al. (2012). Still, Kokutse et al. (2004) measured densities in Togolese teak plantations and found a positive relation between density and diameter. Whereas discussion remains on the influence of the diameter, the positive influence of age is described in Africa (Kokutse et al. 2004), South and Central America (Williamson and Wiemann 2010a; Williamson et al. 2012) and South Asia (Nock et al. 2009), and confirmed by this study. Nelson et al. (1999) even advise to derive density of a sample of trees that do not vary much with age, also suggesting density variations with age.

No reports were found on within-tree density variations in natural forests in sub-Saharan Africa, apart from Henry et al. (2010). They observed that density decreases from pith to bark in Ghana if different species were grouped. No increasing trend was visible in pioneer species (Henry et al. 2010). In our study on a long-lived pioneer species, density increases from pith to bark, similar to Costa Rican pioneer species (Wiemann and Williamson 1988), *Gmelina arborea* Roxb. plantations in Venezuela (Espinoza 2004) and several shade intolerant and intermediate species in Thailand (Nock et al. 2009). All these heliophilous (long-lived) pioneer species typically have high juvenile growth rates, combined with low densities, and adjust their stability if they reach maturity with higher densities to defend the tree against attack from outside (Nock et al. 2009; Wiemann and Williamson 1988). The percentage of change in density from pith to bark (30 %) is comparable to the values observed for shade intolerant and intermediate tree species (24 to 38 %) in Thailand but not as extreme as for the very shade intolerant *Melia azedarach* (70 %) (Nock et al. 2009). This confirms the heliophilous character of *T. superba* but also pinpoints that this species can withstand shade during smaller periods of its lifespan (Chapter 4).

The theory of Williamson and Wiemann (2010b) considers the density at 1/3 of the trees' radius as a good estimate for the total trees' density. Although this is considerably easier and faster, such approach resulted in significantly higher densities than the measured average densities. This theory probably does not hold for pioneer species as *T. superba* where the increase in radial density is too high. The presence of a considerable percentage of lighter juvenile wood at breast height (basal area), not incorporated in samples of Williamson and Wiemann (2010b), only strengthens the overestimation of density.

Juvenile wood has a significantly lower density than mature wood. Nepveu (1976) also observed this lower density during the first 15 years in *Terminalia ivorensis* A. Chev. in Ivory Coast and related this to the presence of juvenile wood. Apart from the hypothesis of Nepveu (1976), this difference in density between juvenile and mature wood was not yet analyzed on tropical trees without heartwood formation. Only Bauch and Dünisch (2000) found that the density of juvenile wood was slightly lower than mature wood of *Carapa guianensis* Aubl. in the Central Amazon, probably because of thicker cell walls in mature wood. As described in chapter 5, juvenile and mature wood reveal differences in wood anatomical variables but no quantitative data were collected to further study the link between microscopic wood structure and density. Also, no universal methodology exists to separate juvenile from mature wood, thus hampering comparison. In our study, individual growth curves were used to mark the border between juvenile and mature wood (double regression), whereas the study of Bauch and Dünisch (2000) and Chaturvedi et al. (2012) used fixed but different distances from the pith, resp. 4 and 10 cm. Our method with double linear regressions permits to follow the growth of every tree separately instead of fixing one value but there are also some disadvantages. First, two maxima of the combined R^2 can occur which was the case in about 20% of the samples. In that case, the decision was based on visual inspection. Second, the maxima of R^2 can be rather broad, meaning that, e.g., 5 years before or after the maximum of the combined R^2, values of R^2 can still be quite similar. However, with portions of juvenile wood ranging from 2,5 to 27 cm, one fixed portion of 4 our 10 cm would probably lead to considerable higher errors in the estimates of juvenile and mature wood density.

Contrary to the observations of Kokutse et al. (2004), variability in density does not stabilize with age. This is also visible in the density graphs based on tree age, derived from measured and crossdated tree ring profiles (see chapter 3). This type of analysis is rare for tropical trees. Schöngart et al. (2011) incorporated tree-ring data from Brazil in a model to follow carbon stocks through time, stressing the importance of tree-ring analysis in the tropics (see 1.4.2).

T. superba can contain cavities and/or false heartwood (Groulez and Wood 1985). These cavities were found in four samples and only represented 1 % of the total basal area of the sampled stem disks, comparable to the percentage in closed forests in Brazil (Nogueira et al. 2006). Hollow trees were mostly larger trees less abundant in inventories, also explaining the small influence on volume and biomass (Nogueira et al. 2006). However, the average pith-to-bark density of *T. superba* trees with cavities was higher than the density of trees without cavities. This is logical because cavities are not represented in the calculation of average density. Cavities were also present in older trees and age and density are positively related, resulting in above average density for trees with cavities. On the other hand, false heartwood is often related to wetwood and thus lower density (Chapter 5). The lower density values within the false heartwood zone are often harder to prove because false heartwood is mostly found in the juvenile wood part and it is not sure whether the decrease in density can be related to false heartwood or to juvenile wood only. In several cases, density reaches a local maximum just inside or before the false heartwood zone. Eckstein and Sass (1994) also observed this compartimentalisation for temperate species and Rinn et al. (1996) interpreted this as a defense mechanism against fungal attacks. The peak in density also explains the higher regression coefficient (*beta*) within false heartwood density profiles of *T. superba*. The influence of cavities and false heartwood on density and AGB as such is most probably less important than radial density variations and density variations with age.

Differences in density can also be compared for different heights on a limited set of two trees with the highest density at the top of the trees. Espinoza (2004) also found that density decreases from the stump to halfway the trunk and increases again towards the top, similar to what is found in sample tree B7. The collection of more stem disks per tree on different heights could allow for mapping density volumetrically similarly to the example S2, instead of the currently used basal area.

6.4.2 Density variations and carbon stocks

The best models for AGB in both Cameroon (Djomo et al. 2010) and the DRC (Ebuy et al. 2011) included density. Also in Ghana, site specific models with density were preferred above general allometric models (Henry et al. 2010). Still, all these models only use a single mean density value per tree or even per tree species. Carbon stocks and volume culminate at the same time if one fixed density value is used. Moreover, cumulative carbon stocks were overestimated if the outer density or even the mean density of the increment core was used. Although the volume culminates rather fast in *Terminalia*, the carbon stock culminates many years later, while diameter only increases slightly. For sample tree S2, carbon stock increments culminate 18 years and 4 cm later than volume increments. Apparently, more carbon could be stocked in an older tree than a young tree because of decreasing ring-widths and increasing density from pith to bark. Schöngart et al. (2011) studied the distribution of carbon stocks in relation to age and also found higher carbon stocks in older forest patches and lower carbon stocks in younger forest patches.

Schöngart et al. (2011) were the first to include annual densities in estimates of carbon content of a pioneer species of the Pantanal, *Vochysia divergens* Pohl, but their methods differ from our method. Our study is less destructive because a small number of samples is used and every tree-ring width is related to an annual density value. Schöngart et al. (2011) used a large sample of trees with different diameters and ages and estimated annual density variations by measuring average densities of these stem disks or increment cores. They also stressed the importance of correct measurements of density variations. The lack of information on density variations introduces significant mis-estimations, contributing up to 90% of the uncertainty in AGB estimates (Schöngart et al. 2011). The cumulative carbon content of Schöngart et al. (2011) was lower than in our sample tree (1500 kg C in 100 years vs. > 2500 kg in 137 years) but we only had one sample tree that was older than the average *T. superba* and older than most *V. divergens* trees. The maximum MAI_c was quite similar and equal to about 20 kg C year^{-1}. Further research on more samples is necessary to confirm these first results and to get a view on the errors of estimating annual carbon stocks.

However, as a test case, we already calculated the annual carbon stock with some commonly used pantropical models and species-specific volume models that were multiplied with annual density values (Fig. 6.6). The overestimation that Bombelli et al. (2009) mention for the African continent, appears to be confirmed: all pantropical models resulted in significant higher carbon stocks, even if taken into account that these models estimate total tree carbon stocks instead of carbon stock of the stem only. Eq. 2.2 was the only model that included wood density next to diameter but in this case, the overestimate was even larger than for the other pantropical models. Also, the volume equation (Eq. 2.7) developed in chapter 2 for Congolese plantations, does not appear valid for natural Ivorian trees. Although this species-specific model is an improvement compared to the pantropical models, overestimates remain considerable, e.g., because of the difference in diameter-height relation in both forest regions (see next paragraph). The classical formula for volume with a fixed form factor of 0.68 (Eq. 2.1) and multiplied with the annual densities approaches the real carbon stock the closest but again relies on tree-ring data and detailed height measurements of the sample trees. Once more, more trees are necessary to prove these significant overestimates of carbon stocks.

The construction of a diameter-height or age-height relation was only possible for sample tree S2 as such carbon stocks for the other trees were based on basal area and annual density values. These relative measurements were possible in nine of the sample trees and bootstrapping was applied to gain insight on the variability of estimates. Again, fixed density values overestimated the relative measures of cumulative carbon stocks. Differences increase with age as growth rates decrease but density increases with age. The MAIs of basal area and relative carbon stocks nevertheless culminate almost the same time. This could be explained by the limited increase in density of the 9 sample trees (from 470 to 570 kg m^{-3}) compared to sample tree S2 (from 400 to 700 kg m^{-3}). Also, the nine sample trees were bootstrapped with an age limit of 50 years whereas sample tree S2 was > 100 years old. Additionally, bootstrapping data will never generate ‘better data’ than the original dataset. A few larger or older trees in a small dataset like ours make a significant difference if one aims at estimating the time necessary to stock the optimum quantity of carbon or the simplified quantity of ‘BA x density’. In Fig. 6.8, two trees are fast-growing with diameters > 60 cm. The inclusion of these trees for bootstrapping results in a later culmination of MAIs of BA and BA x density. On the other hand, the exclusion ignores the largest fast-growing trees and could give too much weight to the slower-growing trees. So, bootstrapping results should be interpreted with caution and larger sample sets are recommended.

6.4.3 *Density estimations with drilling resistance measurements*

Until now, most research focuses on the relation between average density and average drilling resistance values, e.g. Acuña et al. (2011), Johnstone et al. (2011), Lin et al. (2003), Rinn et al. (1996). In those studies and in our study, unique for tropical Africa, drilling resistance and density values revealed positive (significant) correlations. Lin et al. (2003) and Rinn et al. (1996) only worked with air-dried wood samples, whereas Johnstone et al. (2011) found similar significant correlations for drilling resistance values on standing trees (fresh wood) and air-dry densities. In our study, both air-dry and wet drilling resistance were related to air-dry density. Average drilling resistance values were lower on air-dry wood than on fresh wood but both were generally significantly correlated with average density values. Lin et al. (2003) studied the effect of moisture content in *Taiwania* plantations and confirmed that average drilling resistance decreases with decreasing moisture content.

Although average drilling resistance and density values correlated significantly, variations in drilling resistance profiles do not always correspond with variations in density profiles. Chantre and Rozenberg (1997) state for Douglas fir that, although a positive correlation between average density and drilling resistance is found, density variability cannot be estimated by drilling resistance measurements. Recently, Johnstone et al. (2011) concluded similarly for eucalypts in Australia. In our study, the air-dried drilling resistance profiles more accurately corresponded with density variations than the wet drilling resistance yet only in 60% of the samples. Therefore, the resistograph cannot be used as a general field method to estimate density variations. Several reasons are suggested for this failing correspondence:

the drag of the needle and differences in moisture content (Johnstone et al. 2011), the location of sampling and the drilling features of the needle (Rinn et al. 1996).

Normally, the drag of the needle leads to an increase in drilling resistance further away from the bark because rotation movements of the needle consume more energy (Johnstone et al. 2011). This is not the case in drilling resistance profiles of *T. superba* (except for G2R3), where both drilling resistance and density decrease with increasing distance to the bark. We did often observe a lower correspondence the first centimeters of the drilling, possibly related to the needle instability at the start of a drilling. Differences in moisture content of *T. superba* are not studied as such the influence of pith-to-bark moisture content remains unknown. Rinn et al. (1996) reports that abrupt changes in density are often more gradually in drilling resistance profiles because the top of the needle absorbs about 10 % of the drilling resistance. A lag in peak in drilling resistance profiles from bark to pith is sometimes visible from 170 mm onward and could be linked to this phenomenon (Chapter 5). This can explain why regression coefficients of density profiles are steeper than regression coefficients of drilling resistance profiles. The location of both drilling and density measurements is also never equal, also reported by Rinn et al. (1996). It is not feasible to use the same sample paths and therefore, local density variations can influence the regression coefficients of profiles to a certain extent, yet probably only slightly.

Although the resistograph drilling resistance measurements did not result in prediction of density variations for complete or parts of the wood sample, only a few samples did not show any correspondence with density profiles. These sample trees have a high age (> 100 years) and the presence of false heartwood. This suggests that drilling resistance might become less reliable in old trees with false heartwood formation. In other words, successful correspondence between drilling resistance profiles and density profiles was more observed for younger trees with mainly juvenile wood than for older trees with relatively less juvenile wood.

6.4.4 Conclusion

Density is primarily influenced by age, radial position and the presence of juvenile wood. Therefore, simplified methods like Williamson and Wiemann (2010b) overestimate the average density for species such as *T. superba*. Volumetric based carbon stock estimates based on one tree of *T. superba*, give evidence that annual density values resulted in different carbon stocks than a fixed density value. Carbon stocks based on one fixed density value tend to result in overestimations. Additionally, average density values differ considerably in literature and depend strongly on the size and location of the sample, which is mostly not mentioned: an entire increment core, a smaller sample just underneath the bark, a sample at breast height or at another height, etc. Annual density values do not resolve all variations regarding the location of a sample but already provide accurate information along the sample radius and during the whole lifespan of a tree, e.g., taking into account differences between juvenile and mature wood. Relative measures of carbon stocks excluding height (basal area x density) also revealed overestimates based on a fixed density value. In contrary to sample tree S2, we did however observe similar ages at which MAIs of relative carbon stocks based on fixed and annual density values optimize. We are confident that the method combining tree-ring analysis and X-ray scans is promising for carbon estimates in tropical forests but larger sample sets with older trees are recommended to support the implementation and interpretation of bootstrapping results. Further research on density variations at different heights (1) allows for estimates of carbon stocks at a larger scale and (2) might permit to formulate recommendations about the height at which density profiles should be sampled to reflect the trees' average density profile. Although the resistograph appears useful to predict average density in the field and on air-dry samples, it cannot estimate trends in density. Differences in moisture content within and between samples, the different locations of measurements, the presence of older trees with false heartwood and the characteristic behavior of the drilling needle could partly explain the failure of the resistograph to estimate density variations.

Chapter 7

Conclusions, implementation and potential for additional research

7.1 Tree-ring analysis and wood density data of *T. superba* as combined tool for implementation in sustainable forest management

The study of tree rings in two West and Central African study regions confirms the annual character of tree rings in *T. superba* in natural and planted forests. Along with the findings of Mariaux (1969) and Worbes et al. (2003), annual tree rings are now observed in the DRC, the Republic of Congo, Cameroon and Ivory Coast, ascertaining the annual character of tree rings of *T. superba* throughout its large distribution area. Tree-ring analysis of this long-lived pioneer species thus holds considerable potential to: (1) study the link with climate, (2) calculate useful parameters for sustainable forest management (SFM) (minimum logging diameter; MLD, biological rotation age; BRA, need and timing of silvicultural treatments) and, (3) estimate volume growth and carbon storage. These three research subjects can be studied over the entire distribution area and especially in forests where *T. superba* is abundant (e.g., gregarious species in the Mayombe Forest), the results can even be important at the forest level.

The relation with climate was clearer in the Mayombe than in Ivory Coast and tree-ring borders were also more distinct in the Mayombe. This is probably due to the microclimate of the Luki Biosphere Reserve that still enables the growth of *T. superba* in a region with a minimum rainfall normally hampering the installation of the tree species. Trees at the edge of their distribution area and with a clear limiting factor generally have a higher climate-sensitivity (Cook and Kairiukstis 1990; Fritts and Swetnam 1989). However, the lack of long time-series of precipitation could also hinder significant correlations with tree growth in Ivory Coast. To overcome this lack of local climate data, we compared tree growth with regional (SSTs) and global (ENSO) variables. This analysis was successful in both study regions and resulted in relations between El Niño 3.4 indices, October-November precipitation and tree growth. Larger ring-widths were associated with higher autumn precipitation during La Niña years in the Mayombe whereas higher autumn precipitation during El Niño years in western Ivory Coast also resulted in larger tree rings. As far as we know, this is the first study, particularly in tropical Africa, that succeeds in detecting significant relations with global climate indices at both sides of the equator although a link with local climate could not be found in both regions. Therefore, the use of regional and global climate variables is highly recommended in tropical areas with short time spans of instrumental data on local climate like precipitation.

Tree-ring analysis allowed also for the calculation of growth events and variables for SFM such as MLD and BRA. The good silvicultural characteristics described by Humblet (1946) and Groulez and Wood (1985) were confirmed. Moreover, tree rings proved that, in natural as well as planted forests, *T. superba* generally does not suffer from harsh competition to reach the canopy. Growth releases mostly occur during the first 20 years so if one thinning is to be recommended in production forests, it should be done during this juvenile phase to increase growth of slower-growing juvenile trees. Lianas can be removed at the same time, securing forest workers and possibly avoiding forked trees. The timing of the final harvest and the MLD of *T. superba* were also calculated based on basal area increments that were derived from growth curves of the sample trees. If height measurements are available and a diameter-height relation exists, volume based MLD/BRA could also be estimated. These values were higher than basal-area based MLD/BRA in both natural and planted forests.

High-resolution density data could be extracted on the same increment cores that were used for tree-ring analysis. These density data were directly measured using a state-of-the-art X-ray scanner and a sample holder made from a reference material with a known density. This way, we did not only observe a distinct increase in density from pith to bark, we could also relate density to tree growth and concluded that density in general also increases annually. This information was then used to calculate absolute (with height measurements) or relative carbon stocks (without height measurements, only based on tree rings and density data). In both cases, commonly used AGB models with fixed density mostly overestimate the actual carbon stocks. Bombelli et al. (2009) already suggested that most AGB models overestimate carbon stocks on the African continent. Evidence is given in chapter 2 where the carbon stock of plantations was estimated in two ways: as the product of volume (using a site-specific volume model) and a fixed density taken from literature (0.55 g cm^{-3}) and based on four pantropical models of Chave et al. (2001, 2005) and Brown (1997). All pantropical models resulted in much higher carbon stocks than the product of volume and density. Still, without real biomass and/or density measurements, no conclusive answer could be given on the best method. In chapter 6, sample tree S2 was neither weighed for AGB but detailed density and tree-ring data resulted in a more reliable and accurate estimate of the tree's carbon stock than the plantations in chapter 2. The four pantropical models from chapter 2 were run for this sample tree, along with the classical volume formula and the derived volume model. All these models lead to significant overestimations of carbon stocks (Fig. 6.6). Subsequently, the estimated values of carbon stock in chapter 2 based on the product of volume and density are probably also overestimates but more still more accurate than the estimates of the pantropical models. As only one sample tree was involved in this analysis and pantropical models are generally not developed to estimate individual tree's carbon stock, these results should be interpreted with caution. The inclusion of annual instead of a fixed density from literature could however further refine and probably lower the carbon stocks of the Mayombe plantations.

Finally, our objective was to study the collection of data for SFM and carbon stocks in the tropics in a less destructive, fast and inexpensive way. Our results prove that these conditions were mostly fulfilled. Building a tree-ring chronology with only increment cores appears not possible in the tropics but a limited number of stem disks is sufficient to study tree ring anomalies, after which tree-ring series of increment cores can be compared and used to build up regional chronologies. Stem disks were also often collected from trees that could be traded on local or international wood markets, avoiding the exploitation of trees for research purposes only and mostly respecting a minimum diameter of 50 cm, close to the legal MLD of 60 cm. The increment cores for density research were extracted from the Ivorian stem disks so no additional sampling was necessary. The increment cores of the Congolese plantations could be used for future density measurements without pre-treatment, marking the semi- to non-destructive character of both tree-ring analysis and density measurements. The collection of stem disks and increment cores was done quite fast but the subsequent tree-ring analysis is rather time consuming. Still, the result of long-term growth data is a lot less expensive than measuring permanent sample plots (PSPs) over 50 years and more. Density measurements with a customized helical scanning protocol and in-house developed software saved a considerably amount of time compared to the classical Archimedes method and was an improvement of 2D densitometry. More work has to be done to optimize this technique for a different range of species (especially fine-tuning of software, programming) and to allow other scientists to use this scanner in a more user-friendly way.

Fieldwork can be done by trained foresters and does not require large teams or expensive equipment. The equipment for tree-ring analysis (measuring table, stereomicroscope, TSAP-Win license) and especially X-ray scans is nevertheless expensive. The research laboratory at the Luki Biosphere Reserve that was set up in collaboration with the Royal Museum for Central Africa, is one of the rare laboratories in tropical Africa that has an operational measuring table and TSAP-Win software. Nowadays, tree-ring modules are also programmed in the freely available R software, providing low cost alternatives for qualitative tree-ring analysis in the tropics. Still, one should always keep in mind that dendrochronology has the inherent disadvantage of only including the ‘fittest’ trees that reach the canopy stage, encouraging the combination with studies on germination and mortality to gain more inside on the actual forest structure. Then, for density measurements, X-ray CT scanners such as the scanner at the Laboratory of Wood Technology of the Ghent University, are not readily available but the ongoing hard- and software improvements will make this more and more accessible; X-ray CT will be a very important tool in future wood research in general. Research partners or companies can send increment cores for density measurements but the X-ray scanner is not only used for this type of measurements and serves a large scientific community. A low-cost device for density measurements based on 3-dimensional scans is not yet available and a field method for fast and accurate measurements of density variations in the tropics is currently lacking. The tested drilling resistance method could be used to estimate cavities and heart rot and appeared useful to indirectly estimate mean density values. However, this technique largely failed to estimate density variations.

7.2 Potential for additional research on the tree level

Tree-ring analysis and density measurements with the CT X-ray scanner appeared perfect alternatives for PSPs to collect long-term qualitative data on SFM and carbon stocks. Valle et al. (2006) concluded that growth measurements of PSPs were biased by, e.g., limited length of monitoring and the diameter of first measurements, leading to overestimated volume growth. Tree-ring analysis countered these short periods with life spans of trees from pith to bark but this method is most advantageous in combination with classical inventories as the one described in chapter 2. Inventory data are still important and therefore we share the opinion of Zuidema et al. (2012) who consider tropical tree-ring studies and PSP-based approaches as two complementary research techniques. You could also look at it from another point of view: if an inventory is planned, increment cores could also be a part of it. PSPs deliver rates of recruitment, mortality and growth for all species over a short time period whereas tree-ring analyses yield lifetime growth rates and physiological responses to environmental changes for a subset of species at an annual resolution. *T. superba* could certainly be a part of such subsets of species, especially in monodominant forests such as the Mayombe. The Luki Biosphere Reserve has some old colonial sample plots that were recently remeasured (Couralet 2010), offering possibilities for the establishment of a PSP in the future. The combination of inventory data and tree-ring analysis could, e.g., be used for the determination of sustained yield. By using tree-ring data, you can get a good estimate of the wood annual production, also per hectare (the unit mostly used in forest management plans). Numbers on ingrowth and mortality of trees/ha could have an important influence on this annual production so if you have information on these phenomena, this might help to estimate the annual wood production at long term (management plans for 20 years or more). For example, the annual wood production can be high right now but if the tree is not found in regeneration studies, 'sustainable' harvests based on the results of tree-ring analysis only could still lead to depletion of certain tree species.

Height is another variable that could be measured in PSPs or during classical inventories. Although measurements of height are difficult in the tropics due to low visibility in complex forest structures, stem heights to the first large branch were quite easily measured during the leafless dry season in the Mayombe plantations (ca. 10 % of the sample trees of the inventory). The height of felled trees in the natural forests of the Mayombe and Ivory Coast could be measured accurately on the logs with a measuring tape. However, this task was often obstructed by abundant undergrowth and inclination of sample sites, masking the forest floor and creating large risks for the operator. These factors lead to a smaller number of height data on natural sample trees.

How crucial is height for the estimate of variables for SFM and carbon stocks? This study does not provide a conclusive answer but our results suggest that height is an important variable that changes the evolution of volume production and carbon stocks over time. Long-lived pioneer species like *T. superba* are characterized by fast growth, in diameter as well as in height. Measurements of height in young Mayombe plantations by Tutula (1968) and Mbenza (1978) showed that planted *T. superba* trees reached mature stem heights after 20 to 25 years. Height tends to level off at maturity and height increment may approach zero (Bowman et al. 2013). This can also be derived from the diameter-height curve of the plantations in chapter 2. The juvenile phase of *T. superba* combines large tree rings with fast height growth, probably leading to higher values of MLD/BRA than those that were only based on basal area. If volume growth is influenced by height growth, this will also be the case for cumulative carbon stocks.

Apart from the use of tree-ring analyses and PSPs, one of the largest problems often encountered in the tropics is the limited sample size. Sampling in the tropics is difficult and loggings were restricted or forbidden for several reasons: no felling permits in parts of the concessions, difficult angles for the exploitation of large trees, conflicts with local populations, regulations by local authorities or harassment during different stages of the transport of wood samples, etc. On a total of more than 70 analyzed stem disks/increment cores, about 10 trees were older than 100 years. A larger sample size is better, together with measurements of tree rings at different known heights along the trees, taking into account (if possible) a large range of diameters and ages. This strategy could lead to a more representative sample that could lengthen and strengthen the regional chronologies, avoid the sample biases listed by Bowman et al. (2013), lead to a more reliable estimate of the culmination of growth variables and thus provide a solid base for bootstrapping of growth curves.

Longer regional chronologies based on a larger number of trees are useful to test whether the long-distance relations in growth are maintained (Chapter 3). If so, regional chronologies could be merged into a species chronology. Chronologies of *T. superba* will probably not be longer than 200 years and not useful for reliable dating of wooden objects. Still, those chronologies can be compared with growth patterns of neighbouring species and the relation with climate can also be studied over large areas, covering different forest and climate types. If strong links between growth and local climate variables are observed, proxies of, e.g., precipitation could be reconstructed beyond the limited time span of instrumental data.

Bowman et al. (2013) mention different types of sample biases that can be minimized by well-designed studies that control for age, size, and tree competition. In chapter 4, the different individual growth curves from Ivory Coast are presented in Fig. 4.3a. A few slower-growing trees are distinguished as the lowest growth curves with high ages and moderate diameters. If these slower-growing older trees are included in calculations as they are now, they could cause the ‘slow-grower survivorship bias’. Hypothesizing that slow-growing trees generally live longer than fast-growing trees, the oldest rings will originate from the slowest-growing trees, because the faster-growing cohort would not have survived long enough for sampling (Bowman et al. 2013). Yet, for long-lived pioneer trees such as *T. superba* that date from the same period of disturbance, slower-growing trees will probably only be smaller than fast-growing trees. A larger range of ages and tree sizes in Ivory Coast would still substantially facilitate the selection of an appropriate set of growth curves for carbon or volume calculations, documenting the elimination of biased growth curves.

Logically, this larger range would then lead to more representative and reliable estimates of cumulative growth variables as well as the culmination of increments of diameter, height, volume and carbon stocks. The same example can be used here: what happens if we remove the slowest-growing trees from the dataset of Ivory Coast? In chapter 4, the link between a possibly unrepresentative set of sample trees and low values for MLD/BRA was already suggested. It certainly appears that the slowest-growing trees played a considerable role in the low MLD/BRA values because the basal-area based MLD/BRA increases for both the actual data set and the bootstrapped MLD/BRA values.

However, the MLD/BRA based on the actual sample trees still does not fall within the distribution of MLD/BRA values generated by bootstrapping, even if the slowest-growing Ivorian trees are removed. Naturally, bootstrapping results heavily depend on the original growth curves. If this sample population is not representative, bootstrapping can help in assessing this but it does not transform the results into representative data. The removal of the three slowest-growing trees in Ivory Coast leads to higher values but with a sample size of less than 30 trees, it remains difficult to remove trees statistically based on outlier theory. Thus also for bootstrapping larger sample sizes with a large range in age and tree size are necessary. As such diameter and age limits that are set for bootstrapping can be better documented and the number of inconclusive simulations could decrease.

7.3 Potential for additional research on the inter- and intra-annual level

Nowadays, relations between growth and climate are mainly based on tree-ring widths, as described in chapter 3, but a relation between tree growth and climate is not always found (e.g., Ivory Coast). As an alternative to classical tree-ring widths and growth curves, the use of inter- and intra-annual densities of some Ivorian sample trees compared with precipitation is shortly explored in this paragraph, paving the way for further research.

X-ray volumes of cores were corrected, taking into account the angle of tree rings and grain, resulting in accurate microdensity profiles. Further details of this technique can be found in Van den Bulcke et al. (under review). These corrections were not performed in chapter 6 for annual density variations. They are nevertheless recommended for detailed comparison with climate, especially because inter-annual densities were not standardized the way tree-widths normally are, e.g., the elimination of age trends resulting in tree-ring indices for dendroclimatology. Tree rings were marked on the corrected X-ray volumes and dated with the aid of the existing tree-ring series from classical tree-ring analysis. Not all tree rings could be marked due to the resolution of the scans (50 µm) and the presence of very small rings that could not be distinguished. A total of about 330 tree rings was marked on 15 Ivorian increment cores. The density pattern of every tree ring was extracted from the X-ray scans in ImageJ, together with an average annual density value. These time-series of annual densities were related with tree-ring widths over the same period as in chapter 3 (1959-1996). Comparison between inter-annual densities and precipitation was also performed from 1959 to 2006 to enable comparison with the results of chapter 3.

Except for ring-porous species, the relation between tree-ring width and density is generally believed to be negative. However, Wimmer and Downes (2003) reviewed existing literature and concluded that this hypothesis cannot be generalized. Most of the literature only reports weak negative correlations, whereas other studies found no significant relations at all. For the given time span (1959-1996), correlations between annual density values of *T. superba* and tree-ring widths were mostly negative, with exceptions in 1962, 1981, 1982 and 1990 (Fig. 7.1). Those years were not associated with extreme values of tree-ring width, density or precipitation. Results should be interpreted with caution because some years are represented by only two trees and other, more recent years, are represented by eight trees.

The interruption in Fig. 7.1 means that only one tree represented 1965. The overall correlation between the mean curve of annual densities and the mean raw tree-ring widths was also significantly negative (r = -0.41; p < 0.01).

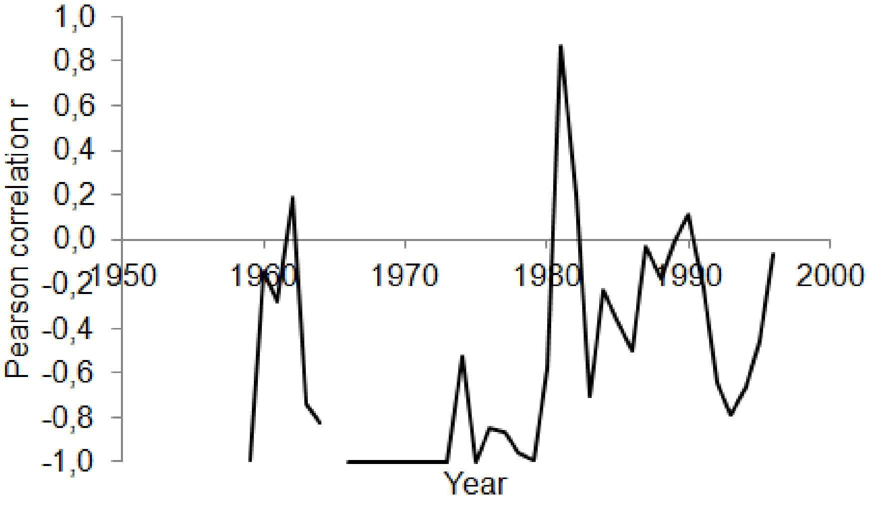


Fig 7.1. Annual Pearson correlations between density and unstandardized tree-ring widths. For every year, correlations were calculated between the tree-ring widths and densities of two to eight sample trees, also explaining the correlation coefficients of -1 based on only two trees.

Based on this negative correlation between tree-ring width and annual density and the positive influence of precipitation on growth in the Mayombe, a negative correlation could be expected between time-series of precipitation and density. In fact, correlations are fluctuating but May precipitation is significantly negatively correlated with the time-series of densities (Fig. 7.2). Higher December precipitation appears to induce higher densities but the precipitation at that time probably doesn’t matter as the growing season is finished. May is the wettest month during the first half of the rainy season, only preceded by June. Summarized, high rainfall in May, during the first half of the rainy season, leads to low annual density values and thus, larger tree rings. However, the limited dataset used here can only suggest that annual density values show a higher climate-sensitivity than tree-ring widths for certain regions. Although this is a preliminary result, wood anatomical features like, e.g., vessel density and vessel area, already proved to lead to better correlations with climate than tree rings (Campelo et al. 2010). The use of density profiles might substitute for labour-intensive wood anatomical studies if these studies of wood anatomy confirm the link with density of *T. superba*. The latter is most probable given that density variations are often largely explained by variations in wood anatomy. Moya and Tomazelo-Filho (2007) also ascribe intra-annual density variations of *Gmelina arborea* to variations of cell wall thickness of fibres and vessel percentage.

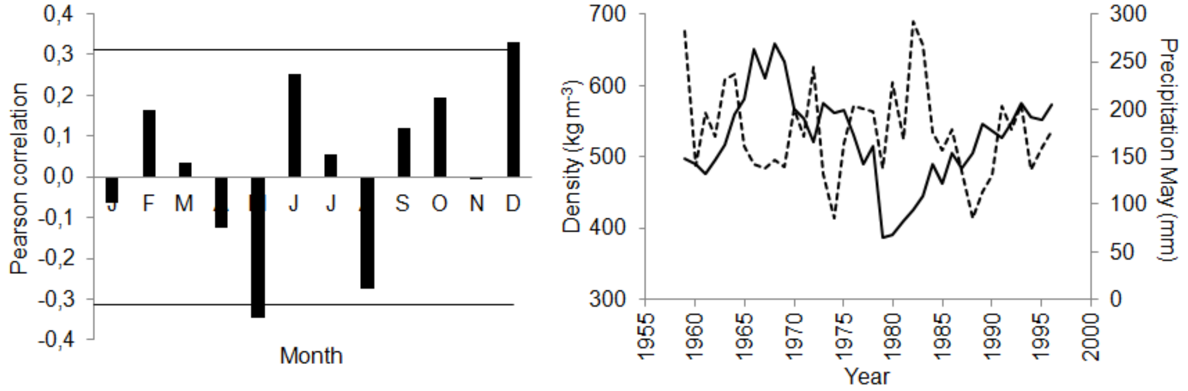


Fig 7.2. Pearson correlations between time-series of density and monthly precipitation are shown at the left. Vertical lines delimit significant correlations at the 0.05 level. The significant negative correlation between annual densities and the precipitation of May is shown at the right. The precipitation curve is a dashed line and the time-series of density are represented as a solid line.

On an intra-annual level, density shows a slight decrease at the start of the growing season and then increases slowly or more explicitly until the end of the growing season (Fig. 7.3a). This pattern was observed in ca. 80 % of the tree rings. The other 20 % of the tree rings often show higher densities in the first part or an increase in the middle of the tree ring (Fig. 7.3b).

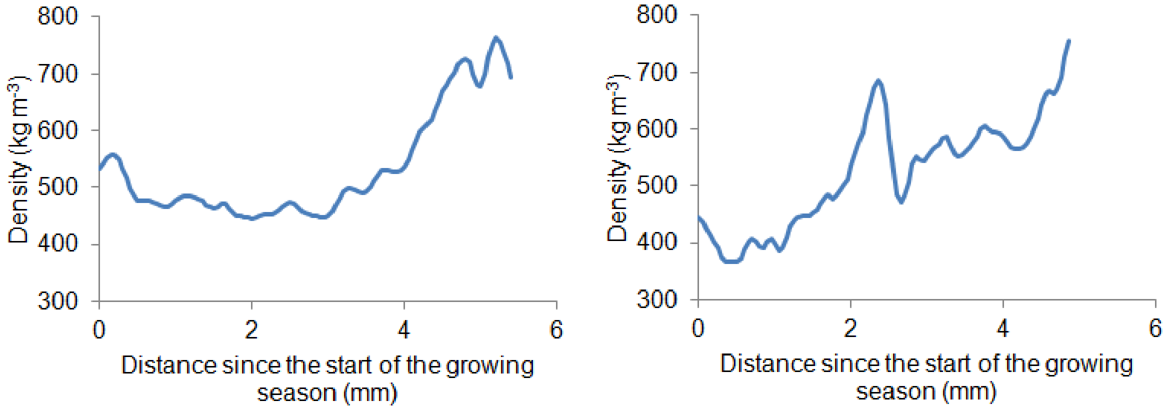


Fig 7.3. ‘Normal’ (left) and ‘deviant’ (right) intra-annual density patterns. The left graph shows the density pattern of B5R1 in 1994. The right graph shows the density pattern of S2.2R5 in 1942.

Deviant patterns of intra-annual density do not necessarily correspond to extremely dry or wet years, nor to ENSO events. Comparison between intra-annual density profiles and monthly precipitation data is not straightforward because intra-annual density patterns do not have a distinct temporal scale. Cambial marks at higher time resolution (monthly instead of annually), together with monthly (or even weekly) precipitation data would offer an interesting framework to interpret intra-annual density patterns and the possibly related wood anatomical variables.

7.4 Concluding remarks

This work gives evidence that the combined use of tree-ring widths and wood density data of *T. superba* is essential for accurate and long-term data on SFM and carbon stocks. It also suggests recommendations for future sampling. The combination of tree-ring analyses and PSPs at the same location offers new possibilities to generate accurate, reliable long-term data for SFM and the estimation of carbon stocks, whereas the addition of cambial marks and wood anatomical data could further document climate-growth relations that remain inconclusive with classical dendroclimatology. In general, wood density data based on helical X-ray CT are possible for all tree species, whereas Bowman et al. (2013) comment that dendrochronological studies are geographically and floristically more restricted due to the need of annual growth rings. Zuidema et al. (2012) nevertheless counter this with a list of almost 70 species from tropical lowland rainforests, all having annual tree rings. They believe this list will increase rapidly, given that annual ring formation is currently being tested in many more species. We share this opinion and recommend to include tree-ring analyses as a part of growth studies conducted in the framework of large projects like CarboAfrica and the Afritron network. This way, the methods analyzed in this work could be applied on growth data of other tropical tree species, further documenting the growth of Africa’s tropical forests.

12 May 2013.

		SERVE	
FORESTIERE DU [illegible]AS-FLEUVE			
[illegible]ESTIER THEY[illegible]			
PANGI			
-KIMALELE	52/210/56	678,00	67
-LUFU	52/224/59	816	53
-ZINGI-ZINGI	52/211/56	1 600,00	
-C.L. LUFU	52/220/59	92[illegible]	
-C.L. [illegible]GIL	19 BO 52/522/59	210,00	15
	—	404	
[illegible]ICE	—	3.280	
[illegible]BUNDI I	—	101	
[illegible]BUNDI II	—	268	
	—	1806	262
	TOTAL	11.1[illegible],00	1.761
[illegible]MAG			
-MAG	52/75/52	1.931,00	
-MAMI	52/252/56	3.111,00	
-ZIMI	—	1.678,00	
	TOTAL	6.7[illegible],00	10.[illegible]
[illegible]			
[illegible]M.28	52/252/58	2.600,00	
-BOMA-BUNGU	52/654/59	253,00	
-KIFULU	—	446,00	—
-BOMA	—	[illegible]	—
-TSHIKAYI	—	221,00	—
	—	400,00	—
	TOTAL	3.920,00	—
[illegible]TIER F[illegible]ST KIEM[illegible]			
[illegible]-KIEM	52/638/59	980,00	
-PATU BLOC I	52/443/55	200,00	—
-KIEMI-TETI	—	1.715,00	—
-KIEMI-LUKANGA	—	640,00	—
-KIEMI-TUBA	—	830,00	—
-LAC VONDO	—	4.300,00	—
-[illegible]UBA	—	12.244,00	—
-NZENZE	—	200,00	—
-KIMA[illegible]	—	720,00	—
	TOTAL	22.149,00	—	1
	TOTAUX	43.95[illegible],00	1.771,00	9[illegible]
[illegible]ERE DES CARACTES			
[illegible]SER[illegible]			
[illegible]MATENDU (Matendula)	—	± 360,00	—
[illegible]VA (Maliva[illegible])	—	± 1[illegible],00	—
[illegible]NASAU (Grande-Nasala)	—	± 250,00	—
[illegible]	—	300,00	—
[illegible]	—	500,00	—

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CURRICULUM VITAE

PERSONALIA

Maaike De Ridder
Place and date of birth: Ghent, 24/3/1982
Nationality: Belgian
Marital status: married to Lieven Schelstraete
Children: Elodie (10/04/2010) & Otto-Jan (20/01/2012)
Home address: Ferd. Vanlaerstraat 5, 3060 Bertem
Phone (mobile): +32 476 33 30 53
E-mail: Maaike.DeRidder@ugent.be / maaikedr@gmail.com

EDUCATION

1994-2000: Lyceum Wachtebeke, Wiskunde-Wetenschappen

2000-2005: Bio-engineer Land and Forest Management, option Forest and Nature Management. Graduated at the Ghent University with high distinction.

> Dissertation: Dendrochronologische monitoring van luchtverontreiniging in de Gentse Kanaalzone.
> Promoters: Prof. dr. ir. Joris Van Acker & Prof. dr. ir. Roeland Samson.

PROFESSIONAL CAREER

Function	*Institution*	*From (d/m/y)*	*To (d/m/y)*
Environmental officer	Municipality of Zelzate	12/07/05	31/08/05
Scientific researcher	Royal Museum for Central Africa (RMCA), Tervuren	01/10/05	30/09/07
PhD student VLIR (VLADOC)	Ghent University	01/11/07	31/10/12

PUBLICATIONS

A1:

-De Ridder M, Hubau W, Van den Bulcke J, Van Acker J, Beeckman H (2010). The potential of plantations of *Terminalia superba* Engl. & Diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo). Annals of Forest Science 67:501

-De Ridder M, Van den Bulcke J, Vansteenkiste D, Van Loo D, Dierick M, Masschaele B, De Witte Y, Mannes D, Lehmann E, Beeckman H, Van Hoorebeke L, Van Acker J (2011). High-resolution proxies for wood density variations in *Terminalia superba*. Annals of Botany 107:293-302

-De Ridder M, Trouet V, Van den Bulcke J, Hubau W, Van Acker J, Beeckman H (2013). A tree-ring based comparison of *Terminalia superba* climate-growth relationships in West and Central Africa. Trees (published online March 2013)

- De Ridder M, Van den Bulcke J, Beeckman H, Van Acker J (accepted). Tree-ring analysis of an African long-lived pioneer species as a tool for sustainable forest management. Forest Ecology and Management (revision accepted)

- De Ridder M, Van den Bulcke J, Beeckman H, Van Acker J (in preparation). The influence of density variations in *Terminalia superba* Engl. & Diels on aboveground biomass quantification.

C1:

- De Ridder M, Haneca K, Beeckman H, Samson R, Van Acker J (2007). Dendrochronological monitoring of air pollution in the Ghent canal area (Belgium). Proceedings of the Dendrosymposium 2006, April 20-22 2006, Tervuren, Belgium:188-195

- De Ridder M, Van den Bulcke J, Beeckman H, Van Acker J (2008). In the heart of the limba tree (*Terminalia superba* Engl. & Diels): detection methods for heart rot and false heartwood. Proceedings of the International Conference on Wood Science for Preservation of Cultural Heritage, November 5-7 2008, Braga, Portugal

Overige:

- Beeckman H, Boeren I, Couralet C, De Ridder M, Schmitz N, Tavernier W, Toirambe B, Verheyden A (2007). De zwarte doos van Afrikaans hout. Het Afrodendro-project van het KMMA. Science Connection 18:10-14

- Beeckman H, Tavernier W & De Ridder M (2008). Houtbiologie en verantwoord houtgebruik. Houtnieuws 161:34

CONFERENCES, LECTURES, FIELDWORK

Conferences as a participant:

- TRACE, April 20-22, 2006, Tervuren, Belgium.
Poster: Dendrochronological monitoring of air pollution in the Ghent canal area.

- Eurodendro, May 28-31, 2008, Hallstatt, Oostenrijk.
Poster: In search of the true color of limba (*Terminalia superba* Engl. & Diels).

- COST IE0601 WoodCultHer, November 5-7, 2008, Braga, Portugal.
Poster: In the heart of the limba tree (*Terminalia superba* Engl. & Diels): detection methods for heart rot and false heartwood.

- International Symposium, Developing Countries facing Global Warming: a Post-Kyoto Assessment, June 12-13, 2009, Brussels, Belgium.
Poster: Combating global warming by planting trees? Some case studies from tropical Africa.

- COST IE0601 WoodCultHer, October 7-10, 2009, Hamburg, Germany.
Oral presentation: Changes in density of archaeological waterlogged wood.

- Eurodendro, September 19-23, 2011, Engelberg, Switzerland.
Oral presentation: Limba (*Terminalia superba* Engl. & Diels), a pioneer species in tropical dendrochronology?

- Xylaredd symposium, November 30, Brussels, Belgium.

Poster: Tree-ring analysis of an African long-lived pioneer species: A tool for sustainable forest management?

- International Symposium on Wood Structure in Plant Biology and Ecology, April 15-20, 2013, Naples, Italy.
Oral presentation: A tree-ring based comparison of *Terminalia superba* in West and Central Africa: growth, climate and density relationships

Conferences as a member of the local organizing committee:

TRACE 2006 and COST-conference WoodCultHer (7-9 June 2007), Tervuren (Belgium).

Lectures:

- Infolunch Royal Museum for Central Africa (February, 2008): Bosinventarisatie van limba plantages in Luki (DRC).
- InnovaWood (January, 2010): The relevance of measuring wood density for sustainable tropical forest management.
- Katholieke Hogeschool Campus Sint-Niklaas (May, 2008/2012/2013): Sustainable forest management under tropical conditions.
- Paul Scherrer Institute (Switzerland) (November, 2009): Neutron scans of tropical and cultural heritage wood samples.
- Several lectures for African trainees at the Royal Museum for Central Africa.

Fieldweeks, fieldwork and short term scientific missions:

- Winter School in Wood Anatomy, Nov 25-Dec 1, Davos, Switzerland.
- Short term scientific mission at the Paul Scherrer Institute, June 14-19, 2009, Villigen, Switzerland
- Fieldwork in the Luki Biosphere Reserve, DRC (January 2007 and June-July 2008) and in western Ivory Coast (January-February 2009).