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Cambial activity, growth rings analysis and wood density variability of planted teak (*Tectona grandis* L.f. (Lamiaceae)) in Ivory Coast

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

By the Authority of the Rector,
Prof. dr. Anne De Paepe

Dutch translation of the title

Cambiale activiteit, groeiringanalyse en variabiliteit in volumegewicht van plantage teak (*Tectona grandis* L.f. (Lamiaceae)) in Ivoorkust

Cover page: Structural changes in the cambial zone of 24-year-old teak (*Tectona grandis* L.f.) collected in April 2007 (during earlywood formation) in the Séguié Forest Divisions (Ivory Coast).

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Préface

"*De Celui qui mange est sorti ce qui se mange et du fort est sorti le doux*. (Juges 14v14)" C'est un prodige, c'est l'oeuvre du Puissant de Jacob, du Fort d'Israel, de Jehovah Sabahouth.

A ma sœur, ma sœur et mère Béatrice Glon Epse Klohi. Tu avais promis de me téléphoner tôt ce matin-là. J'ai attendu ton appel, en vain. Alors j'ai compris que tu étais partie. Mais tu restes à jamais présente dans mon cœur et ta voix résonne encore comme pour me dire: «Fonce, vas-y, tu y arriveras». Je promets que je foncerai encore et toujours pour achever la course.

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A ce stade du parcours de la vie, j'ai réalisé que Dieu agit envers l'homme par des gens de bonne volonté qui acceptent de se mettre à sa disposition. Je voudrais reconnaître tout le soutien de quelqu'un qui, sans être mon père, a agi comme s'il l'était: Professeur Joris Van Acker. D'aucuns considéreraient cela logique et y trouveraient même des raisons humaines. Cependant, seul lui et Dieu qui l'a guidé savent le pourquoi de cette attention particulière qu'il m'a accordée en se rendant disponible chaque fois que besoin était. Au-delà de son esprit critique aigu et constructif dans le contexte scientifique, l'homme est doté de quelque chose qui fait de lui un véritable Humain. Bedankt, beste Professor!

J'avais entendu parler de ceux qui scrutent les étoiles: Les Mages d'Orient l'ont fait. J'ai aussi entendu parler de ceux qui lisent les cartes ou dans les lignes de la main de l'homme, pour prédire l'avenir. Mais je n'avais encore pas rencontré quelqu'un qui lit dans les lignes du bois, jusqu'au jour où j'ai découvert un visage qui a l'aspect des savants de l'histoire. C'est cet homme Hans Beeckman qui, volontairement et avec passion, m'introduisit au cœur du bois, au cœur du teck, pour décrypter l'information qui y était enfouie depuis des temps reculés. Et j'ai compris que le cœur du bois regorgeait plus de secrets que n'en contient le cœur de l'homme. Depuis ce jour, chaque fois que je lis et lirai dans les lignes d'un bois, une reconnaissance montera de mon cœur vers, toi, cher Hans. Merci de m'avoir accueillie au Laboratoire de Biologie du Musée Royal de l'Afrique Centrale dont la Direction est priée de recevoir, ici, l'expression de ma profonde gratitude.

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Avant d'oublier ce qu'est une âme sensible, avant d'oublier que blanc et noir ont le même sang circulant dans leurs veines et avant de me laisser emporter par la beauté des pages qui suivront, je voudrais reconnaître le soutien sans faille, sans contestation d'un homme, d'un fils du Père, d'un frère de sang: Philippe Julien Wouters. Il se serait substitué à moi devant tous les défis de la vie durant cette période. Les mots sont faibles pour te manifester ma reconnaissance; le dire serait trop insignifiant. Cependant, *Verba volant, scripta manent*, c'est pourquoi je dis et j'écris: Merci. Chaque lettre de ce mot renferme quelque chose de spécial pour toi, *Philou*. Nos chemins se sont croisés et je crois que le véritable but de notre rencontre ne sera révélé qu'au banquet de l'Agneau, dans la Félicité céleste.

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Mo Nkolo NZambe shao diky diky yeo yeba? Mo Nkolo NZambe mo kom sao bi lobaloba yeo yeba? (DR Congo)

L'on naît avec sa conception au sujet de certaines notions. Pour certains, la famille est l'ensemble des individus liés par le sang. Pour moi, cette période doctorale a déchiré le voile qui couvrait mon esprit et m'a permis de revoir la définition de la famille, la vraie. Ainsi Benjamin Toirambe Bamoninga (Yaya, accepte que j'écrive tout ton nom) et Laurent N'senga m'ont démontré cette autre dimension de la famille. Recevez, chers frères, la bénédiction de notre Père pour avoir affronté et relevé les défis dans les contextes de la foresterie et de la famille. Merci d'avoir fait de la RDC, ma seconde patrie, où je suis devenue plus que populaire sans y avoir mis pied. J'ai bien peur que la haie d'honneur qui m'accueillera à l'aéroport de Kinshasa provoque un état d'urgence de la part du gouvernement central. Merci à mes frères Patrick Konjo et John Tshibamba Mukendi, mes soutiens indescriptibles et inconditionnels. Aux autres frères de la RDC: Jean-Maron Maloti, N'Tamwira, Prospère Sabongo, Bhely, vieux N'Dunga. Que tous ceux dont le nom ne figure pas ici, soient cléments. Le linge sale se lave en famille; on est ensemble.

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There has never been a defined border between Ghana and Ivory Coast. We were just one people. I think there should be a blood link crying out somewhere. That is probably the reason why any Ghanaian family always welcomes me immediately as part of theirs. Pastor and Mum Set, Nana and Mercy, Pastor and Antie Danso, Dina Danso (my lovely Angel) "*Me da se*". Thanks to Sam N'ketiah, Ernest Foli, Victor Agyeman, Lucy Amissah, and Emanuel Ebanhyele, all from the Forest Research Institute of Kumasi/Ghana (FORIG). Special thanks go to Michael Abedi-Lartey, thanks for everything and for always being there.

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Yobô seô (South Korea)

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Glanmangné kpa tou ha drou mein. Diman kpoun de yahibo! (Guéré, mother tongue)

Chez les Dié comme chez les Ivoiriens en général, la charité bien ordonnée ne commence pas mais plutôt finit par soi-même.

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Agathe Dié, 20th January, 2016

Summary

Although they currently absorb more carbon than they release, tropical forests suffer disturbances generated by human activities and amplified by global warming. Therefore, forest plantation, based on fast-growth fuelwood and timber species such as teak, becomes an option to counteract the risk of loss of these natural biomes.

For its various advantages (ecological plasticity, good behaviour in plantation, fast-growth, high natural durability and wood density), teak (*Tectona grandis*) is introduced under different climatic conditions along the inter-tropical belt, occupying 75% of the world tropical timber plantations. However, this species remains highly sensitive to climate, suggesting that disturbances in the rainfall rate and intensity are expected to negatively affect tree growth and, consequently, induce variations in the derived wood properties. Therefore, to be successful, in response to the high demand for high quality wood, teak based reforestation programs should be underpinned with reliable and accurate information based on field data on tree growth rate and wood density dynamics. Because growth rate (reflected in ring widths) and wood density represent the main two functional traits that portray tree sensitivity/vylnerability to environment (climate). Information on the dynamics of growth and wood density remains, therefore, crucial to control and predict planted stands productivity, biomass estimate and the wood quality in regions marked by ongoing climatic variability like in Ivory Coast.

Our study addressed the following questions: (i) What are the determining factors of wood formation and its fluctuations in teak planted in Ivory Coast? (ii) How does the precipitation variability influence managed and non managed tree growth? Is there a large-scale climatic signal in the tree growth rate (ring width), in addition to local the precipitation signal? (iii) How to assess the degree of variability of wood density in teak planted in Ivory Coast? Does climate variability affect teakwood density?

To address these research questions, monthly cambial sampling was carried out in an evergreen forest and tree-ring analysis was performed in trees from 2 stands: a managed plantation located in an evergreen forest close to the Atlantic coast and an unmanaged semi-deciduous forest situated in the Central West Ivory Coast. Microdensity measurements were implemented on trees also from the evergreen forest, in order to assess the variations in wood density.

Cambial activity showed that a 3 months dry season induced growth interruption and resulted in the formation of an annual xylem growth ring with 2 phloem rings over the same vegetative season. Anatomical quantification of the structural changes occurring in the cambial zone was closely correlated to monthly precipitations. Growth anomalies, induced by climatic and phenological variations during the growing period, were visualized through the formation of intra-annual xylem growth zones.

Tree-ring analysis revealed higher growth rate in the managed trees than in the non-managed forest. In the deciduous forest, teak growth was only sensitive to the wet season precipitation while trees reacted to both wet and annual precipitation in the semi-deciduous forest. Anomalies in the sea surface temperature of the Gulf of Guinea also influenced trees growth. Moreover, growth patterns reflected the effect of three major El Niño events in the southern forest. Overall, climatic influence was more pronounced (slightly high correlation) in the non-managed teak plantation compared to the managed one as a consequence of the lack of sylvicultural intervention in the non-managed stand. This indicates the role of sylviculture in enabling trees to cope with a water deficit resulting from climate disturbances. The results reveal clear and direct effect of the broad-scale climate on tree growth, in addition to local precipitation recordings.

Microdensitometrical profiling revealed that wood density was more variable within the tree than between trees. Intra-tree density variations reflected fluctuations occurring in the intra-ring xylem anatomy. Direct and significant correlations were found between October rainfall and the total ring wood density ($r= 0.37$; $p<0.05$) and latewood density ($r= 0.41$; $p<0.05$) which also correlated with the post-wet season rainfall ($r=0.47$; $p< 0.05$). The intra-ring anatomy related density changes led to the occurrence of the alternating pattern of intra-ring denstiy variation which best supported the correlation with the bimodal monthly precipitation. Inter and intra-annual density variations were high and persistent in the mature wood portion, indicating that the cambial age was not the main driving factor of the density variability.

This research work, founded on original field data and unique for this region, provides highly useful results for teak plantations management in West-Africa. This scientific data evidences the sensitivity of teak growth to climate at both local and global scales. As a result of this climate sensitivity, (1) growth slowed down during years of low precipitation and (2) in response to intra-annual precipitations disturbances, trees formed intra-ring anatomy fluctuations which, in turn, result in the intra-ring density variations, the main source of the mean tree density variability.

As a perspective to future research, a weekly cambial sampling could test the hypothesis on the intra-annual xylem growth zones formation which affected tree-ring density and, consequently, mean tree density. Monitoring of thinnings and pruning operations, combined with tree-ring analysis, and the monitoring of leaf area index, evapotranspiration and soil water content, could be a key to unravel the mechanism through which the managed stand trees adapt to water deficits. Heritability study could allow to establish the degree of the genetic control on wood density namely the earlywood features which could contribute to stabilize the mean tree wood density.

Résumé

Les forêts tropicales absorbent, actuellement, plus de carbone qu'elles n'en libèrent et subissent des perturbations anthropogéniques amplifiées par le réchauffement climatique global. Dès lors, les plantations forestières d'essences à croissance rapide et à vocation de production de bois-énergie et de bois d'oeuvre, comme le teck ou *Tectona grandis* (Lamiaceae), deviennent une option visant à contrer le risque de déperdition des biomes forestiers tropicaux naturels.
La plasticité écologique, le bon établissement en plantation, la croissance rapide, la durabilité naturelle et la forte densité de bois sont les atouts majeurs qui ont valu au teck de coloniser divers types de climat à travers la ceinture inter-tropicale. Les teckeraies occupent, actuellement, 75% des plantations mondiales d'essences de bois d'oeuvre. L'espèce reste, toutefois, sensible au climat; ce qui signifie que la variabilité du climate local et/ou global est susceptible de perturber et d'affecter négativement sa croissance et causer une variabilité des propriétés du bois, par modification de la structure du xylème. Dès lors, la réussite des programmes de reboisement, en réponse à la demande de bois d'œuvre, devrait reposer sur la disponibilité de données précises et fiables sur la vitesse de croissance et l'effet de ses variations sur les propriétés du bois. Ces données devront permettre (i) de contrôler et estimer les rendements des peuplements et la qualité du bois et (ii) de relayer les méthodes sylvicoles empiriques en vue d'améliorer la productivité ligneuse dans un contexte de variabilité climatique qui prévaut en Côte d'Ivoire.

Le présent travail visait à résoudre les questions suivantes: (i) Quels sont le déterminisme et les facteurs contrôlant la formation du bois dans le teck planté en Côte d'Ivoire? (ii) Comment la variabilité climatique influence la croissance des arbres dans les peuplmts aménagés et non aménagés? Existerait-il un autre signal climatique influençant la croissance des arbres, outre les précipitations locales? (iii) Comment évaluer le degré de variabilité du bois? La variabilité climatique expliuerait-elle les fluctuations de la densité du bois?

Un échantillonnage mensuel de la zone cambiale a servi à l'étude de la formation du bois. L'étude de la sensibilité de la croissance au climat s'est effectuée à l'aide d'une analyse des variations de la largeur de cernes dans deux plantations: une plantation aménagée localisée en zone sempervirente proche de la côte atlantique et une autre, non aménagée, située au centre-ouest du pays, en zone semi-décidue. La variabilité de la densité du bois a été examinée à l'aide d'une analyse microdensitométrique du bois.

L'activité cambiale montre que 3 mois de saison sèche causent un arrêt de croissance, résultant en la formation d'un cerne de croissance du côté du xylème et deux cernes de phloème, pendant la même saison végétative. Les variations morphométriques de la zone cambiale sont étroitement corrélées aux précipitations des mois de d'échantillonnage. Les anomalies de croissance – résultant des fluctuations phénologiques induites par les variations du climat – se sont traduites par la formation de zones de croissance intra-annuelle.

Les arbres aménagés présentent un rythme de croissance plus rapide que ceux qui ne le sont pas. En forêt semi-décidue, le teck est uniquement sensible aux précipitations de la saison humide tandis qu'en forêt sempervirente, les arbres ont réagi, à la fois, aux précipitations annuelles et à celles de de la saison humide. Les anomalies du champ thermique océanique du golf de Guinée exercent une influence significative sur la croissance, légèrement plus élevée en forêt semi-décidue qu'en forêt sempervirente. En forêt sempervirente, la croissance a enregistré l'effet de trois épisodes majeurs El Nino. Dans l'ensemble, l'influence du climat était plus accentuée sur les arbres non aménagés; conséquence du manque de traitement sylvicole dans ce site.

L'analyse microdensitométrique révèle que la densité est plus variable au niveau intra-arbre qu'à l'échelle inter-arbres. Les variations intra-arbres, essentiellement dues aux variations intra-cernes, sont engendrées par les fluctuations de l'anatomie du xylème. Les précipitations de la période post-saison humide et d'octobre ont un effet significatif sur la densité totale du cerne et sur la densité du bois final. Les variations intra-cernes de la densité persistent fortement dans le bois mature. Ceci indique que l'âge cambial ne constitue pas la source principale de variabilité de la densité.

L'étude actuelle, basée sur des données originales, fournit des résultats très utiles pour la gestion du teck en Afrique de l'Ouest. Elle met en évidence la sensibilité de la croissance face au climat local et global. Cette sensibilité du teck s'est traduite par le ralentissement de la croissance pendant les années de baisse des précipitations. En réaction aux perturbations pluviométriques intra-annuelles, les arbres forment des zones de croissance intra-annuelles qui causent des fluctuations de la densité du bois. Ces variations intra-annuelles représentent la principale source de la variabilité de la densité moyenne de l'arbre.

Des études futures devraient réaliser un échantillonnage hebdomadaire de la zone cambiale, en vue de tester l'hypothèse sur la genèse des zones de croissance intra-annuelles qui affectent la densité moyenne de l'arbre. Une étude intégrant l'analyse de l'activité cambiale et des cernes de croissance couplée à un suivi du régime des éclaircies, de l'indice foliaire, de l'évapotranspiration, et de la réserve utile du sol permettra (i) d'approfondir le mécanisme par lequel les arbres, sous traitements éclaircies, réagissent au déficit hydrique et (ii) de déterminer le seuil de déficit hydrique tolérable par le teck. Une étude génétique permettra d'établir le degré d'héritabilité de la densité des composantes de la densité, notamment la proportion et la densité du bois initial qui représenteraient une forme de stabilisation de la densité moyenne de l'arbre.

Samenvatting

Tectona grandis L., beter gekend als teak, is een tropische boomsoort met hoogwaardig hout en een aanzienlijk potentieel voor koolstofopslag. Deze soort, intensief gebruikt in herbebossingsprogramma's in Ivoorkust, heeft eveneens een hoge klimaatgevoeligheid. Verstoringen in lokale neerslagpatronen en globale klimatologische fenomenen zouden dus de boomgroei van teak kunnen stimuleren of afremmen en/of leiden tot afwijkende groei. Die veranderingen in groei zijn mogelijks te linken met variaties in houtkenmerken als densiteit (volumegewicht) die veroorzaakt worden door variaties in de structuur van het xyleem.

Succesvolle herbebossingsprogramma's met teak gaan hand in hand met betrouwbare en nauwkeurige gegevens om te beantwoorden aan de hoge vraag aan kwaliteitshout. Deze gegevens zijn gebaseerd op veldwerkdata rond de groei en variaties hiervan. Deze variaties hebben op hun beurt implicaties op de houtstructuur en de houtanatomische eigenschappen. Al deze informatie is cruciaal om de productiviteit en de houtkwaliteit van plantages te controleren en te voorspellen, met inbegrip van de invloed van klimaatsverandering hierop. De belangrijkste objectieven van dit werk zijn: (i) de analyse van houtvorming en variaties gelinkt aan cambiale activiteit, (ii) de analyse van groeiresponsen van teak op lokale en globale klimaatsvariabiliteit en het mogelijke effect van bosbouwkundige behandeling en (iii) de analyse van variaties in houtdensiteit van teak door middel van microdensitometrische profielen.

Voor de eerste twee objectieven werden maandelijks cambiumstalen genomen gedurende 18 maanden en werden jaarringen opgemeten in een beheerde en een onbeheerde plantage. Voor het derde objectief werden microdensiteitsmetingen uitgevoerd om variaties in houteigenschappen als houtdensiteit en vezellengte te analyseren.

Cambiale markeringen tonen aan dat een droog seizoen van drie maand leidt tot een groeistop en de vorming van een jaarlijkse groeiring. Terwijl het cambium een groeiring produceert in

het xyleem, produceert het twee ringen per groeiseizoen in het floëem. Cambiale seizoenaliteit wordt ook gekenmerkt door de aanwezigheid van kristallen –al naargelang het seizoen- in de cambiale zone. Gegevens rond veranderingen in anatomische structuur van de cambiale zone zijn sterk gerelateerd met de maandelijkse neerslag. Groeianomalieën, verbonden met klimaatsgedreven fenologische variaties gedurende de groeiseizoen, zijn zichtbaar onder de vorm van groeizones binnen het xyleem van dat groeiseizoen. Jaarringanalyses bewijzen de hogere groeisnelheden van beheerde plantages ten opzichte van niet-beheerde plantages. Teak vertoont een variabele groeirespons in relatie tot klimaat. In het bladverliezende bostype was de groei enkel gerelateerd met de neerslag van het regenseizoen terwijl bomen uit het semi-bladverliezende bostype zowel reageerden op de jaarlijkse neerslag als de neerslag binnen het regenseizoen. Anomalieën van de oppervlaktetemperatuur van de Golf van Guinea hebben ook een invloed op de groei van teak. Bovendien werden drie grote El Niño jaren ook teruggevonden in de jaarringpatronen van het zuidelijk gelegen bos. Algemeen gezien is de invloed van het klimaat duidelijker in de niet-beheerde plantage dan in de beheerde plantage als gevolg van het gebrek aan bosbouwkundige interventies. Dit resultaat illustreert de rol van bosbouwkundige ingrepen die bomen toelaten om hun waterdeficiet bij lagere neerslag, veroorzaakt door klimaatsverstoringen, te omzeilen. Zowel globale (oppervlaktetemperaturen oceanen/El Niño) als lokale (neerslag) klimaatsvariabelen hebben dus een direct en duidelijk effect op de groei van teak.

Microdensitrometrische profilering heeft aangetoond dat het volumegewicht (densiteit) meer varieert binnenin bomen dan tussen bomen. Variaties tussen bomen weerspiegelen schommelingen in de intra-ring xyleem anatomie. Significante correlaties zijn gevonden tussen de neerslag in oktober en het volumegewicht van de totale groeiring ($r= 0.37$; $p<0.05$) en het volumegewicht van het zomerhout ($r= 0.41$; $p<0.05$), welke ook gecorreleerd is met de neerslag die valt na het natte seizoen ($r=0.47$; $p< 0.05$). De veranderingen in volupmegewicht gerelateerd aan de intra-ring anatomie leidde tot het vóórkomen van een wisselend patroon van de intra-ring dichtheidsvariatie welke het beste de correlatie ondersteund van bimodale maandelijkse neerslag. Inter- en intrajaarlijkse variaties in volumegewicht zijn hoog en persistent in het mature houtgedeelte. Dit duidt erop dat de leeftijd van het cambium niet de hoofdoorzaak is van de variabiliteit in volumegewicht.

Dit werk, gebaseerd op authentieke veldgegevens, uniek voor deze regio, is nuttig voor het beheer van teakplantages in West-Afrika. Deze wetenschappelijke gegevens bewijzen de gevoeligheid van teakgroei ten opzichte van het klimaat, zowel op lokale als op wereldwijde schaal. Ten gevolge van deze klimaatgevoeligheid, (i) verminderde de groei tijdens de jaren van lage neerslag en (ii) vormden de bomen intra-ring schommelingen als een reactie op de intrajaarlijkse neerslag verstoringen. Deze resulteerden in de intra-ring variaties in volumegewicht, de hoofdoorzaak van de gemiddelde boom variatie in volumegewicht.

Als perspectief voor toekomstig onderzoek, is een wekelijkse monsterneming van het cambium nuttig om te testen of de hypothese met betrekking tot de vorming van intraannuele xyleemgroeizones klopt. Deze intraannuele xyleemgroeizones beïnvloedden het volumegewicht binnen de groeiring en, ten gevolge hiervan, ook het gemiddelde volumegewicht van de boom. Monitoring ven dunnings- en snoeiactiviteiten, in combinatie met groeiring analyse, kan een sleutel zijn tot het ontrafelen van het mechanisme hoe de beheerde bomen reageren op watertekorten. Bemonstering in verschillende ecologische gebieden zouden het mogelijk maken om onze resultaten van de microdensitometrische profilering te generaliseren, waarbij de intra-ring anatomie gerelateerde volumegewichtsvariaties toelaten om de klimaatgerelateerde groeigevoeligheid te interpreteren.

Acronyms

AD: Alternating pattern of intra-ring density variation from earlywood to latewood
ADp: African drought episods
ANOVA: Analysis of Variance
AXGR: Annual xylem growth ring
CDMs: Clean Development Mechanisms
CNRA: Centre National de Recherches Agronomiques
Crd: radial diameter of fusiform cambial cells
CRR: rainfall reduction at the country level
CT-scan: Computed Tomography scanning
CV: coefficient de variation
CZ: Cambial zone width
Dg: Harvest diameter
DS: Dry season
dt: differentiating tissues (xylem and phloem)
DXZ: Differentiating xylem zone width
e: Espacement entre arbres/ spacing between individual trees
ENSO: El Nino-Southern Oscillation
EPS: Expressed Population Signal
PET: potential evapotranspiration
EwD: Earlywood Density
Ewp: Earlywood proportion
FAA: Fixative solution of Formaldehyde Acid and Alcohol
FAO: Food and agriculture organization,
FC: fusiform cambial cells
FC-Séguié / FC-Téné: Forêt classée de Séguié ou de Téné
Fl: Fibre length
Glk: Gleichläufigkeit
GPY: growth pointer years
GW: Great wet season
H_0: commercial log total height
IAWA: International Association of Wood Anatomists
ID: Increasing pattern of intra-ring density variation from earlywood to latewood
Ip: Index of productivity
ITCZ: Intertropical Convergence Zone
ITTO: International Tropical Timber Organization
Ld: lumen diameter
LwD: Latewood density
Lwp: Latewood proportion
NOAA: National Oceanic and Atmospheric Administration

PDF: Plan Directeur Forestier
p.p.r.: percent of parallel run
sds: small dry season
ms: Mean sensitivity
rc: initials of the xylem ray
rD: Vessel radial diameter
REDD+: Reducing Emissions from Deforestation and forest Degradation
RW: Ring width
S (%): spacing factor
SEM: Scanning electronic microscopy
SODEFOR: Société de Développement des Forêts
SODEXAM: Société de Développement et d'Exploitation Aéronautique et Météorologique
SRR: rainfall reduction years at the forest site level
SSTs: Sea Surface Temperatures
sws: small wet season
tD: Vessel tangential diameter
TotrD: wood density of the total growth ring
WAM: West-African Monsoon
WDD: water displacement density
WRR/WAD: Rainfall reduction in West-Africa or West-African drought episods
WT: wall thickness
XGZ: Intra-annual xylem growth zone
X-rayD: X-ray derived density

Table of content

Chapter 1: Outline of the thesis

1.1. General framework of the study

Tropical forests are key in biodiversity conservation, water resources regulation and atmospheric carbon sequestration. They also contribute to improving living conditions of the neighboring populations, preserving the existing ecosystems, ensuring timber resources production and use. However, notwithstanding their various vital functions, the survival of these tropical biomes is being threatened by an increasing rate of deforestation. A recent estimate imputed 11 to 15% of the global emissions of greenhouse gases to deforestation in the tropics (Peters *et al*., 2011). Excessive and uncontrolled exploitation of timber species remains one the main causes of tropical deforestation, particularly in West Africa, including Ivory Coast (N'Guessan *et al*., 2006; Heubes, 2012).

1.1.1. Deforestation in Ivory Coast

Ivory Coast covers an important part of the tropical rain forests of the Guineo-Congolian domain known for its rich biodiversity and its numerous endemic and threatened species (White, 1983). The country represents, unfortunately, one of the sub-Saharan African regions experiencing high rate of deforestation since the recent decades. Excessive forest logging seems to be the main cause of forest degradation in Ivory Coast. Furthermore, in Ivory Coast, the annual timber production from plantations is, currently, estimated at more than 100000 m^3. Timber species logging and forest industry represent a substantial source of revenue and employment. The wood/timber sector is reported to be the fourth largest economic sector of the country in terms of exports. This logging, partially compensated by an annual reforestation rate of 8000 ha, appears to be carried out without sustainable policies, due to lack of technical and scientific assistance (Ministère de l’Environnement et du Développement Durable, 2012).

The increasing agricultural development plays a significant role in land use in Ivory Coast. The country appears as the first and third worldwide producer of cocoa and coffee respectively and is among the top group of African producer of palm oil, banana etc. These crops are shade demanding plants that are also mainly subjected to the annual and inter-annual rainfall regime. The ongoing rainfall disturbances since some decades probably cause a decrease in the agricultural yields, leading farmers in search of new appropriate lands. Furthermore, logging of high quality wood consists of the removal of the most valuable timber species. These logging activities also cause damages to the remaining forest stands through roads construction; which facilitates the penetration and establishment of both local populations and landless migrants in search for agricultural lands. This uncontrolled exploitation of high quality timber species thereby results in the depletion of the rainforest area appropriate for the aforementioned shade demanding crops.

The increasing agricultureal development combined with the uncontrolled forest logging remains the main cause of forest degradation and depletion in Ivory Coast; resulting in the decrease of the tropical dense forest cover from 9.10^6 ha in 1955 (Guillaumet & Adjanohoun, 1969) to 2.10^6 ha in 1993 (Dao, 1999). The annual national monitoring of 2012 reported a forest cover loss of 110 000 ha/year over the period 1980-2000 (Ministère de l'Environnement et du Développement Durable, 2012). Recent unpublished data (BNETD, 2010) confine the forest area and gGuineo-Congolean savanna below the 8th parallel (Fig. 1.1).

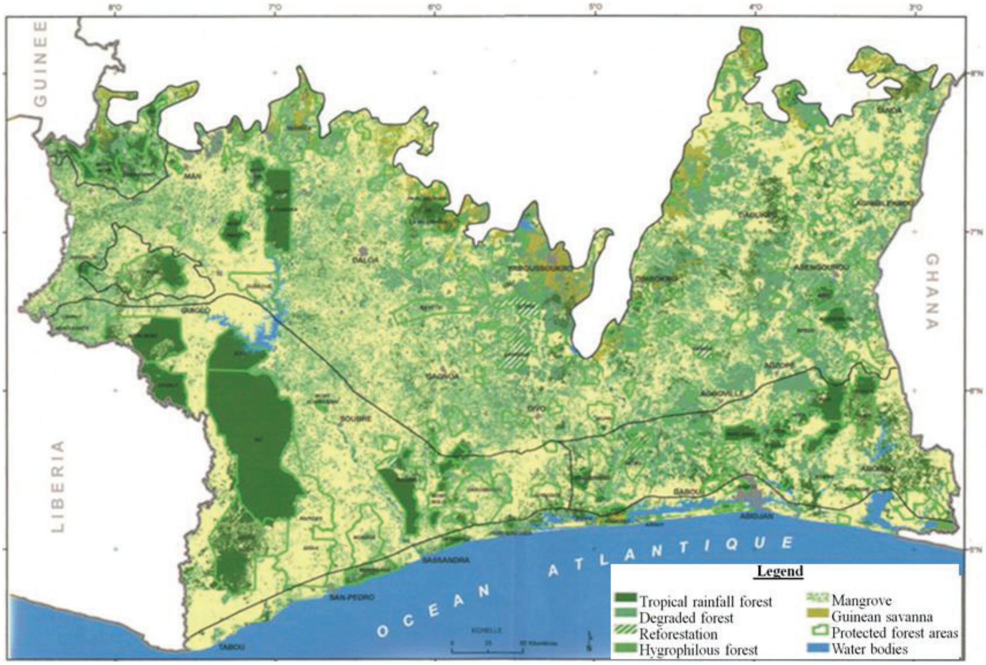


Figure 1.1. Current distribution of the moist dense forest area and Guineo-Congolean savanna, produced by Bureau National d'Etude Technique pour le Développement (BNETD, unpublished, 2010)

1.1.2. State Policy for a sound sustainable forest management

Forest logging in the rural domain, which provides up to 90% of the annual harvested timber logs in Ivory Coast, is still being carried out without a sound management plan. It is actually only using simple logging maps. The latter serve as road map and are based on a preliminary survey for the annual timber supply planning. This survey applies merely to the existence, number and quality of trees destined for logging. While the planting and management (sylvicultural treatments) rules should be adapted to each species group in order to promote sustainable tree growth and to ensure the species regeneration and forest resources renewal.

In order to mitigate the risk of natural forest depletion, resulting from uncontrolled forest logging, a Forest Master Plan or Plan Directeur Forestier, covering the period 1988-2015 (PDF-1988-2015), has been elaborated by the State (Maldonado & Louppe, 2000). A State Policy of 1995 (Réforme Forestière 1995 or Réforme 1995), integrated into the PDF-1988-2015, was elaborated towards improving the forest management and restoring the degraded areas through timber species planting.

The Réforme 1995 was issued through the Decree n° 95682 of September 6, 1995 (Ibo & Kessié, 1998) and aimed to regulate the formerly uncontrolled forest logging confined within the rural forest zone (Domaine rural). The Réforme 1995 intended to (1) slowdown the increasing rate of deforestation (300 000 ha of forest loss per year by the time of the policy issuance) and (2) to accelerate the restoration of the forest cover by involving both the Forest and Wood stakeholders and companies. This policy addressed several objectives:

- Establishing protecting belts around the State Forest Reserves (Forêts Classées)
- Regulating the forest logging taxation
- Planting 1ha of trees for 250 m^3 or 150 m^3 of wood harvested in the dense forest area or in the savannah zone.
- Prohibiting forest logging beyond the 8th parallel

The logging companies opted for teak (*Tectona grandis* L.f.) as a reforestation species, due to its various advantages namely its ease in planting, fast growth and high quality wood. These advantages made teak to take the lead over the other reforestation taxa known as first class timber species and partly comprising *Entandrophragma angolense*, *Guarea cedrata*, *Guibourtia ehie*, *Khaya anthotheca*, *Mansonia altissima*, *Nesogordonia papaverifera*, *Pterygota macrocarpa*, *Pycnanthus angolensis*, *Triplochiton scleroxylon* (Maldonado Louppe, 2000; Kouadio *et al.*, 2007).

Previous forest inventories reported that some local species, such as samba, cedrela and framiré show highest or similar harvest diameter at an earlier age compared to teak (Dupuy *et al*., 1999; see also table 1.1). However, teak took the lead and became the main reforestation species due to its multiple advantages such as its high growth and productivity rate. Teak is also a fire-resiliant species. Wood products derived from teak plantation thinnings can be used, at an early age, as good quality material for solid applications. Owing to its wood quality, teakwood enjoys a higher economic value compared to local timber species.

Table 1.1. Wood productivity of teak compared to some fast-growing local species

	Harvest age (year)	Harvest diameter (cm)	Mean annual increment (m^3/ha/yr)
Tectona grandis (teak)	35	50	13
Triplochiton scleroxylon (samba)	24	50	14
Cedrela odorata (cedrela)	28	55	16
Terminalia ivorensis (framiré)	32	48	11

These first class species (both exotic and local) are mainly destined to produce quality wood for solid applications like exterior and interior carpentry and timber construction.

1.1.3. Teak plantations as an option to enhance natural forest recovery

Due to its high ecological plasticity, its fast growth and its high quality wood, teak is planted as an option to restore the degraded lands in both the rural domain and the State forest reserves in Ivory Coast. The species is introduced in all climate zones under persistent climate variability. Massive reforestation based on teak resulted, in 2000, in 70 000 ha covered by teak plantations out of the 162 000 ha of reforested area (Koné *et al*., 2010). As such *Tectona grandis* has become the main source of timber in Ivory Coast, the country being the largest producer of teak in terms of planted area and exported volume, outside Asia. In addition to its high growth rate, *Tectona grandis* produces wood with high density, high dimensional stability, ease of drying, strong rigidity and high resistance to biodegrading agents such as fungi and termites (Moya *et al*., 2009; Izekor *et al*., 2010;. Niamké *et al*., 2011; Shanbha & Sundararaj, 2013; Wanneng *et al*., 2014.). These physico-mechanical and technological properties confer a high economic value to teakwood which has, thereby, become a substantial source of income for Ivory Coast. Teak logs, added to those of gmelina, currently represent about 88% of the total exported logs. Wood products derived from thinnings can serve as stakes, poles and posts on the local market. They are also used in the small carpentry. The stumps of the felled trees (base of the tronc) serve as energy wood (charcoal fabrication) for rural and urban urban households. Teakwood charcoal sector also provides direct and indirect permanent jobs.

Owing to its fast-growth, its natural durability and high density wood (Bhat *et al*. 2001; Kokutsé *et al*., 2006; Niamké *et al*., 2011), teak is also an interesting species for atmospheric carbon sequestration. The species falls within the framework of the Clean Development Mechanisms (CDMs) and REDD+ files (Reducing Emissions from Deforestation and forest Degradation). Studies reported an atmospheric carbon storage capacity of 120 $tC.ha^{-1}$ and 72 $tC.ha^{-1}$, respectively in 20 year old teak plantations in Panama and in a 14 year old stand in Ghana (Kraenzel *et al*., 2003; Watanabe *et al*., 2009). The high carbon storage performance of teak reflects the tree high growth rate which, in turn, depends strongly on both the quality of the biological material (seedlings or plants) used for reforestation, the planting techniques and the silvicultural treatments applied (Koné *et al*., 2010; Kollert and Cherubini, 2012). High growth of a woody plant involves strong cellular metabolism, i.e., high absorption of the atmospheric carbon which represents the main greenhouse gas, and thus, the main source of global warming (Terakunpisut *et al*., 2007). The absorbed carbon is used for synthesizing the polysaccharides (lignin embedded cellulose and hemicellulose matrix) which represent the main component of the xylem cell walls (Plomion *et al*., 2001).

In consideration of the above advantages, planting fast-growing timber species such as teak can represent a realistic option aiming at (i) relieving the strong human pressure on the natural forest of the rural domain, (ii) restoring, on a long-term basis, the natural forest cover for biodiversity preservation and (iii) reducing the atmospheric carbon, through carbon storage in plant tissues. It is obvious that the reforestation, alone, cannot resorb all of the planet's green house gas emissions. However, almost all the environment scientists and experts agree that woodland restoration contributes, significantly, to curbing climate change.

1.2. Study objectives

The Ivorian forest research programs were interrupted due to lack of effective control over forest logging resulting from lack of essential data on stand dynamics (Ministère de l'Environnement, des Eaux et Forêts de Côte d'Ivoire, 2012). Without such data, it is almost impossible to implement accurate estimate of the potential supply in terms of wood volume (Ministère de l'Environnement, des Eaux et Forêts de Côte d'Ivoire, 2012). Estimating the potential wood supply (wood production) from a forest stand is important in determining efficient standards aiming to control the forest logging.

The wood production of a forest stand, referring to the output or the amount of wood formed in trees during a period of time, depends on the wood productivity. The latter is the wood increment per time unit, i.e., the dynamics or rate of wood formation. Wood production allows to determine stand yield which is defined as the volume of wood produced per time and area units.

Wood productivity, production and stand yields are key concepts needed (i) to assess tree growth rate and its variations and stand dynamics, (ii) to predict the wood volume to be harvested and (iii) to estimate carbon storage capacity. These three concepts essential for sustainable forest management cannot be, accurately, determined using only on bark diameter measurements as it is the case for Ivory Coast (Tariel, 1966). Therefore, for accurate estimate of wood productivity, production and stand yields, it is essential to:

(i) know the amount of wood formed during a vegetative period (annual layer of wood or growth ring) and

(ii) use this short-time wood unit (growth ring) to make a reliable estimate of the current and mean annual increments, wood production and stand yields.

In addition to the data on growth dynamics, it is important to identify the growth influencing factors likely to affect the quality of the derived wood and assess the extent of its quality. Because high quality wood material can stand diverse wood degrading agents. Determining wood quality and its possible variations can, therefore, help towards wood properties improvement if needed; which will lead to the durable use of the material.

This comprehensive information of growth dynamics and wood properties is, unfortunately, scarce for timber species of the rural area which provides about 90% of the harvested wood in Ivory Coast. Examing the secondary growth metabolism of fast-growing timber species is important to optimize their cultivation. Planting and producing wood from such species will help, on a long-term basis, to limit the use of natural forest and thus contribute to the restoration of the degraded areas.

From the concern of the Ministère de l’Environnement de Côte d’Ivoire, it is obvious that the forest sector of Ivory Coast needs a sound management. For that purpose, we consider important to investigate and understand the growth dynamics of the forest species used in relation to the growth conditions such climate which remains the main factor controlling tree growth in the

tropics (Wagner *et al*., 2012 & 2014). We also investigate the extent of wood variability in trees (teak) by evaluating the degree of wood density variability. Because wood density is not only the key indicator of general wood properties but it also represents one of the two main functional traits in which tree sensitivity/vulnerability to climate can be mirrored (Baker *et al*., 2004; Chao *et al*., 2008). The current extent of climate change does not seem to be detrimental to forest growth in the country. Our research, however, aims to provide methodological tools to evaluate growth responses under the predicted future climate change (IPCC, 2007).
The main objective of the present study consisted of studying timber species growth responses to the climate variability affecting Ivory Coast, i.e., examining growth dynamics and its variations in relation to both local and global climate change and investigating the effect of growth variations on wood properties. For this purpose, we use *Tectona grandis* as a model species owing to its ecological plasticity and high climatic potential which are relevant criteria to achieve the objectives of the present work.

1.3. Study outline

In the current study, we addressed the following research questions:

1. What are the characteristics and determining factors of teakwood formation in a tropical dense forest of Ivory Coast? Can the factors controlling the xylogenesis influence the properties of xylem cells?

2. How do the precipitation variations affect the growth rate in teak planted in Ivory Coast? Do trees from the managed stand exhibit growth patterns and climate sensitivity similar to those of trees from the unmanaged stand? Do growth responses reflect the effect of global climate change other than the local precipitation?

3. How to assess the degree of teakwood density variability? What are the driving factors of the density variability within a stand? Could the density variability be related to site precipitation fluctuations? Could the radial (pith-to-bark) density variations help to define the juvenile wood phase?

Subsquent to the present chapter (**Chapter 1:** Outline of the thesis), the second chapter (**Chapter 2**) describes the study species, presents some concepts of the West African forest biomes and addresses some consequences of water deficit (due to severe decrease in precipitation) on tree growth.

After these introductory chapters, the following chapters are linked to the specific aforementioned objectives:

- Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (*Tectona grandis*) in Ivory Coast(**Chapter 3**): To the effect of studying the cambial activity, cells divisions and differentiation were investigated in 24 year-old teak trees through monthly cambial zone sampling.

- Tree rings show a different climatic response in a thinned and a non-thinned plantation of teak (*Tectona grandis* L.f.) in West Africa (**Chapter 4**): This chapter examines the climate-growth relationships of managed teak trees compared to unmanaged trees through tree-ring analysis. The effect of local and global climate is also investigated. The possible role of sylviculture in increasing trees resistance to water stress is discussed.

- Assessing wood density variability of *Tectona grandis* L. through microdensitometrical profiling shows latewood sensitivity to climate (**Chapter 5**): This chapter aims to assess wood density variability, to identify the possible factors and examine their mechanisms of influence.

The content of each chapter is consistent with the published paper it is based on. However, some side observations carried out, when implementing the activities related to each chapter, gave additional and important data which allow a better understanding of the described phenomena or processes. These additional informations are compiled in text boxes as "Additional data to chapter…" inside or at the end of the related chapter or in appendices at the end of the PhD manuscript.

Finally, follows **Chapter 6** which concludes on the contribution of the current study to assessing teak growth, the growth variations, sources/factors of variability and the implications of growth variations on the derived wood properties. Addressing the above research questions will help to understand how the monitoring of the cambial activity can provide the key to gain insightful information on tree growth variations and their effects on wood properties. Different methodologies were applied in chapters 3, 4 and 5. Therefore, the specific material and methods are explicitly laid down in the related chap

Chapter 2: Study framework

Introduction

This chapter aims to present the study species. The description of the species is mainly based on observed data and complemented with some literature details. Additional anatomical observations were carried to accomplish this. This illustrative first section is followed by a brief description of the West African forest environment and its climatic challenges. Finally, some concepts of water pathways in vascular plants are addressed in order to understand the sensitivity of trees to water stress caused by the climate change.

One main reason motivated the choice of teak as a model tree for the present study. Teak was introduced in Ivory Coast since 1926, using the Togolese provenance seeds (Bellouard, 1957), with the first trials in 1927 in the Banco Forest Reserve (Trial, 1965). The planting activities spread to reach the Central region namely Bamoro (Bouaké) in 1929 (Dupuy, 1990). The small teak stands developed quickly into large-scale industrial plantations that were intensified within the framework of the forest reform of 1995. Its fast-growth and high quality wood made teak to become the main species for the reforestation programs in the country and the main supplier of high quality wood. The species thus colonized all the ecological zones of the country. Depending on their size (diameter and height) teakwood products from relatively short rotations are used for several purposes: stakes, poles, posts, sawn timber (Voui Bi, 2008).

Furthermore teak growth is known to contain a high climatic signal (Pumijumnong *et al*., 1995; Ram *et al*., 2011; Pumijumnong, 2012). Related to that, the precipitation variability, prevailing in Ivory Coast as it is the case for the whole West-African region, is likely to affect tree growth and, thereby, generate modifications in the derived xylem structure. Structural changes of the xylem features can cause significant variations in the wood properties. This can represent a major concern for a forest management aiming to produce quality wood from relatively young trees (from short rotation forests).

2.1. Teak: a native Asian timber tree that became a pan-tropical species

2.1.1. Description, ecology and global distribution

The genus Tectona includes four species namely *Tectona abludens* Koord. & Valeton endemic to the island of Java, *Tectona grandis* Linn. f. (India, Malaysia, Laos, Thailand), *Tectona hamiltoniana* Wall (Burma) and *Tectona philippinensis* Benth & Hook. f. (Philippine

Islands). Our study species (*Tectona grandis*) is the most widespread one, due to its ecological plasticity and to the properties and the economic value of its wood.

Description

The present description of our study species is based on the following previous and recent works: Ouattara (2009), Neha and Sangeeta (2013) and Nidavani and co-authors (2014).

Kingdom: Végétal
Superdivision: Spermatophyta - Seed Plants
Division: Magnoliophyta - Flowering Plants
Class: Magnoliopsida - Dicotyledons
Sub-class: Gamopetalous
Series: Tetracyclic
Order: Lamiales
Family: Lamiaceae
Sub-family: Claroteinae
Genus: *Tectona*
Species: *Tectona grandis* L. f.

Teak (*Tectona grandis* L. f.) is a tall tree of 40-50 m high in natural forests and 30 m in plantations with a densely clothed with yellowish grey tomentum trunk presenting a quadrangular section (Dupuy & Verhaegen, 1993). Trees form ovate-elliptic to ovate, simple, opposite, cuneiform, decussate, large deciduous and 20-40 cm x 15-20 cm broadleaves (Fig. 2.1B).

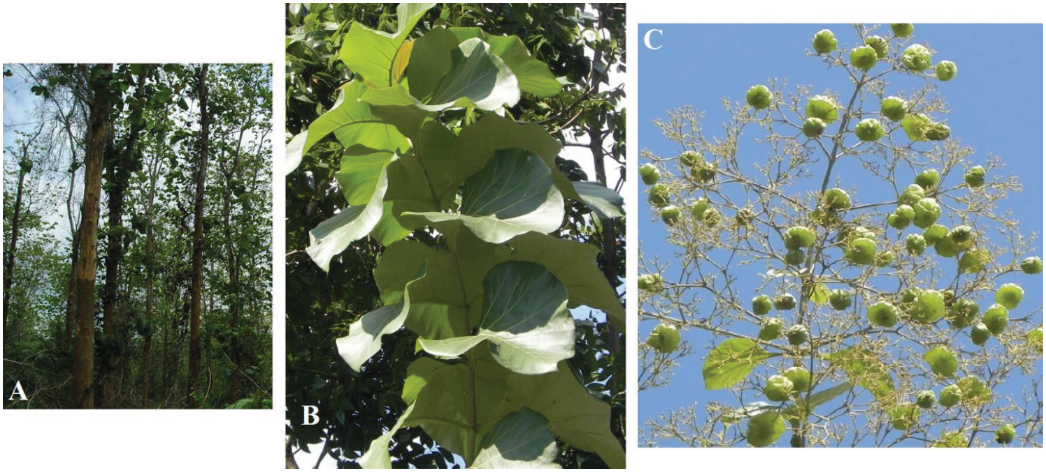


Figure 2.1. Teak stand in the Séguié forest (A), leaves and fruits from Bangladesh (B and C).

The gamosepalous calyx can reach a diameter of 2-3 cm. Flowers are small, whitish, hermaphroditic and grouped in panicles which can contain thousands of floral buds (Neha & Sangeeta, 2013). Only a few of these buds break during the flowering period which lasts 2-4 weeks. The fruit is a drupe with 4 chambers, round, hard and woody, enclosed in an inflated, bladder-like covering; pale-green at first, then brown at maturity (Sattler, 1997; see Fig 2.1C.). Each fruit contains 0 to 4 oblonga and brown seeds enclosed in bony endocarp. Only one or two of these seeds are fertile.

Ecology

In general, teak prefers deep, porous, fertile, metamorphic or alluvial and well-drained soils with good water retention (Behaghel, 1999; Krishnapillay, 2000). Teak shows its best growth performances under annual rainfall of 900-2500 mm and temperatures ranging between 18 and 43 °C. Typical growth sites are characterized by a 6 or 7-month rainy season and with monthly precipitation of 200 mm, followed by 5 or 6 months of dry season (Purwanto & Oohata, 2002; Suzuki *et al*., 2007).

In its new geographic regions, precipitations intensity and its monthly and yearly distribution seem the relevant for teak growth. Related to the precipitation intensity and rate and the degree of soil fertility, teak plantations have been classified into site of high, medium and low productivity (Dupuy & Verhaegen, 1993). In plantations teak can also tolerate an annual rainfall of 600-800 mm as it is the case in the northern plantations of Ivory Coast.

In both natural and planted forests, the growing site precipitations should alternate with a pronounced dry season of 2-4 months (Pardé, 2002); a dry period sufficient to induce trees defoliation and lead to growth interruption (Dupuy, 1990; De Mattos *et al.*, 1999). Precipitation resumption (in the following growing year) triggers active tree growth. The growth interruption alternating with growth resumption results in the annual growth ring formation (Worbes, 1995; Borchert, 1999; Stahle, 1999). This climate related growth sensitivity explains the continuous use of *Tectona grandis* (L.f.) in dendrochronological and dendroclimatic studies.

Phenology

Teak phenology is closely related to climate seasonality in both natural and planted forests. The duration of new leaves sprouting and full foliage being present corresponds to that of the wet season. In natural forests as well as in plantations, trees shed leaves during the dry season and leaf sprouting begins with the onset of the rainy season (Béhaghel, 1997). The species flowers during the peak of the rainy season and fruit setting begins one month later. The fruit maturation and trees defoliation occur in the dry season.

In Ivory Coast, trees shed grually their leaves in the moist forest areas during the dry season (mid-November to mid-February) whereas trees experience complete defoliation in the deciduous forest and savanna zones. Flowering and fruit setting occur as in natural forest.

The species shows early fruiting in both the natural forests (from the 6th growth year) as well as in plantations such as in Ivory Coast (from the 2nd growth year, Dupuy & Verhaeghen, 1993). These authors also reported that 7-years old clone-seed orchards could produce mature seeds though with a weak germinative ability.

Distribution

Asia is the only source of natural teak forests. Teak growth performances and wood quality account for the extensive establishment of plantations within and beyond the species native range (Pandey & Brown, 2000). The increasing worldwide demand for teakwood, and the decline in the currently available resources, has resulted in intensifying teak planting activities since the early 1970s (Keogh, 2000). The graph (Fig. 2.2) below shows an illustration of the worldwide distribution of teak plantations.

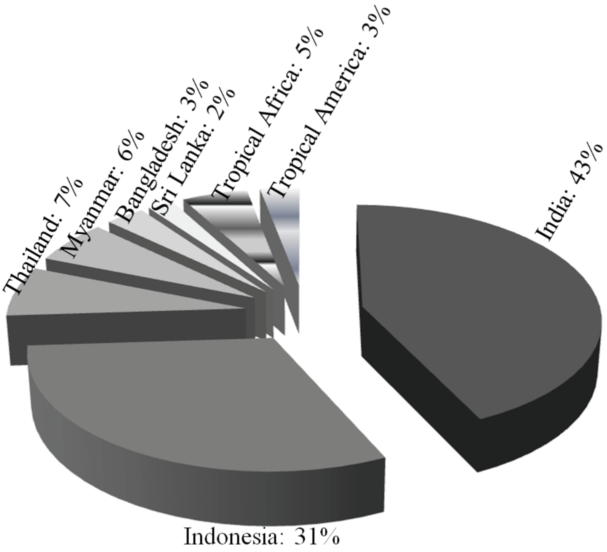


Figure 2.2. Global distribution of teak plantations with Asia being the predominant continent in terms of total planted area. Source: ITTO, 14/1-2004.

The successful teak forests management led to obtaining an estimate of harvest wood volume of 500 000 m^3 and 1 500 000 to 2 000 000 m^3 in natural forests and in plantations, respectively (Kollert & Cherubini, 2012).

2.1.2. Sylviculture and heritability

2.1.2.1. Reproduction

- *Taungya method*

The Taungya planting method, formerly applied in South Asia, was initially used for teak cultivation In Ivory Coast (Tariel, 1966). The Taungya method necessitates the participation of local farmers who cultivate local crops (rice, yam, cassava, maize…) along with teak seedlings with an initial planting density of 2500 stumps/ha. Farmers are allowed to cultivate these crops during 2 to 3 consecutive years. In that way, they not only clear the land destined for reforestation but also take charge of weeding the young teak plantations while taking care of their crops. The procedure allowing to obtain the stumps used in the Taungya method is the same applied in the seed forest regeneration system explained below.

Although it seems safe and less expensive (no cost for land clearing and young plantation weeding), the Taungya method could not be a realistic approach for an intensive reforestation program. The forest zones required for teak growth are also highly desired by the farmers. This prompted the installation of teak plantations in less populated areas far from human influence but with a necessary use of the mechanization to execute the related activities.

The installation of large scale mechanized plantations is now being implemented through two main planting systems: seed regenerated forest and coppice system.

- Seed regenerated plantation

In this regeneration system and prior to the planting, seeds undergo a treatment aiming to soften their endocarp, in order to facilitate their germination (Dupuy, 1998). The hardness of this membrane, although detrimental to the germination, allows long-term conservation of the seeds germinative capacity (over several years) if the following storage conditions are provided: low moisture content of the seeds before the storage and no fluctuations of the temperature and humidity over all the storage period. The pretreatment is similar to that described by Rachmawati and co-authors (2002): seeds are soaked overnight and sun dried over a day; a treatment repeated over 1-2 weeks. Another procedure consists in oven-drying seeds at 50°C for 1-5 weeks or at 80°C for 48 h (Ouattara, 2009). Beside this heating procedure, foresters of Ivory Coast practice artificial bush fires during the dry season (after dry seeds have fallen on the ground). This allows to treat a large amount of seeds at once. Another procedure consists in soaking the seeds in a concentrated solution of sulfuric acid (H_2SO_4) over 15 minutes. Then seeds are washed in water and finally air-dried overnight (Pramono *et al.*, 2011). These various pretreatment methods all aim to soften and permeabilize the seed membrane (endocarp) in order to trigger and facilitate the germination, a process through which the hypocotyl breaks the cotyledonary envelope (Dupuy, 1998).

The treated seeds are sown in polybags filled with fertile soil. Some weeks later, the roots apex and old leaves of the polybagged seedlings are cut off to obtain the stumps (the remaining part of the seedling), which are later transplanted on the land prepared in advance for reforestation. The stumps are planted in the vertical position, with the collar at the ground level; a planting mode that confers an initial strong growth dynamism to the plants. In this regeneration system, deriving from a sexual reproduction mode (pollination, fruiting and seeds harvest), trees reach the regular fruiting stage before any logging activities (Koné *et al.*, 2010).

- Coppice system

In this regeneration system based on the use of shoots, after trees are cut, the remaining part of the trunk is trimmed back to stumps level (20-50 cm above ground level). At the onset of favourable soil moisture conditions (due to precipitation), the buds sprout out from the stumps, giving rise to new teak plants that develop into a new trees stand. Due to the presence of a pre-existing root system on the stem, the derived shoots show an initial faster growth than seedlings (plants derived from seeds). The coppice system is a regeneration mode that does not imply the genetic recombination (Dupuy, 1998) and ensures a continuous supply of small poles and mature logs. Two types of buds are involved in teak cultivation through the coppice system:

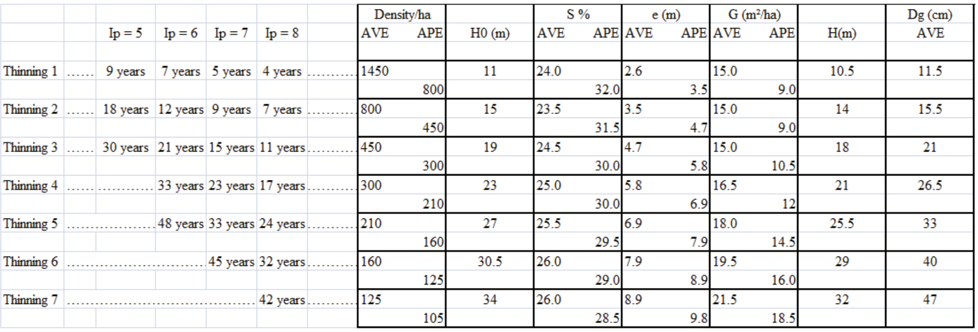
. Adventitious buds: They develop on the wound (swelling) around the stem or root section.

. Proventitious buds: These buds form during first growth year along with the adventitious buds. Located under the bark, they remain quiescent during the rest of trees' lifespan and resume only after trees felling i.e, after the cutting of the stem axis.
Others plantations are made of the mixture of the combination of both regeneration modes.

2.1.2.2. Sylvicultural treatments

Teak production table (tab. 2.1), that motivated and enhanced the sylvicultural treatments in Ivory Coast, was developed in 1983 (Maître, 1983).

Table 2.1. Teak productivity table in relation to the site fertility in Ivory Coast. Source: Maître (1983).



					Density/ha			S %		e (m)		G (m²/ha)			Dg (cm)
	Ip = 5	Ip = 6	Ip = 7	Ip = 8	AVE	APE	H0 (m)	AVE	APE	AVE	APE	AVE	APE	H(m)	AVE
Thinning 1	9 years	7 years	5 years	4 years	1450		11	24.0		2.6		15.0		10.5	11.5
						800			32.0		3.5		9.0		
Thinning 2	18 years	12 years	9 years	7 years	800		15	23.5		3.5		15.0		14	15.5
						450			31.5		4.7		9.0		
Thinning 3	30 years	21 years	15 years	11 years	450		19	24.5		4.7		15.0		18	21
						300			30.0		5.8		10.5		
Thinning 4		33 years	23 years	17 years	300		23	25.0		5.8		16.5		21	26.5
						210			30.0		6.9		12		
Thinning 5		48 years	33 years	24 years	210		27	25.5		6.9		18.0		25.5	33
						160			29.5		7.9		14.5		
Thinning 6			45 years	32 years	160		30.5	26.0		7.9		19.5		29	40
						125			29.0		8.9		16.0		
Thinning 7				42 years	125		34	26.0		8.9		21.5		32	47
						105			28.5		9.8		18.5		

Ip: productivity/fertility index; AVE: before thinning; APE: after thinning; e: spacing between individual trees; H0: total height; S (%): spacing factor; G: basal area; H: log height; Dg: haverst diameter.

The above production table recommended 3-7 thinnings, depending on the soil ferility index: thinnings are more (7), earlier (from the 4th growth year) and more freqent in the most fertile soil site (Ip = 8).
Thinnings, pruning and monitoring of the tree health status are the main sylvicultural treatments applied to teak plantations in Ivory Coast. In addition to this, forest managers detect and select the "plus trees" i.e. trees that show cylindrical and straight stems. Such trees are selected and used in the vegetative propagation that aims to improve the production of quality wood. The works of Maître (1983) and Dupuy and co-authors (1999), serving as a basis for the application of the sylvicultural treatments, made the following recommendations:

(i) Applying a high initial stand density of 1500 stumps.ha^{-1}. However the current initial stand density of 2500-3000 stumps.ha^{-1} is significantly higher. High initial stand density aims to reduce of the plantations maintenance cost. Teak often forms branches at a very low height in its initial growth phase and close stand leads to better natural pruning. The close canopy of the young stands hinder weed development (Tariel, 1966). In addition, high initial density also aims to maximize the number of plants that will reach the rotation or harvest age, after the death of non-viable individuals and after the multiple thinnings.

(ii) Applying a time intervall of 3 and 5 years between two thinnings in young and mature stands respectively.

(iii) Removing a basal area of less than:
- 40 % before the age of 12 years;
- 30 % between 12 and 25 years;
- 25 % after the age of 25 years.

The success of the sylvicultural treatments, added to the genetic improvement (section and vegetative propagation of the plus trees), resulted in enhancing growth performances and improving stand yields in worldwide teak plantations. This allowed the forest managers to reduce the rotation period or trees harvest age. The current international teak market is, thereby, mainly supplied with wood from relatively young plantations of about 20 years (Kollert & Cherubini, 2012; see Fig. 2.3). The prevailing age class distribution is an indication of increased efforts to establish and manage teak plantations in the past 20 years and this pattern is very likely to persist in the future.

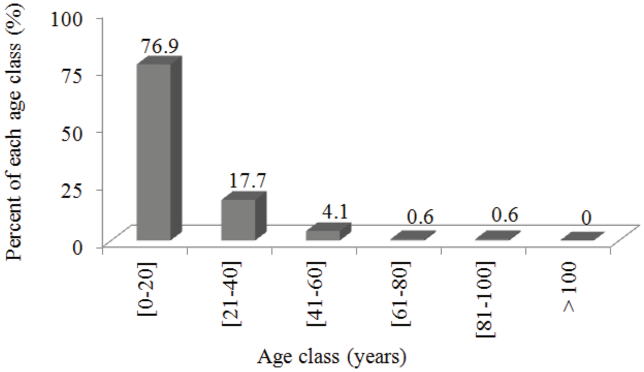


Figure 2.3. Teak harvest age class distribution on the international market with data provided by 38 countries. Source: Kollert & Cherubini (2012).

2.1.2.3. Heritability

The genetic characterisation revealed that about 95% of teak planted in Ivory Coast orignated from North India (Fofana *et al.*, 2008; Verhaegen *et al.*, 2010). *Tectona grandis* shows heritability for growth performances, namely tree height and diameter (Narayanan *et al.*, 2009; Solórzano *et al.*, 2012; Fofana *et al.*, 2014) as well as for wood properties when dealing with parameters considered as prime wood quality indicators in living trees, namely knots and buds index (Narayanan *et al.*, 2009; Verhaegen *et al.*, 2010; Solórzano *et al.*, 2012; Fofana *et al.*, 2014). Solórzano co-authors (2012) also showed a genetic influence on wood mechanical properties, tangential and radial shrinkage and dynamic elasticity modulus of dry wood. However trees juvenility can mask the expression of these indicators of growth and wood properties (Solórzano *et al.*, 2012; Fofana *et al.*, 2013).

Fofana co-authors (2009; 2013 and 2014) revealed the existence of genetic variability in which each population exhibits specific characteristics. Genetic selection, therefore, allows to identify population or individuals of best phenotype which are later used in the vegetative propagation aiming to establish stands with high growth performances in view of high quality wood production.

2.1.3. Pests and diseases

Insects and fungal attacks remain the major pests affecting teak growth and wood productivity (Nair & Sudheendrakumar, 1986; Vongxomphou, 2001). The Forestry Department of Tamil Nadu Agricultural University identified and characterized five (5) insects that attack living teak trees:

- *Hyblaea purea*, known as old leaves skeletonizer. The larvas defoliate the living trees.
- *Hapalia macheralis*: the larva causes a uniform skeletonization of the leaf.
- *Sylllepta straminea*: the larva rolls the tough and hard leaves.
- *Nodostoma bhamoense*: known as teak borer, it creates holes on tender shoot.
- *Dichocrocis punctifearlis*: this insect feeds on the fruit by boring the pod.

However, out these five insects, *Hyblaea purea* is well known as the main teak defoliating insect in India and Laos (Nair & Sudheendrakumar, 1986; Vongxomphou, 2001), in natural forests as well as in plantations. The attack of these insects on trees can reduce the growth rate (Priya & Bhat, 1997) and decrease the stands productivity and yield (Beeson 1941; Nair *et al.*, 1985).

In Ivory Coast, intensive and prolonged rainfall leads to fungal attack (mainly *Fomes lignosus*) of the roots, which causes root decay and is known as the main pest affecting teak growth and productivity in West Africa and particularly in Ivory Coast (Maillet *et al.*, 1985; Ganglo & Lejoly, 1999).

2.1.4. Functional anatomy

The different steps of wood formation, namely the mitotic activities and cells differentiation, are strongly under the influence of the site precipitation (Rao & Rajput, 1999; Dié *et al.*, 2012). Cells divisions start with the onset of the wet season and the cell differentiation ends along with the end of the wet season, induced by decreasing precipitation. Vessels are the first xylem cells to differentiate; then follow the fibres and parenchyma surrounding the vessels (Dié *et al.*, 2012). Although the role of the thin-walled fibres surrounging the earlywood vessels is not yet clarified, studies suggested that the wide earlywood vessels serve to the water conduction for the ongoing cambial activities (Marcati *et al.*, 2006 and 2008; Dié *et al.*, 2012). An anatomical quantification, performed in a 21 years old Indian teak stand, shows the following proportions for the different cell types (Bhat & Priya, 2004): 67% (fibres), 24% (parenchyma cells) and 9% (vessels). The paragraphs beneath present some cellular features.

Vessels and wood porosity

Teak is a tropical ring-porous timber species which indicates that the wood exhibits a sharp variation in vessels diameter from the latewood of one growth ring (small diameter vessels) to the earlywood of the following ring (wide diameter vessels, Fig. 2.4).

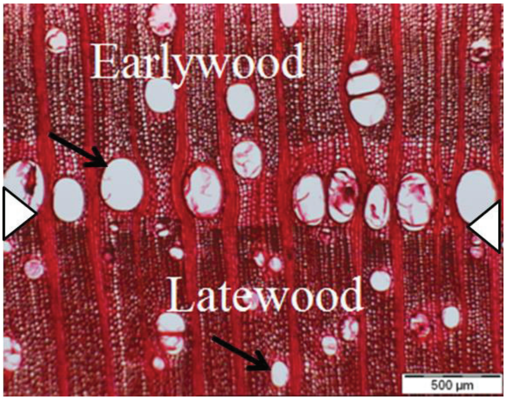


Figure 2.4. Sharp transition between latewood and earlywood in teak indicated by the white arrow heads. Black arrows point at vessels. Scale bar: 500 µm.

Own measurements, carried out on ten 35 years trees, revealed a noticeable variation in vessel diameter from the earlywood region to the latewood zone. Vessels show a mean diameter of 206 µm in the initial earlywood (first millimeter), 140 µm in the middle of the ring and 100 µm in the latewood. The above described vessels diameter represents the average of both the radial and tangential diameters (rD and tD, respectively). This mean diameter served to caluculate the hydraulic diameter (dh, Fig. 2.5) per growth ring as follows (Jacobsen *et al.*, 2005; Gea-Izquierdo *et al.*, 2012):

$$dh(\mu m) = \frac{\Sigma d^5}{\Sigma d^4} \quad \text{with } d(\mu m) = \frac{(rD + tD)}{2} \qquad \text{(equation 2.1)}$$

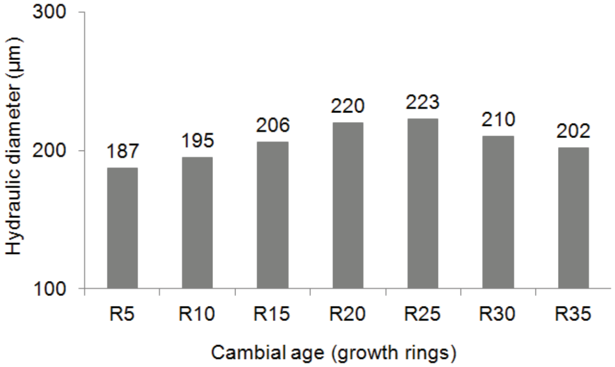


Figure 2.5. Variation of teak hydraulic diameter in relation to cambial age.

The vessel hydraulic diameter refers to vessels that actually contribute to the greatest part in the xylem water ascent (Sperry *et al*., 1994). Xylem features such as hydraulic diameter provide fundamental information (i) on plant ecophysiology, i.e., the plant's capacity to supply water for photosynthetic and growth activities (Tyree & Zimmermann, 2002) and (ii) on plant sensitivity to environmental stress such as drought. Tree drought-sensitivity can be of major concern if the drought episod occurs during the vegetative period (cambial active phase). In our study dealing with cambial activity, vessels diameter was used to characterize the intra-annual xylem growth zones (XGZ) formed as a consequence of the physiological fluctuations (Chapter 3).

Some species seem to produce smaller lumen diameter vessels under extreme water stress in order to prevent cavitation risks (Hacke *et al*., 2001). While in their study on Costa Rican teak, Moya and co-authors (2009) reported that trees from the dry climate site formed wider lumen vessel compared to those from the humid climate site. And under the same climatic conditions, trees from the low growth stand produced wider vessels compared to those of the high growth rate stand. Furthermore, high/fast growth rate trees of the humid climate site showed the highest percentage of multiples vessels. The results of Moya and co-authors (2009) indicate a climate influence on vessel size and grouping in teak. The knowledge of the hydraulic diameter typical to a given species and the variations of this diameter due to rainfall fluctuations can help to assess the climate sensitivity of the examined species.

The same trees used to calculate the hydraulic diameter showed a vessels frequence (number of vessels per square milimeter) of 2-4 cells in the earlywood and 4-6 cells in the latewood (Fig. 2.6).

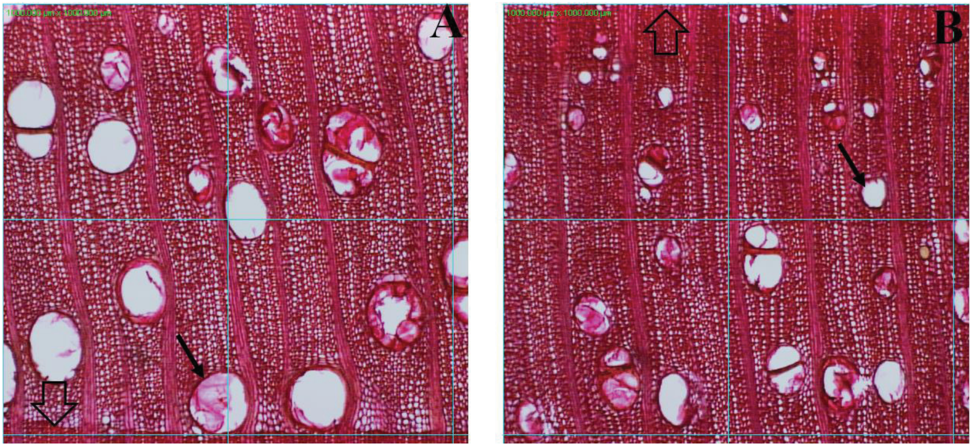


Figure 2.6. Variation of vessels frequence (number of vessels) from earlywood to latewood (25th growth ring, sample Tw59769). Empty arrows (A) point at the ring lower boundary in A and at the upper boundary in B. Black thin indicates the decrease in vessel diameter from earlywood (A) to latewood (B). The length of each square side is of 1 mm (1000 µm).

Differents types of vessel wall pitting were observed in the examined mature rings. The outer or primary wall shows bordered pits with elliptical openings (Fig. 2.7).

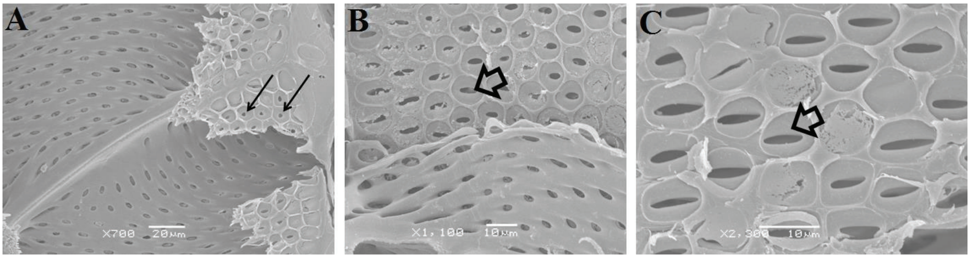


Figure 2.7. Structure of the vessels primary (outer) wall observed under a scanning electronic microscope: Bordered pits with circular opening on the primary or (outer wall) indicated by arrows (A) and with elliptical opening (empty arrows, B). Image C is the magnification of elliptical pits. Scale and magnification: A (20 µm; x700), B (10 µm; x1100) and C (10 µm; x2300).

The inner (secondary) wall shows two sub-types of elliptical vessel pits (Fig. 2.8). Sub-type 1 consists of stretched pits with an opening partially covered by the fold of the inner wall (Fig. 2.8 A-D). Sub-type 2 consists of pits, more or less, similar to those found on the primary wall (Fig. 2.8 E-F).

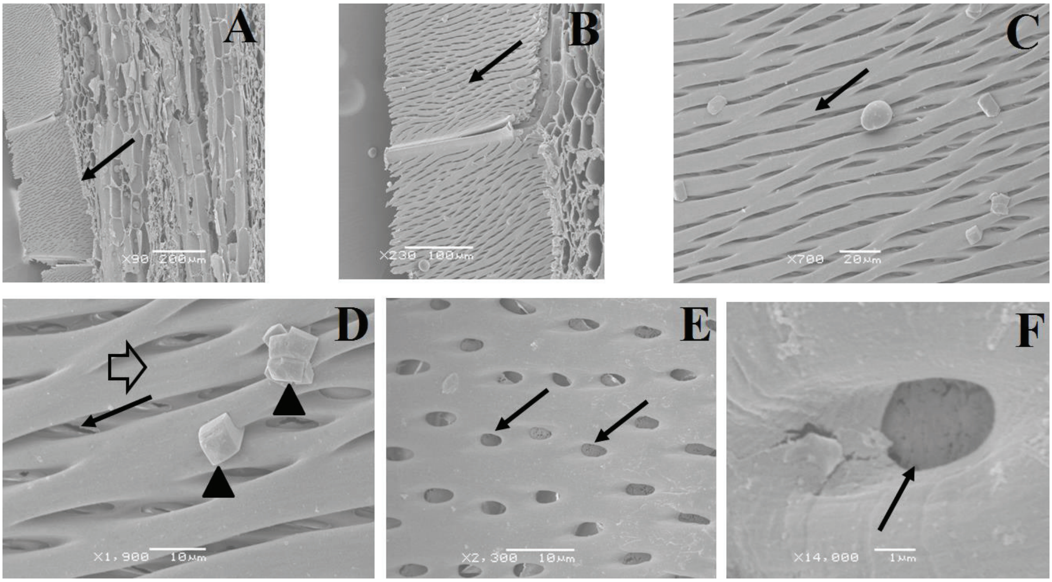


Figure 2.8. Structure of vessels secondary (inner) wall showing two sub-types of pits observed under a scanning electronic microscope: Different magnification of stretched pits with an opening partially covered by the fold of the inner wall (see thin arrows in A-D). Panel D shows the inner folding (empty arrow), a pit opening (thin arrow) and crystals at the pit openings (black arrow heads). Panels E and F indicate bordered pit with circular to elliptical openings. Scale bars and magnification: A (200 µm; x90), B (100 µm; x230), C (20 µm; x700), D (10 µm; 1900), E (10 µm; x2300) and F (1 µm; x14000).

Fibres length and wall thickness

Measurements carried out on cambial samples and on mature growth rings indicated that the lowest value of fibre wall thickness is found in the earlywood (1.5 µm) and the highest value of wall thickness is found in the latewood regions characterized by thick-walled fibres (4-5 µm).

Fibre length also varies along the earlywood-to-latewood gradient within the growth ring. Personal measurements showed a mean fibre length of 1615 µm. Fibre length reaches its mature phase at an early age i.e. from the 7th year of the tree life. Fibres quantitative features (length and wall thickness) are presented in the below figure (Fig. 2.9).

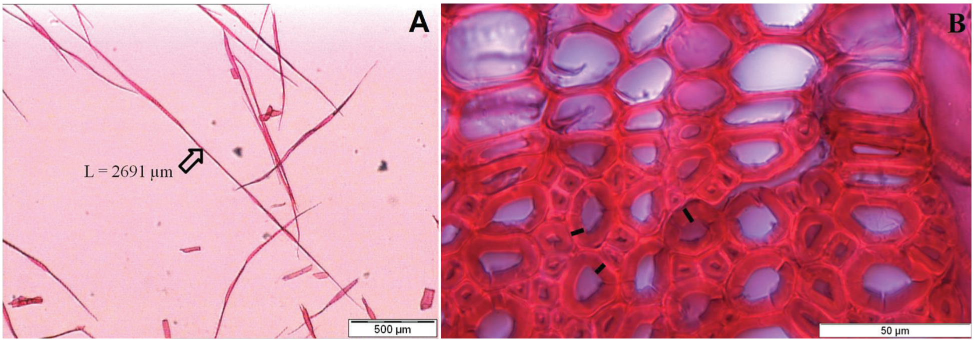


Figure 2.9. Quantitative analysis of xylem fibres in *Tectona grandis*: separate fibre length indicated by the empty arrow (A) and individual latewood fibre wall thickness on a transversal micro-section indicated by the black bars (B). Scales bars: 500 µm (A) and 50 µm (B).

Xylem rays

Teak xylem rays are, mostly, multiseriate and contain, on average, 3-4 cells in their median parts (Fig. 2.10). Results from Costa Rica, obtained from 10 years trees, indicate that xylem rays reach their mature phase from the 5th year of trees lifespan (Moya *et al*., 2009).

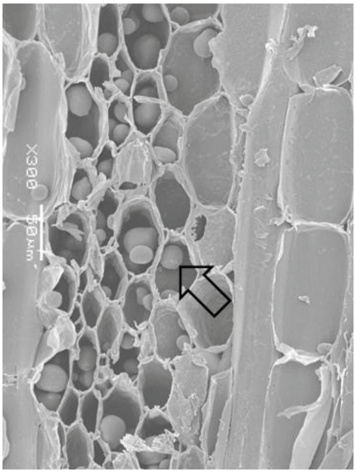


Figure 2.10. Tangential view of xylem rays of *Tectona grandis*, observed under a scanning electronic microscope, with the arrow pointing at starch grains in the ray cells. Scale bar and magnification: 50 µm x 300.

2.1.5. Various properties and utilizations of teak

2.1.5.1. Wood products

In Ivory Coast, the economic value of teakwood made the species to become what gold represents among the metals and diamonds among the stones. Due to its properties such as its high proportions of heartwood (Fig. 2.11), high wood density, hardness, high modulus of elasticity (MOE) and modulus of rupture (MOR), high natural durability (Bhat *et al*., 2001; Cordero & Kanninen, 2003; Bhat & Priya, 2004; Kokutsé *et al*., 2004 and 2010; Niamké *et al*., 2011), teak wood is used as plywood, house building material, as well as a material for railways construction and shipbuilding. Studies evidenced the presence of mineral inclusions such as calcium crystals which increase the wood density (Kjaer *et al*., 1999). Figure 2.11 shows mean proportions of heartwood measured in teak from three different locations in Ivory Coast.

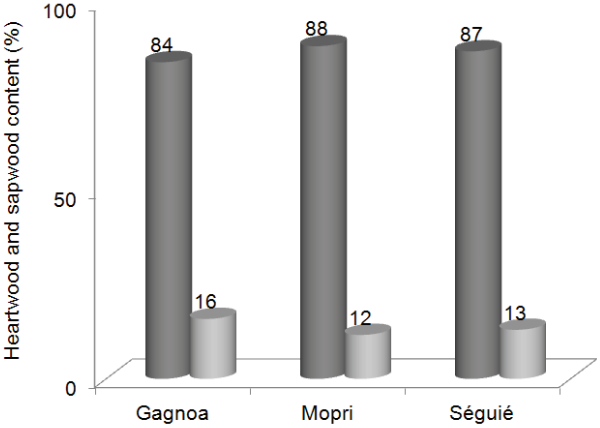


Figure 2.11. Percentage of teak heartwood (dark-grey) and sapwood (light-grey) measured in three stands with different age: Gagnoa (37 years), Mopri (24 years) and Séguié (35 years).

Teak became an important species in the context of wood biomass production and atmospheric carbon sequestration due to its fast-growth and high wood density. The quality of its wood explains the predominance of teak on the international market of high quality tropical hardwoods (Thulasidas *et al*., 2006; Miranda *et al*., 2011; Niamké *et al*., 2011). This leads to an increase of the economic value of teakwood, mainly harvested from relatively young rotation plantations (20-30 years) as indicated by the 2013 annual report of the International Tropical Timber Organization (ITTO, see Fig. 2.12).

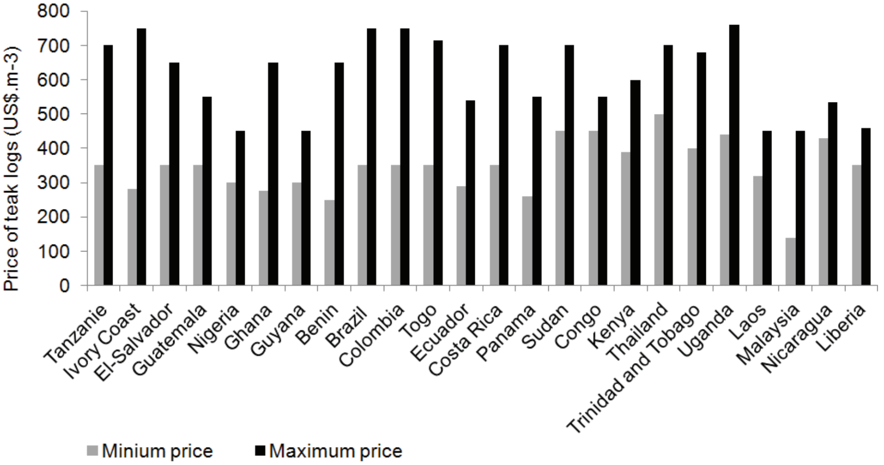


Figure 2.12. Teak logs price accross the producing countries. Source: International Tropical Timber Organisation (ITTO, TTM Report of 1-15 November 2013).

In Ivory Coast, teak showed a mean annual volume increment (MAI) of 7-10 $m^3.ha.year^{-1}$ between 45 and 60 years in the Preforest zone and a MAI of 10-16 $m^3.ha.year^{-1}$ between 35 and 50 years in the rainforest forest zone (Dupuy *et al.*, 1999). Ivoran teak can serve for various utilisations, depending on the logs diameter and height. The following dimensions (D (cm): diameter and H (m): height) are currently used in the country:

- Stakes (D < 10 cm and H < 3 m):
- Poles (10 cm <D < 15 cm and 3 m < H < 8 m):
- Posts (15 cm <D < 21 cm and 8 m < H < 18 m):
- Sawnwood (22 cm <D < 35 cm and H > 18 m):
- Millwood (D > 35 cm and H > 18 m):

In addition, the byproducts of forest logging serve as wood energy in rural areas. Alongside its above uses, teakwood shows medicinal properties (Neha & Sangeeta, 2013). The wood aqueous extracts are acrid, cooling, laxative, sedative to gravid uterus, useful in treating piles, leucoderma and dysentery. Oil extracted from the wood is best for headache, biliousness, burning pains particularly over a region of liver and also in the treatment of acute liver disease. The wood ethyl acetate extract shows an antioxidant activity.

2.1.5.2. Other wood products and non-wood products

Root and bark

Teak bark is used as astringent, anti-constipation, anthelmintic and depurative, in treating bronchitis, hyperacidity, dysentery, verminosis, burning sensation, diabetes, difficult labour, leprosy and skin diseases. The root methanolic extract of *Tectona grandis* shows a hypoglycemic effect. Naphthoquinone isolated from the roots is used in the treatment of ulcer (Neha & Sangeeta, 2013). The ethyl acetate extract of *Tectona grandis* Linn bark shows an antiasthmatic activity (Goswami *et al*., 2010; Neha *et al*., 2010).

Leaves

Teak leaves contain various chemical compounds namely the steroids, tannins, saponins, anthocyanins, coumarins, alkaloids, proteins, amino acids, carbohydrates, flavonoids, diterpenes, phytosterols, phenol, anthraquinone (Ghareeb *et al*., 2014; Godghate & Sawant, 2014). The ethyl acetate-soluble portion, some of the isolated compounds and hemisynthetic derivatives show an antiplasmodial activity (Kopa *et al*., 2014). Chloroform extract of leaf showed inhibition to the growth of *Staphylococcus aureus* and *Klebsiella pneumoniae*. Teak leaves contain also an important quantity of phenols which explain their antioxidant activity (Ghareeb *et al*., 2014; Nidavani & Am, 2014) and, probably, their antifungal activity against fungi that cause teakwood rot (Neha & Sangeeta, 2013).

Flowers and seeds

Bitter and acrid, teak flowers are used in the treatment of bronchitis and liver conditions. Oil extracted from the flowers serves to treat scabies and strengthens hair growth. Methanol extracts of the flower present an analgesic, antidiabetic, antihyperglycemic and antioxidant activity (Neha *et al*., 2010; Ramachandran *et al*., 2011; Neha & Sangeeta, 2013). Teak seeds show a hair growth stimulating activity.

2.2. West-African forest biomes and climatic challenges

The West African territory covers a wide range of climatic zones (from the Sahelian regions to the equatorial climate according to Koppen-Geiger: Koppen, 1936). This climatic gradient led to the vegetation subdivision into five (5) biomes from the North to the South of the region: Desert, Grassland, Savanna, Deciduous, Semi-deciduous and Evergreen forests. West Africa shelters a large part of the Guineo-Congolian forest domain that extends over 570 420 km^2, from the Republic of Senegal to the Democratic Republic of Congo and is interrupted by the Dahomey corridor formed by Togo and Benin (Fig. 2.13).

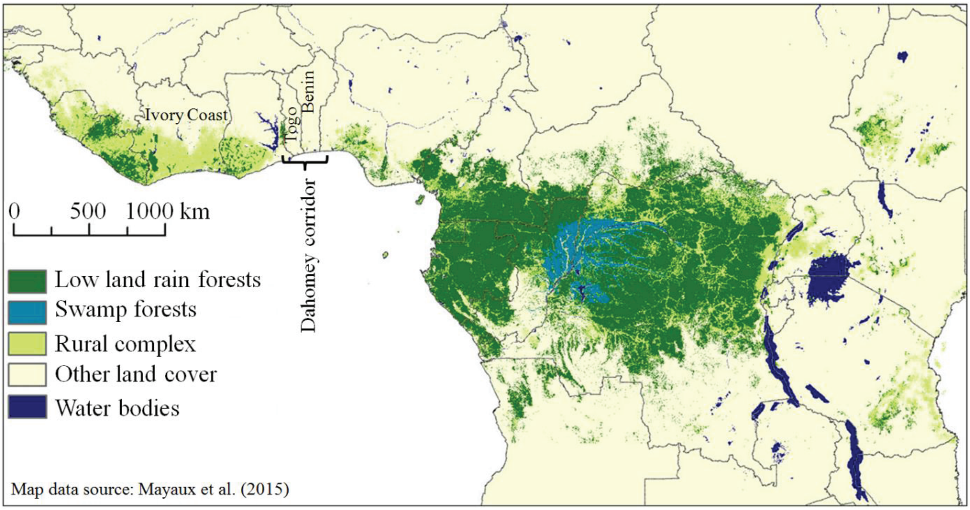


Figure 2.13. Spatial distribution of the African rainforests derived from MODIS data (Mayaux *et al*. 2015).

The region experiences high annual precipitation unevenly distributed. Annual precipitations are comprised between 1600 and 2000 mm and can, sometimes, amount to 4349 mm in Guinea-Conakry, where daily rainfall can reach 80-100 mm during the moonson (White, 1986; Béavogui *et al*., 2011). West-African forest subdivision provided by White (1986) gave rise to the following vegetation types: Guineo-Congolian wet rainforest, Guineo-Congolian dry rainforest, the mosaic of the two types, rainforest corresponding to the transition between the Guineo-Congolian region and a large island of Afro-montane region, swamp forest, the mosaic of transition and swamp forests, mosaic made of the Guineo-Congolian wet rainforest and secondary grassland.

These forest formations - which include about 8 000 plants species with more than 80% of endemism (White, 1983 and 1986) - are fragile ecosystems threatened by anthropogenic activity in a region with a population growth rate of 4 % per year (FAO, 2010). Excessive and uncontrolled exploitation of timber species remain the main cause of deforestation in West Africa (N'Guessan *et al*., 2006; Heubes, 2012). In this region, forest logging and the impact of persistent climatic changes are responsible for the disappearance of a current rate of 1.17% of the forest cover per year (FAO, 2007). West-African climate variability represents a major risk to the sustainability of the different biomes including the forest species. These climate changes cause both functional and structural modifications of the West African forest landscape (Root *et al*., 2003; Fauset *et al*., 2012; Wagner *et al*., 2014). Forest inventories, conducted in 19 plots covering various types of forests (Fauset *et al*., 2012), revealed that the ongoing changes of the West-African climate, reflected in precipitation decrease, results in the expansion of the deciduous forest at the detriment of the rainforest. These qualitative and quantitative changes in the forests species composition are also accompanied by a decrease in wood biomass production. If appropriate measures are not undertaken, towards a sound forest management, the current climate variability added to human activities may cause a forest cover depletion of 5% by 2050 in West-Africa, with an annual deforestation rate of 0.13% (Heubes *et al*., 2011). Extending fast-growing species plantations is, therefore, a realistic option to absorb agricultural activities pressure and limit the deficit in forest products. It can thus contribute to satisfy (1) the demand of the local market for sawnwood and millwood and (2) the need for energy wood. The availability of wood and wood products from plantation can, thereby, limit the use of the natural forest and thus enhance, on a long-term basis, the natural forest regeneration in the degraded lands.

2.3. Moisture conditions and tree sensitivity to climate

2.3.1. Water pathways in vascular plants

Water occupies 80% of the volume of plant tissues and forms a continuous flow from one extremity to the other in plants. Xylem conduits assure about 99% of the water flow in vascular plants (Sperry *et al*., 2003; Award, 2011). These conductive functional elements, namely the xylem vessels show walls embeded with 25 to 35% of lignin, a phenolic polymer, providing the hydrophobic surface essential for water transport (Plomion *et al*., 2001).

Xylem vessels are short, wide and equiped with pits on the outer (primary) and inner (secondary) sidewalls and perforations on the transversal walls (Cruizat *et al*., 2002; Taiz & Zeiger, 2006). Pits assure the lateral intervessel communication whereas the perforations are responsible of the vertical liquid transport. Vessels play the role of water and raw sap transport from the roots to the leaves. The strength of this water column, which circulates through the xylem between the distal parts of the plant, is ensured by the attraction between the partial negative charge of a water molecule oxygen and the positive charge of another water molecule hydrogen (Fig. 2.14). This attraction between water molecules lies on the cohesive strength of the hydrogen bonds.

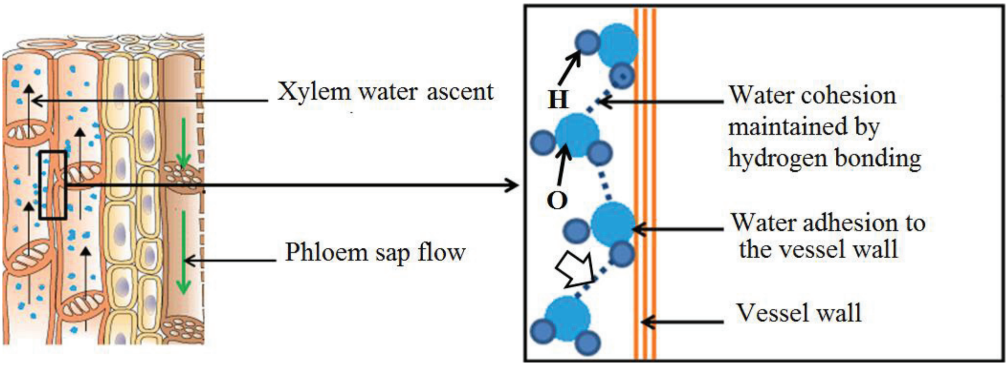


Figure2.14. Xylem water ascent and phloem sap flow. The strength of the cohesion between water molecules is assured by the hydrogen bonding (H). O represents the oxygen (référence image A). The left part of this figure is an online and modified image while the right one has been constructed.

Part of the water absorbed by the roots is released at the leaves level through transpiration (liquid phase) or evaporation (gas phase). Leaf transpiration can cause an important water loss depending on the tree crown volume. The evaporation, occurring at the sub-stomatal chambers level, amplifies this water deficit which, in turn, generates a leaves-to-roots signal. The latter triggers root water uptake. The continuity of the xylem water ascent is assured by the cohesion between water molecules and the water adhesion to xylem vessels wall (Tyree, 1997).

2.3.2. Water deficit

Besides the presence of adequate and permanent water content in their tissues, plants still require a continuous water flow to perform vital processes such as the mineral absorption and photosynthesis. For these processes, the available water is not always sufficient. This unbalance between water supply and plant needs generates the water stress that can, often, be intense and/or permanent.

Plants experience two types of water stress, namely the excessive water availability (flooding) and the lack of adequate water quantity (water deficit). In the case of flooding, a large part of the soil pores are filled with water. The oxygen diffusion and gas exchange between the soil, plants and the atmosphere is, thereby, limited. This results in a reduction of tree growth due to a slowdown of roots functioning. This situation is the major cause of teak root rot during the rainy seasons, in the wetlands of West Africa (Maillet *et al.*, 1985; Ganglo & Lejoly, 1999). The following section deals with the effects of water deficit, the main form of water stress, because (i) of its persistence due to the continuous rainfall disturbances and (ii) of its consequences which are detrimental to trees survival. Water deficit affects plants by reducing the leaf water potential, which in turn, leads to loss of cells turgor and to stomatal closure. This can cause a slowdown of the photosynthesis, tree growth and tree wilting, if the deficit persists (Capron, 2014).

2.3.3. Xylem vulnerability to water deficit: Vessel cavitation and embolism

Cavitation is the phenomenon of vapor-bubble formation in a region of flowing liquid where the pressure of the liquid falls below its vapor pressure. This phenomenon occurs in the xylem of vascular plants when the tension of the sap within a conduit becomes high enough that the dissolved air within the sap expands to fill vessels. As a consequence, vapor-filled (embolized) conduits no longer assure the sap flow continuty. The xylem hydraulic conductance decreases; which can lead to the stomatal closure, and even to leaves abscission, shoot dieback and finally to the plant death (Tyree & Sperry 1989; Capron, 2014). Cavitation can be caused by two types of environmental conditions, namely the freeze-thaw that mostly affects broadleaves tree species in the temperate zones. It can also be caused by the drought induced water stress occurring in the tropical regions during the dry seasons (Meinzer *et al.* 2001; Cruizat *et al.*, 2002; Award, 2011). The following paragraph deals with the risks of xylem caviation likely to be caused in tropical trees due to drought induced water deficit.

Summer water deficit

The intensive drought and decrease in precipitation, during the dry seasons, are responsible of the xylem cavitation in the tropical regions. Pickard (1981) proposed three processes to explain xylem cavitation in tropical species:

a- There may be an interruption of the water column which may be caused by the loss of cohesion between water molecules. This loss of cohesion can result from the breakage of the hydrogen bonds caused by a drought-induced temperature increase (Dougherty, 1998; Lu *et al.*, 2001). There exists a noticeable cooperative strengthening of the hydrogen bonds between the water molecules that the failure of one of the bonds may, consequently, weaken the remaining ones (Heggie *et al.*, 1996).

b- Cavitation can also be caused by a loss of the water-walls adhesion, i.e. a failure of the water-vessel wall interface.

c- The third possible process is that an air-bubble can be pulled through a bordered pit, under atmospheric pressure, from one vessel to another adjacent vessel. This process, which seems to be the more plausible cause of cavitation in tropical trees, can be explained by the air-seeding hypothesis (Zimmerman, 1983). In this hypothesis, a vessel V1 can appear non-functional due to the fact that V1 has undergone its apoptosis. Apoptosis is a programmed cell death, a normal physiological phenomenon resulting from the programmed cell self-destruction which corresponds to the last of the four major stages of xylem cell differentiation (Plomion *et al.*, 2001).

The non-functional vessel (V1) adjacent to a functional vessel V2 (Fig. 2.15), can be filled with air. In such a case, a meniscus forms at the air-sap or air-water interface at the intervessel pit pore level (pit between V1 and V2). Increase foliar transpiration, inducing the loss of the sap or water pressure in vessel V2 (increasing negative pressure), leads to a further increase of the meniscus radius. Microbubbles develop at the meniscus level, once the latter meniscus reaches its resistance limit. The microbubbles are pulled into V2, due to the increase of the negative pressure in V2 (Zimmermann, 1983), swell, expand and fill the cavity of V2. This causes a discontinuity in the sap/water column and results in the loss of hydraulic conductivity in V2 (Cochard *et al.*, 1992).

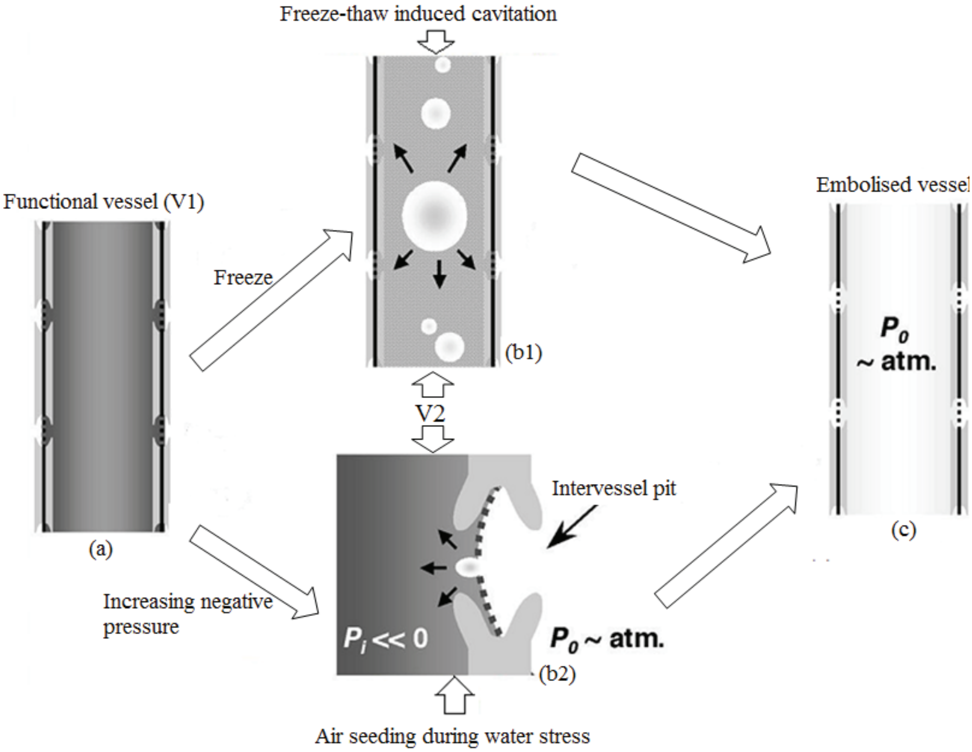


Figure 2.13. Summarizing of the cavitation caused by freeze-thaw (b1) and by air seeding during water stress induced (b2). P_i: negative pressure; P_0: gaz pressure. Source: Hacke & Sperry (2001). Vessel (V2) is isolated in the present figure for illustration purposes. Part b1 illustrates the freeze-induced vessel cavitation and part b2 the air seeding due to water stress during the dry season.

Recent research, dealing with xylem vulnerability to cavitation in 5 temperate angiosperm species, reported that a vascular pressure loss of -2 MPa to -5MPa is sufficient to trigger air-bubbles formation and lead to the loss of vessel hydraulic conductivity (Capron, 2014). The latter becomes total if the vascular pressure loss reaches values comprised between -6 MPa and -2 MPa, depending on the species.

The air-seeding hypothesis, thus, shows that the anatomical properties of vessel pits – such as the pit diameter, its membrane and the biochemical composition of the latter – play a major role in the vessel vulnerability to cavitation (Sperry & Hacke, 2004). The more a vessel shows wide diameter pits (faciliting air entering), the more it is vulnerable to cavitation (Wheeler *et al*., 2005; Christman *et al*., 2009). Interestingly, species with such wide diameter vessel pits are scarce compared to those that show pores impermeable to air (Choat *et al*., 2003; Wheeler *et al.*, 2005). Regardless its origin or causes, vessel cavitation results in reducing or interrupting water supply to the upper parts of the living tree.

2.3.4. Tree’s strategy to resorb cavitation/embolism and to adapt to water stress

Various adaptative processes enable trees to recover from vessel cavitation (Cochard *et al.*, 1992; Capron, 2014). The below section presents some of these processes such as leaves shedding, new xylem conduits formation, variations of cells properties, contribution of other xylem cells.

- ***Effects of leaves shedding***

Studies evidenced the role of stomatal closure in delaying the onset of xylem cavitation. However, stomatal closure can lead to photosynthesis reduction and varies between species (Bond & Kavanagh 1999, Cochard *et al.* 2002). The case study of *Juglans regia* provides a clear understanding of the role of stomatal closure in limiting vessel embolism (Tyree *et al.*, 1993). At the onset of the water deficit, stomatal apertures close. Cavitation starts in the petioles which become non functional when the water deficit persists; resulting in leaves yellowing and shedding. Only the branches show significant resistance to cavitation due to their higer water potential compared to that of the leaves. The defoliation entails the reduction of stomatal apertures. This situation results in a positive increase of the xylem pressure which, in turn, induces the air-bulbbes dissolution, a phenomenon essential to resorb the xylem embolism (Cochard et Tyree, 1990; Cochard *et al.*, 1992; Ewers *et al.*, 2001). Since the cavitation has been induced by the increase in the xylem negative pressure. The restoration of the site moisture conditions back to the normal level (favourable to growth reactivation), triggers the resumption of the mitotic activities.

In their study dealing with drought effects on cambial activity of teak seedlings, Priya and Bhat (1998) did not explicitly report seedlings defoliation during the 30-days induced water deficit. However, they observed an interruption of the cell divisions (resulting from the induced drought) followed by growth recovery as a consequence of the restoration of favourable moisture conditions. Second, based on field cambial activities of teak trees (Priya & Bhat, 1999; Rao & Rajput, 1999), it can be assumed that a water deficit, similar to that of the major dry season and occurring during the vegetative season, is likely to induce trees defoliation and growth interruption in tropical dry climate sites.

The role the stomatal closure, in limiting xylem cavitation, suggests the existence of a threshold leaf water potential at which photosynthesis decreased in response to drought.

- *New vascular system formation*

To mitigate cavitation effects and recover from vessels embolism, trees natural reaction consists in forming new xylem conduits. Under extreme water stress, plants seem to develop more small vessels, in order to maintain an efficient water transport system (Hacke *et al*., 2001), as wider diameter vessels are more vulnerable to cavitation (Carlquist, 1975; Christman *et al*., 2009).

- *Influence of vessel pits properties*

Vulnerability to cavitation is related to the vessels diameter and wall thickness (Carlquist, 1975; Jacobsen *et al*., 2005; Christman *et al*., 2009), perforation plates (Janssen *et al*., 2004) and the ultra-structure of intervessel pits (Lens *et al*., 2011). The variation of these anatomical features is likely to influence xylem vulnerability to cavitation according to the above authors. Second, wood shrinkage, due to dehydration for example, is reported to increase vessel pit diameter (Shane *et al*., 2000). Owing to the hygroscopic nature of its cell wall, wood can shrink as a result of dehydration caused by a decrease in air moisture induced by a temperature increase (Derome *et al*., 2012). Wood can also grow in volume with an increase in the air moisture content. The shrinkage of wood cell wall components – such as pectins (cell wall insoluble compounds) – is likely to induce an increase in the dimensions of the pit openings (Zwieniecki *et al.*, 2001).

Trees age is, also, reported as a factor of xylem vulnerability to cavitation (Sperry *et al*., 1991). In addition, the pattern of vessel pits arrangement between outer and inner vessel walls as observed in teak (Fig. 2.8 D-E) and the functioning of these pits is likely to represent a safer way for cavitation prevention in some trees species. .

- *Contribution of the vessels surrounding xylem fibres*

Tree species, likely to exhibit high negative xylem pressure and hence being more vulnerable to cavitation, interestingly form thick-walled vessels. These species, thereby, show high ratio of wall thickness / lumen diameter (Hacke *et al*., 2001; Jacobsen *et al*., 2005), which enables them to be more resistance to cavitation. Furthermore, Jacobsen *et al*. (2005) obtained significant correlation between xylem cavitation-resistance and the properties of the vessels surrounding fibres. Their results suggest that trees species with dense wood, made of thick-walled and narrow lumen fibres, are less vulnerable to cavitation, regardless of the vessels properties.

Tectona grandis trees experience complete defoliation during the dry season in the deciduous and dry forests (Pumijumnong, 1995) while gradual leaves shedding is observed in the evergreen forests (Dié *et al*., 2012). And total defoliation has been reported to be associated with growth interruption in trees (Pumijumnong, 1995; Priya & Bhat, 1999). As such, the species growth can be expected to be negatively affected by the drought exposure likely to increase as a result of the ongoing global climate warming (IPCC 2007) causing decrease in precipitation, especially in West-Africa.

The current literature, on teak growth responses to climate change, has not yet reported any data related to xylem vulnerability to embolism. Nevertheless, the species is known to show high sensitivity to climate change; which explains its common use in dendroclimatology (Ram *et al*., 2011; Pumijumnong, 2012). Furthermore, teak is a ring-porous wood species like oaks which are likely to experience somewhat loss in conductance when the xylem pressure reaches some threshold (Matzner *et al*., 2001). However, even for oaks the discussion on the loss of conductance is somewhat controversial. Since these species can exhibit a protective mechanism by the stomatal regulation; which prevent from embolism risks (Tyree & Cochard, 1996). This can be the case in the functioning of teak.

We suggest that the lack of experimental data on the xylem pressure likely to induce drought related vessels embolism in teak can be explained by some possibilities as follows, in addition to the stomatal regulation:

- *Bark thickness*

The bark (Fig. 2.16) is probably thick enough to prevent xylem shrinkage which could have been caused by the drought induced increasing temperature during the dry season. Measurements carried out on dehydrated samples collected from three Ivorian plantations (Gagnoa, Mopri and Séguié: personal measurement) gave an average bark thickness of about 1.5 cm. Xylem stretching can result in increasing the diameter of the pits membrane pores; which can expose the xylem to cavitation risks (Jacobsen *et al*., 2005).

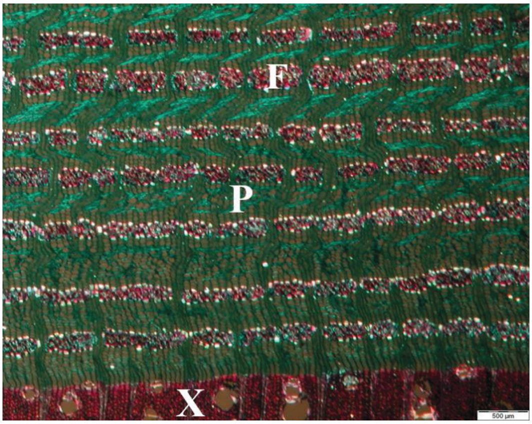
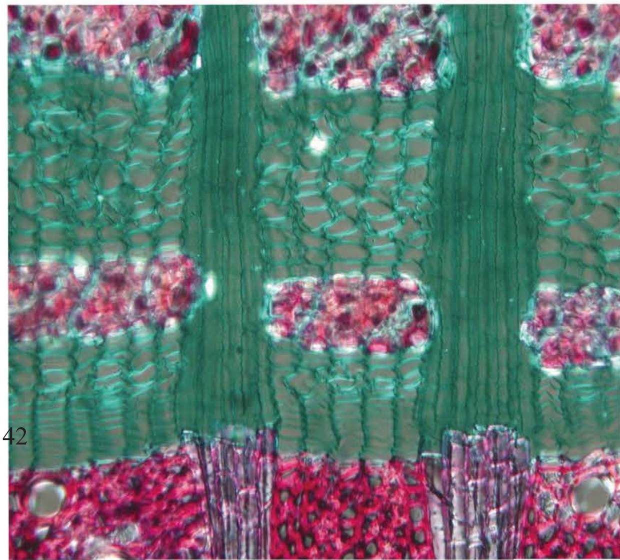


Figure 2.16. Structure of *Tectona grandis* bark showing alterning tangential bands of phloem parenchyma (P) and fibres (F). Scale bar: 500 µm.

- *Cell wall thickness*

Thick cells walls are likely to reduce wood stretching/flexing and hence prevent pit membrane pores from increasing. This increases the xylem resistance to cavitation risks; which can explain the significant correlation between physico-mechanical properties and xylem resistance to embolism (Hacke *et al*., 2001; Jacobsen *et al*., 2005). Teak is a hardwood species (with thick-walled cells) which also shows high sensitivity to climate change. We consider important to present the species cellular properties such as vessel walls pits likely to be involved in tree growth resistance to changing climatic conditions. Addressing the possible variations of teak vessel pits pores in relation to site climate paves a way for further research on pits role in growth sensitivity/resistance to future climate change.



Chapter 3: Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (*Tectona grandis*) in Ivory Coast

This chapter is based on the following paper:

Dié A., Kitin P., Kouamé F.N., Van den Bulcke J., Van Acker J., Beeckman H., 2012. Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (*Tectona grandis*) in Ivory Coast. Annals of Botany 110: 861-873.

Abstract

Tectona grandis is a tropical timber species forming xylem rings carrying records of climate variability and carbon sequestration. These records are only useful when the structural variations of tree rings and their periodicity of formation are known.

Seasonality of ring formation in mature teak trees was examined via correlative analysis of cambial activity, xylem and phloem formation, and climate throughout 1.5 years. Xylem and phloem differentiation were visualized by light microscopy and scanning electron microscopy. Three month dry season induced semi-deciduousness, cambial dormancy and formation of annual xylem growth rings (AXGRs). Intra-annual xylem and phloem growth was characterized by variable intensity. Morphometric features of cambium such as cambium thickness and differentiating xylem layers were positively correlated. Cambium thickness was strongly correlated with monthly rainfall ($R^2 = 0.7535$). In all sampled trees, xylem growth zones (XGZs) were formed within the AXGRs during the seasonal development of new foliage. When trees achieved full leaf, the xylem in the new XGZs appeared completely differentiated and functional for water transport. Two phloem growth rings were formed in one growing season.

At the onset of cambium dormancy (October-November), crystals were absent in cambial cell and abundant in the differentiating tissues. They were present in dry season (December-January) cambial cells and during cambial reactivation (February). Active and full active (March through June) cambial cell contained very few or no crystals.

The seasonal formation pattern and microstructure of teak xylem suggest that AXGRs and XGZs can be used as proxies for analyses of the tree history and climate at annual and intra-annual resolution.

Introduction

Teak, *Tectona grandis*, is a tropical and sub-tropical forest hardwood species, indigenous to regions with monsoon climates in South Asia (Behaghel, 1999; Pardé, 2002). This is a light-demanding and fast-growing species that is prized as one of the most economically important tropical timber trees for its valuable wood (Dupuy *et al.*, 1999; Maldonado & Louppe, 2000; Pandey & Brown, 2000; Cordero & Kanninen, 2003; Rahman *et al.*, 2005). Teak also shows a high potential for carbon storage and biomass production for renewable energy (Kraenzel *et al.*, 2003; Silver *et al.*, 2004).

Teak trees grow best on well-drained and deep alluvium sites with annual rainfall of 900–2500 mm and temperatures between 17 and 43°C (Behaghel, 1999; Enters, 2000; Pandey & Brown, 2000). Typical growth sites are characterized by a 6 or 7 month rainy season and precipitation 200 mm/month, followed by 5 or 6 months of dry season (Purwanto & Oohata, 2002; Suzuki *et al.*, 2007). In contrast to the Asian distribution area of teak, teak plantations in Ivory Coast experience a shorter main dry season (2–4 months) and a 1 or 2 month secondary period of reduced precipitation (around 70 mm/month) in late summer (August) called the small dry season. After September follows a period of resumption of rainfall that lasts 2–3 months, with monthly precipitations sometimes equal to those of the major rainy season (Société d'Exploitation et de Développement Aéronautique et de Météorologie – SODEXAM/Côte d'Ivoire: 1972–2000).

In typical growth sites characterized by seasonality of rainfall and temperature, the wood in teak is composed of ring-porous growth rings resulting from seasonal fluctuation of cambial activity (Nobuchi *et al.*, 1996; Borchert, 1999; Priya & Bhat, 1999; Rao & Rajput, 1999). In contrast, irrigated young trees have been found to form diffuse porous rings with less or no distinction between earlywood and latewood (Priya & Bhat, 1999). It can be expected that due to the worldwide distribution of teak plantations in various tropical climates, the pattern of tree ring formation can be diverse. Moreover, while a number of reports addressed the seasonal variation of cambial structure (Rao & Dave, 1984; Nobuchi *et al.*, 1996; Rao *et al.*, 1996; Borchert, 1999; Rao & Rajput, 1999), little is known yet about the environmental factors that affect xylem cell differentiation and growth ring structure. Investigating the time course of xylogenesis in situ and its relationship to climate is a straightforward way to characterize environmental factors controlling the structure of wood (Worbes, 1995 and 2002; Wimmer, 2002).

Knowledge of the seasonal pattern of xylem formation is important for better assessments of forest management and sylvicultural practices, and can provide means to improve the technological features of the wood product (Denne & Dodd, 1981; Bhat *et al*., 2001; Plomion *et al*., 2001; Wodzicki, 2001). Moreover, teak is an interesting model for studying the formation of tree rings in the tropics because it typically forms a ring-porous wood structure with distinct annual rings as well as false rings (Priya & Bhat, 1998; Bhattacharyya *et al*., 2007). Annual growth rings of teak can provide information on productivity and age structure of the forest stands, and enable dendrochronological research (Pumijumnong *et al*., 1995; Jacoby & D'Arrigo, 1990; Somaru *et al*., 2008).

Studies on the ecology, growth dynamics and carbon sequestration of tropical forests are often hindered by insufficient information on the structure and periodicity of tree rings. In the case of teak, tree ring analysis can be complicated by variations in xylem structure such as different kinds of false rings (Priya & Bhat, 1998) that can be the result of climatic disturbances or non-climatic factors, such as pathogen attacks (Sudheendrakumar *et al*., 1993; Managave *et al*. 2011).

With this study, we aimed to reveal the seasonal pattern of xylogenesis in Ivorian teak trees and identify environmental and physiological factors that affect the cambial activity and annual growth ring structure. In particular, we investigated:

(i) The anatomical features that characterize dormant and active phases of cambial activity;

(ii) The seasonal time course of growth ring formation and structure of xylem and phloem;

(iii) The inter-relationships between cambial activity and phenology in teak, and the climate.

3.1. Material and methods

3.1.1. Study site description

The sampling was carried out from October 2006 to March 2008 (Table 1), in the forest reserve ‘Séguié’ located in Rubino (Southeast Ivory Coast), between 6810′ and 6821′N and 4814′ and 4827′W. The vegetation in the region is classified as an evergreen moist rain forest type and soils are typical acid soils of tropical lowlands (White, 1983). Séguié is the fourth largest of the 48 Ivorian state forest reserves in terms of planted area, covering 19 600 ha, and the second largest teak plantation in the country next to Téné. The vegetation of Séguié is representative of the forest zone reported as the most appropriate site for teak growth and wood productivity (Dupuy *et al.*, 1999). The forest reserve is situated in a predominantly flat terrain and on a hydromorphic soil consisting mainly of sand and clay. The edaphic conditions are classified as one of the most productive sites for teak (Séguié Forest Management Plan, internal document, 1999).

Rainfall data were recorded daily at the forest site during the sampling period and compared with two different precipitation data sets (1986-1998, by Séguié Forest Division at the study site; and 1972-2000 by SODEXAM 50 km away from the study site). The mean annual sum of precipitation is 1298 mm, with a mean annual potential evapotranspiration of 1257 mm. About 83 % of the rains that fall infiltrate the soil, which contributes to a sustained water storage (N’Go *et al.*, 2005). Annual mean relative air humidity is between 70 and 80 % (60 % in December and 80 % during the wettest month). Monthly mean temperature is 26.6 8C (minimum in August, 24 8C; and maximum in February-April, 28 8C) over the period 1972-2000 (Société d’Exploitation et de Développement Aéroportuaire, Aéronautique et de Météorologie – SODEXAM/Côte d’Ivoire: 1972-2000). Phenological observations were carried out during the course of the study.

3.1.2. Collection and preservation of plant material

The study trees were collected from the same stand (same microsite), same age, almost same diameter at breast height. Two to three 36-year-old individuals of *Tectona grandis* were sampled every 28 days. Each investigated tree was sampled once in order to avoid disturbed physiological due to cambium woundings responses (Rao & Rajput, 1999). One block with dimensions approx. 5 × 5 × 5 cm, containing xylem, cambium and inner bark, was removed from the trunk at 1.30 m above the ground using a chisel. The cambial samples were immediately fixed in FAA [acetic acid 5 %, (37 %) formaldehyde 10 %, distilled water 35 %, and ethanol 50 %].

For analysis of the structure of previously formed growth rings, disks from ten individuals (Tw59768, Tw59769, Tw59770, Tw59771, Tw59772, Tw59773, Tw60583, Tw60584, Tw60585 and Tw60586; accession numbers of the Tervuren Xylarium) were cut at 1.30 m above the ground. Wood blocks including annual growth rings 5, 10, 15, 20, 25 and 30 as counted from the pith were cut out from each disk and air-dried.

3.1.3. Determination of cambial activity

3.1.3.1. Light microscopy

Transversal and radial sections with a thickness of 15–30 mm and containing secondary xylem, cambial zone and phloem were cut using a sliding microtome (HM 440E; Microm Laborgeräte GmbH, Germany). The sections were stained with a 0.1 % Safranin O (Merck KGaA, Darmstadt, Germany) solution in 50 % ethanol. They were washed in an ethanol series (50 and 75 %, 5 min in each concentration) and then stained with a 1 % fast green solution (Merck KGaA, Darmstadt, Germany) in 96 % ethanol for conventional light microscopy in order to differentiate lignified and cellulosic cell walls in terms of colour. After staining, sections were dehydrated in increasing concentrations of ethanol, mounted on microscope slides in Euparal (Carl Roth Gmbh + Co. KG., Karlsruhe, Germany) and dried in an oven at 50 8C overnight.

Observations were made with an Olympus microscope (BX60F-3, Tokyo, Japan), equipped with bright-field and polarized light optics, as well as epi-fluorescence using a mercury arc lamp and an Olympus WU filter cube (excitation 330-385 nm, long-pass emission 420 nm). The polarized light was used to detect birefringence from crystals and developing secondary walls. Digital images were obtained using an Olympus Digital Camera (C-3040 ZOOM; Olympus Co. Ltd, Japan). By fluorescence microscopy, yellow or red colour was indicative of lignified cell walls and violet or blue colour indicated cellulosic walls. Whereas Safranin is a well-known fluorophore (Donaldson, 1992; Kitin *et al.*, 2003), fast-green staining is used primarily for conventional light bright-field imaging. The effect of violet or blue fluorescence of cambium and phloem was observed after 1 min exposure of the sections to the fluorescent excitation light, possibly due to bleaching of the Fast-green stain.

3.1.3.2. Scanning electron microscopy

For scanning electron microscopy (SEM), 5 mm cubes containing cambium and adjacent xylem and phloem were excised from the samples and rinsed in running tap water overnight. The cubes were planed on the sliding microtome in order to achieve smooth transverse, longitudinal radial and tangential faces of cambium, xylem and phloem. They were then dehydrated using an ethanol series of increasing concentrations (25, 50, 75 and 100 %) for at least 1 h in each concentration. After three changes in 100 % ethanol for 15-20 min each time, cubes were air dried. The samples were coated with gold in a sputter coater and observed with a scanning electron microscope (JSM-6610LV; JEOL, Tokyo, Japan) operated at an accelerating voltage of 10 kV.

Cambial zone thickness (CZ), number of tangential layers of fusiform cambial cells (FC), radial diameter of fusiform cambial cells (Crd) and thickness of the xylem differentiating zone (XD) were measured in bright-field microscopy images of transverse sections (.50 measurements per sample) using AnalySIS Pro 3.2 software (Soft Imaging System Gmbh, Münster, Germany).

To characterize the variation of vessel diameters across annual ring boundaries, earlywood and latewood vessel diameters were measured in annual rings 5, 10, 15, 20, 25 and 30 in five individual trees (50 vessels per sample). Measurements of Feret diameters (the maximal length straight line that can be fitted into a vessel) were executed automatically in images of transverse sections with ImageJ software (Wayne Rasband, National Institute of Mental Health, Bethesda, MD, USA).

An analysis of variance (ANOVA) was carried out on the monthly variations of CZ, FC, Crd and XD. Tukey HSD multiple comparisons were used to determine pairwise similarity probabilities. Pearson's correlation coefficients were calculated for the inter-relationships between CZ, FC, XD and monthly precipitations. All the statistics were performed using SYSTAT 11.5.

3.1.4. Terminology and definitions

The terms cambial zone or cambium indicate all layers of meristematic cells and their intermediate derivatives between the xylem and phloem (Mahmood, 1971; Rossi *et al*., 2006a). The cells in the cambial zone do not differ from cambial initials in shape. The xylem or phloem differentiating zones comprise the immature xylem cells (newly formed vessel elements, xylem parenchyma, fibres and rays) or phloem cells distinguishable from cambial cells by their shape and the fact that they exhibit various stages of differentiation (growth, primary or secondary wall formation, lignification).

The cambial cells and the differentiating cells with primary walls show no birefringence under polarized light and are stained in green or blue after applying our double staining. Cells with developing secondary walls show birefringent walls under polarized light, and lignified cell walls are stained in red after the Safranin staining. The lignification of secondary walls was additionally confirmed in controls of unstained sections by the stronger autofluorescence of lignin. According to a traditional concept, any growth ring or growth zone which is not annual can be designated a false ring. Such a definition, however, is not suitable in climates where species typically form more than one growth ring in a single year. Knowledge on and proper methodologies for how to identify false rings from true rings is fundamental in tree ring studies. The definition of false rings by Kaennel and Schweingruber (1995) is a step forward because it provides a distinction between false rings and growth zones or density fluctuations which are structurally different from true rings. In this study, we use definitions by the Multilingual Glossary of Dendrochronology (Kaennel & Schweingruber, 1995) adapted as the following:

Growth rings: subsequent growth layers of xylem or phloem suggesting periodicity of growth. For classification of xylem growth rings according to structure and distinctiveness, see IAWA Committee (1989).

Annual xylem growth ring (AXGR): a growth layer produced by cambium in 1 year.

Growth zone: a growth layer of xylem or phloem which can be identified by variations in cell shape, size and wall thickness. Unlike growth rings, growth zones are not produced in subsequent layers and often do not go around the entire circumference of the stem. Growth zones with indistinct or diffuse boundaries are defined as density fluctuations by Kaennel and Schweingruber (1995).

Intra-annual xylem growth zone (XGZ): a growth zone within an annual growth ring which is distinct in structure from the annual ring.

False ring: an additional, apparently complete growth zone with well-marked boundaries, formed within one growing season. In contrast to intra-annual growth zones, false rings cannot be morphologically distinguished from true tree rings, and can only be identified by cross-dating or anatomical analysis of cambial activity and annual xylem growth.

3.2. Results

3.2.1. Climatic conditions and phenology

The study site experienced a wet season of 5-6 months (from February until July), preceding a 3 month dry season (from mid-November until mid-February) long enough to induce trees defoliation. Then occurred a reduction in precipitation in August, followed by a resumption in rainfall from September until mid-November (Fig. 3-1). Monthly precipitation data sets collected at the study site over different periods (1986-1998 and 2005-2008) and 50 km away from the site (1972-2000) are in agreement and show no major disturbance to the typical precipitation pattern during the study period (Fig. 3.1). The only exception was the month of August (short dry period) in 2006 with only 10 mm monthly precipitation. The rainfall in August of 2007 with precipitation of 66 mm was consistent with the typical pattern.

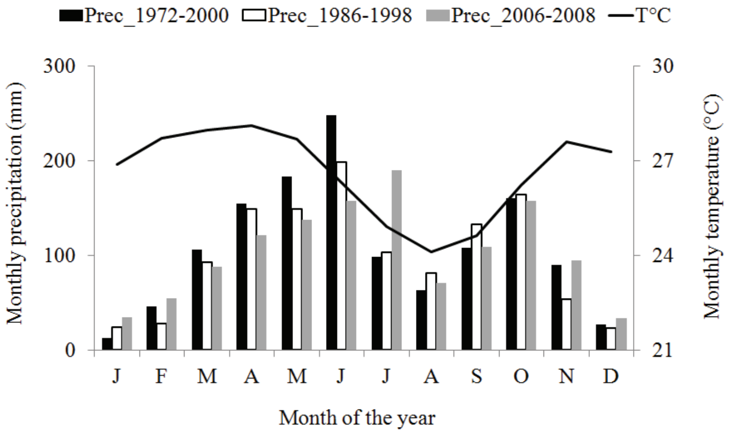


Figure 3.1. Monthly precipitation and temperature variation over three different periods in the study.

In the present study, we monitor the leaves phenology (table in Box 1). Our observations, together with phenological data from the Séguié Forest Division (1999), show that Séguié teak gradually sheds leaves during the dry period, but trees do not become completely leafless at a time. Leaf fall starts between mid-October and early November, and lasts until the end of January or mid-February, after which sprouting begins with the onset the major wet season. Development of current-year leaves is continuous from February to April or May. Trees are in the full foliage in May before the peak in precipitation. Flowering takes place during the full foliage from May to August or September. The fruiting covers 3-4 months (September-December). Leaf phenology is associated to structural changes in the cambial zone (Box 3.1).

Box 3.1. Correspondence between leaf phenology and structural changes in the cambial zone

Leaf phenology	Structural changes in the cambial zone
Leaf yellowing	Decline in cell divisions
Leaf fall	Cambial rest
Leaf sprouting	Cambial reactivation
New foliage development	Increase in cell divisions
Full foliage	Cambium full active phase

3.2.2. Seasonal changes of the cambial zone morphology

Number of tangential layers of fusiform cells (FC)

The cambial zone contained the least FC in the middle of the dry period in December (table 3.1). In contrast, the largest FC occurred during the peak of cambial activity in June. There was the same FC at the end of cambial activity in October and at the onset of reactivation in February.

Table 3.1. Seasonal variation of the morphology of the cambial zone width (CZ) and the number of fusiform cells (FC).

	Width of the cambial zone (µm)	Number of fusiform cambial cells
26 October 2006	47.80±10a	9 ± 2a
25 November 2006	40.32 ± 8a	7 ± 1b
December (27 in 2006 and 29 in 2007)	39.48 ± 15b	4 ± 1c
25 Januray 2007	34.70 ± 7b	7 ± 1b
28 February 2007	40.77 ± 15a	9 ± 2a
March (29 in 2007 and 27 in 2007)	63.38 ± 9c	12 ± 1d
29 April 2007	55.39 ± 12c	11 ± 2d
31 May 2007	81.54 ± 24d	16 ± 2^{e}
29 June 2007	86.04 ± 13d	19 ± 2f
Coefficient of determination R^2	0.80	0.854
F-ratio	227.324	1042.488
P (probability)	0.000	0.000

Values in the table are the average of 50 measurements or counts per micro-section and their standard deviation. Measurements were performed on 2 to 3 trees depending of the sampling month. Values holding the same letter are significantly equal (ANOVA; multiple means comparison of Tukey HSD, $P<0.05$). R^2 represents the part of variation of the studied variable (cambial zone width and number of cambial cells) explained by the cambial seasonality.

The FC during new leaf development in March and April were also statistically different from other months of the year (table 1, Fig. 3.2).

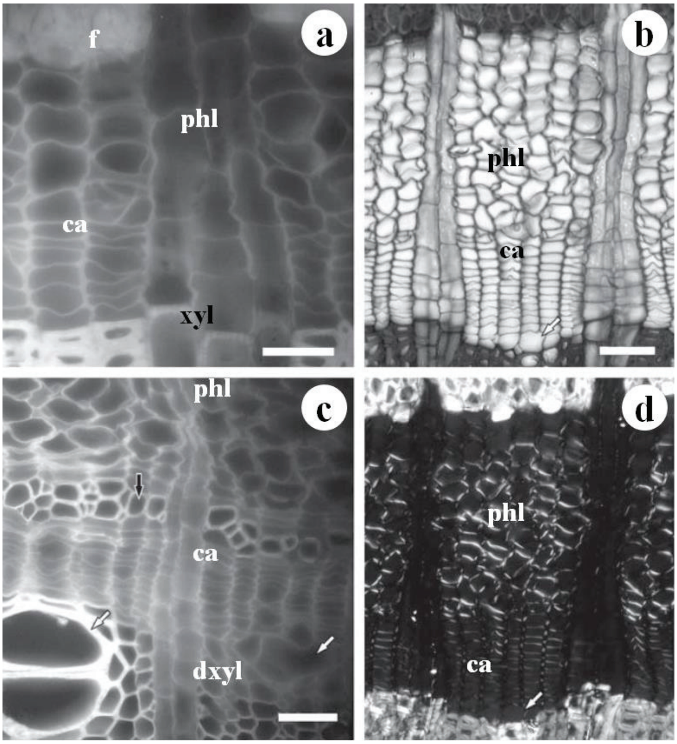


Figure 3.2. Seasonal development of cambium in teak in Séguié Forest. (a) Dormant in November. (b) Cambial reactivation in February. The arrow shows an expanding xylem cell. (c) Image of active cambium in April. The black arrow shows developing phloem fibres, and white arrows show developing vessels. (d) Matching image of the sample in (b) viewed with polarized light. Methods: TS (a–d), FL (a) and (c); BF (b) and PL (d). Scale bars = 25 mm (a); 50 mm (b–d). Abbreviations in all figures. Xylem and phloem development: ca, cambium; df, developing fibres; dp, developing phloem; dxy, differentiating xylem; dxy1, xylem differentiation zone of primary cell wall development and expanding cells; dxy2, xylem differentiation zone of secondary cell wall development and lignification; dxy3, lignified xylem of the current year; f, fibres; phl, phloem; xy, xylem of the previous year. Growth ring structure: XGR, xylem growth ring XGZ, xylem growth zone. Methods: RS, radial longitudinal section; TLS, tangential longitudinal section; TS, transverse section; BF, bright-field light microscopy; FL, epi-fluorescence; PL, polarized light.

Cambial zone width (CZ)

The CZ in October and November (end of the growing season) was significantly thinner compared with the CZ at the peak of the rainy season in May and June. The CZ was further significantly decreased in December and January (a 2-fold decrease relative to the cambium at the peak of the rainy season). At cambial reactivation in February, the CZ increased and became statistically similar to that at the end of cambial activity in October and November (table 3.1, Fig. 3.2). A strong linear correlation was found between the FC and CZ (Fig. 3.3 and table 3.1). There were considerable variations in CZ between different trees (table 3.1). The seasonal change in cambium morphology (CZ and FC) showed a significant correlation with the precipitations of the corresponding sampling months (Fig. 3.3).

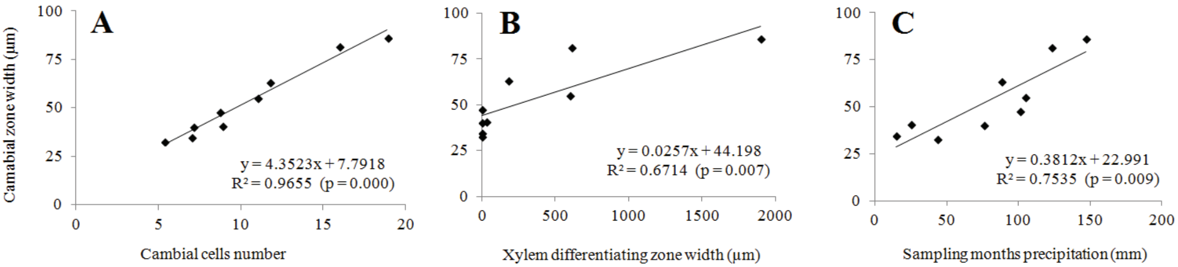


Figure 3.3. Correlations between the cambium morphometric features and the sampling month precipitation ($P < 0.01$): number of tangential layers of cambial cells and cambial zone width (A), cambial zone width and width of xylem differentiation zone (B with $P < 0.05$), cambial zone width and monthly precipitation (C with $P < 0.01$). Trendline equations are shown in the graphs.

Fusiform mother cell radial diameter (Crd)

The Crd in January (before reactivation) was the smallest and, at the onset of reactivation in February, was significantly increased (table 3.1, Figs. 3.2 and Fig. 3.4).

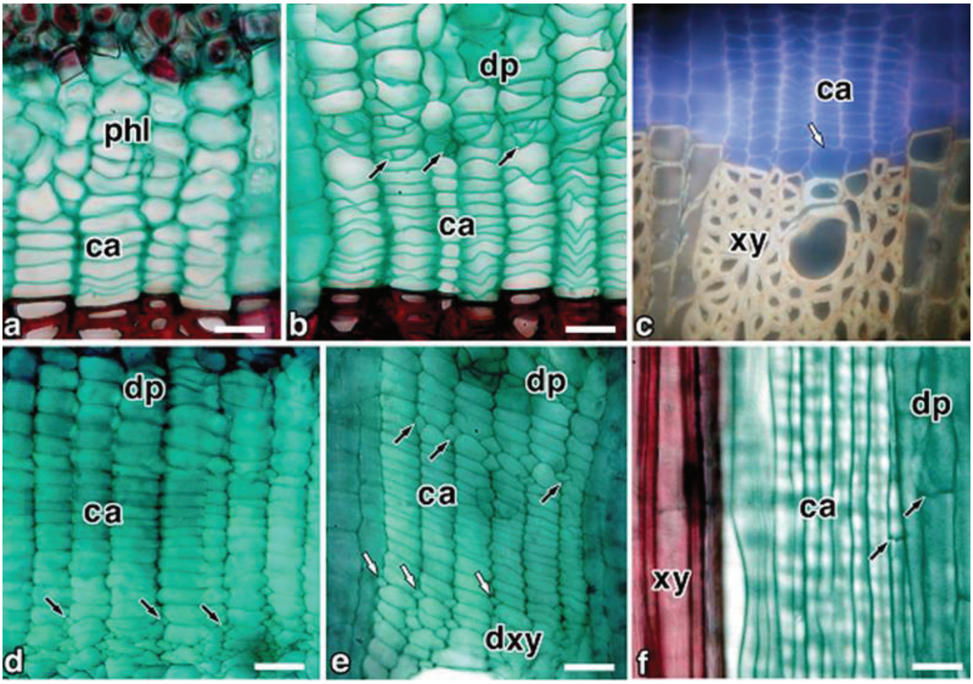


Figure 3.4. Morphology of dormant and active cambium: Dormant cambium in November (a), Cambial reactivation in February (b) with the arrows indicating anticlinal divisions at the phloem side and an expanding cambial derivative at the xylem side (c). Active cambium in May (d) shows intrusively growing tips of developing xylem fibers (IGX, arrows in d). Active cambium in June (e) where the black arrows show anticlinally-divided cells of developing phloem and white arrows point to IGX. Cambium in February (f) with arrows indicating anticlinal divisions of developing phloem cells: dxy = differentiating xylem; ca = cambium; phl = phloem; dp = developing phloem; xy = xylem. Methods: TS (a through e), RS (d), BF (a, b, d, e, f), Fl (c). Bars = 20 µm (a, b, d, e, f), 40 µm (f). For abbreviations, see list at the legend to Fig. 3.2.

Newly derived (daughter) cells may have been overlooked in the measurements because new division plates were not easily visualized by light microscopy. Uneven thickness of the radial walls of cambial cells (primary pit fields) was evident in the period November-February (see dark and bright spots in the radial walls of cambial cells in the radial section in Fig. 3.4).

3.2.3. Relationships between the cambial morphology and the growth ring development in the stem

The seasonal changes in the morphology of the cambial zone were associated with corresponding changes of the XD (Fig. 3.3).

Dormant cambium

There were no enlarging or differentiating cambial derivatives during the main dry period of the year from October until February (Fig. 3.2a-b; Fig. 3.5a-b). However, the CZ in October and November was still significantly thicker than the CZ in December and January (Table 3.1). Cell walls of cambial cells, phloem rays and phloem parenchyma showed little birefringence, in contrast to developed xylem and sieve tube elements which allowed for a clear differentiation between these different types of elements under polarized light (Fig. 3.2d and Fig. 3.5f).

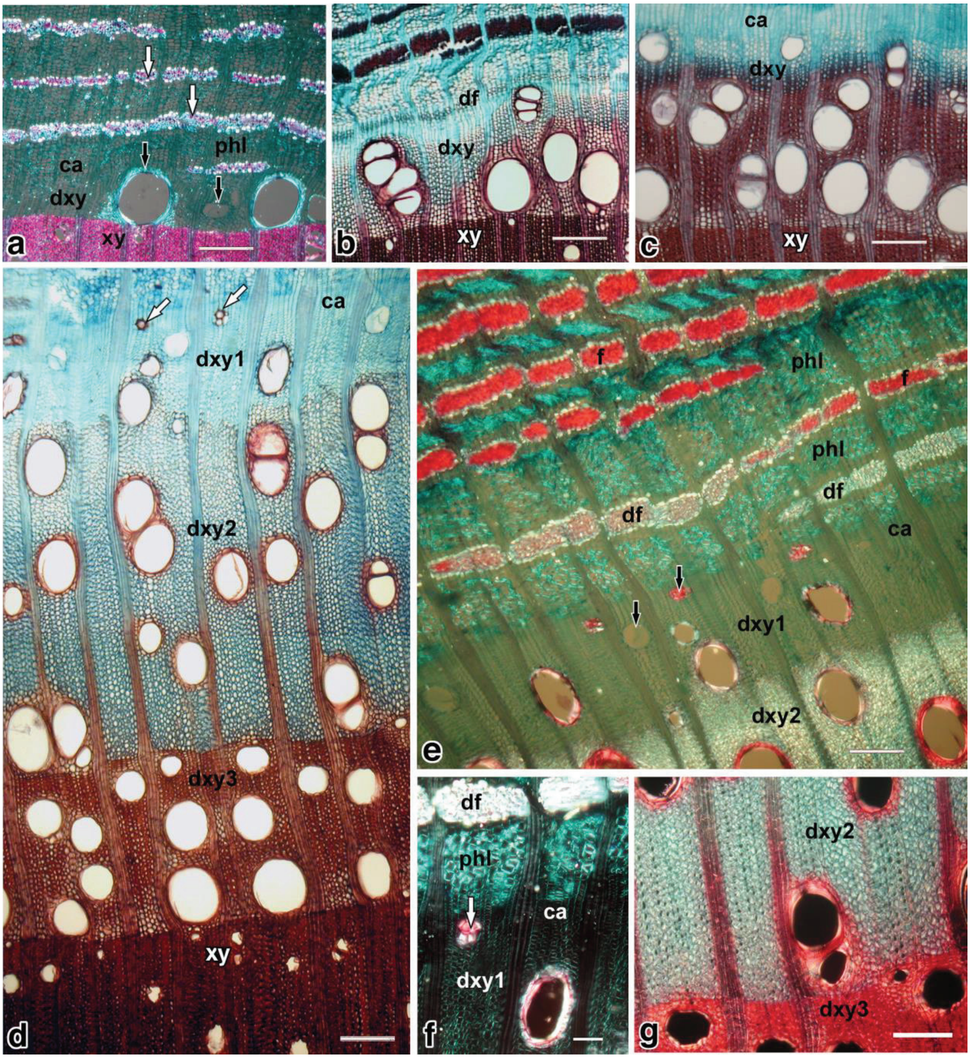


Figure 3.5. Intra-annual pattern of xylem differentiation: Development of earlywood in March in image (a) with vessel elements at different stages of differentiation (black arrows) and fibre bands of phloem from previous years (white arrows). Development of earlywood in April (image b) and May (image c). Development of earlywood and initiation of latewood in June (image d). The differences in colour indicate various stages of differentiation in image (d): ca, dxy1, dxy2, dxy3 and xy (see abbreviations in the legend to Fig. 3-2). Polarized light image of June cambium and differentiating xylem and phloem in image (e). Note the unstained developing fibres (df) and stained red lignified fibres in image (f). Birefringence is seen in differentiating xylem (dxy2), phloem fibres (df, image f) and sieve elements (phl) but not in the cambial zone (ca), and not in differentiating xylem with primary walls (dxy1) or in rays. Arrows point to vessels in different stages of development (red colour indicates lignifying vessel walls). Image (f) shows a magnified view of June cambium and differentiating xylem and phloem by polarized light. The arrow points to a latewood vessel with developing secondary wall indicated by birefringence and red staining. Image (g) is the polarized light image of the sample in (d) showing the border between dxy2 and dxy3 (lignifying cell walls stained red). Methods: TS (images a-g), PL (images a, e-g), BF (b-d). Scale bars: (a-e, g) = 220 mm, (f) = 100 mm. Abbreviations are as in the legend to Fig. 3-2.

3.2.4. Cambial reactivation and initiation of xylem and phloem formation

The first cell divisions were seen in February at the phloem side of the cambium. The reactivation of cambium was preceded by an apparent swelling of the cambial zone (about 17 % increased thickness relative to the January samples) which was associated with increased FC and Crd (table 3.1, Fig. 3.2b; Fig. 3.4bc). The first expanding cambial derivatives were seen in February at the xylem side (Fig. 3.2b; Fig. 3.4c). There was no secondary wall formation in the differentiating cells, indicated by the lack of birefringence in their walls (Fig. 3.2d).

Active cambium

The swelling of the cambial zone in February was followed by an increased mitotic activity evidenced by a statistically significant increase of the FC. In March, the radial enlargement of the CZ was an 83 % increase compared with the dormant stage in January (table 3.1, Fig. 3.2; Fig. 3.4). In March, the xylem differentiating zone included a single layer of earlywood vessels (Fig. 3.5a). Some vessels were still growing while others were fully expanded with developing secondary walls.

Lignification was evident in the fully expanded vessels but not in the surrounding developing cells (Fig. 3.5a; Fig. 3.6ac). The zone of differentiating xylem in April was enlarged > 200 % compared with that in March, and included 2-3 layers of earlywood vessels (table 3.1, Fig. 3.5ab). However, the amount of newly produced xylem cells varied at different positions in the samples. Several layers of xylem cells had developing secondary walls, and lignification was evident in the cell walls of fully expanded vessel elements and adjacent-to-vessels fibres (Fig. 3.5b). Similarly, Ridoutt and Sands (1994) in eucalypts noted that fibres close to vessels started secondary wall development sooner than fibres further away.

The new xylem layer in May had a relatively small increase compared with that in April, showing that xylem formation in May was relatively slow, although statistically significant (table 3.1, Fig. 3.5bc). In June, the cambial activity had become very intensive, resulting in a 3-fold enlargement of the XD compared with the previous month (table 3.1, Fig. 3.5d).

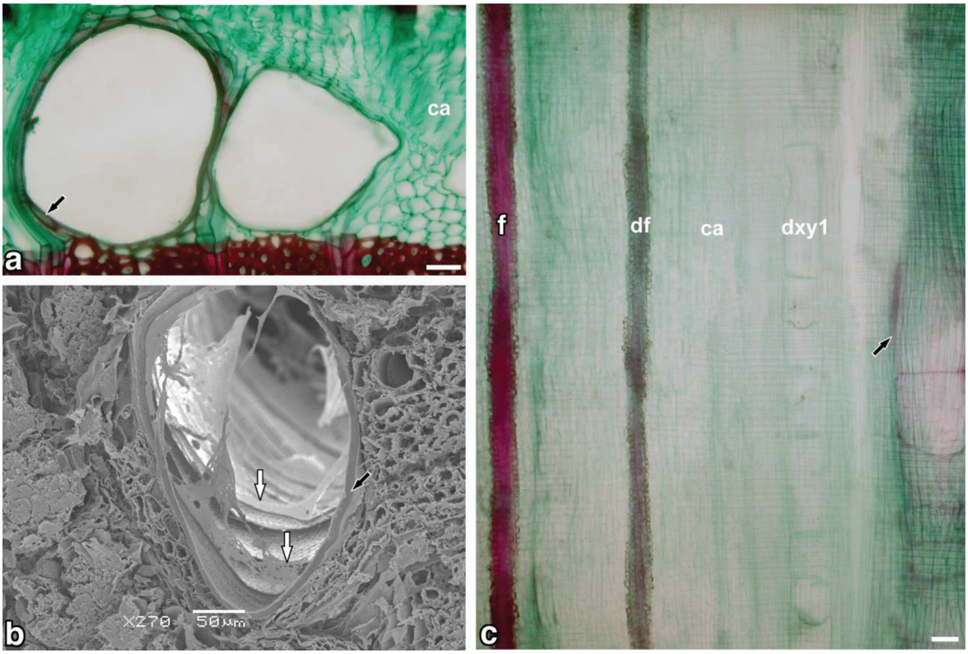


Figure 3.6. Cell wall development of differentiating xylem and phloem cells: Expanding earlywood vessels in March (image a), SEM micrograph of developing vessel wall in March indicated by black arrow in image b and white arrows pointing to membranes of perforation partitions between vessel elements. These perforation partitions have probably been ripped off during sample preparation for SEM. Developing phloem and xylem in June (image c). Red coloration of the secondary wall in developing cells is indicative for beginning of lignification (arrows in images a and b). Methods: TS (a, c), RS (b), BF (a through c). Bars = 50 µm. For abbreviations, see list at the legend to Fig. 3-2.

Moreover, three distinct zones of cell differentiation could be defined in the current xylem ring in June (Fig. 3.5d-g):

- A a zone of expanding cells (dxy1) where only some fully expanded vessel elements had birefringent walls (Fig. 3.5d-f; Fig. 3.6c);

- A zone of secondary wall development (dxy2), where all cells were birefringent and only the vessel elements and a few layers of vessel-adjacent cells had lignifying walls (Fig. 3.5d-g; Fig. 3.7); and
- A zone of lignified xylem (dxy3) where all cells were lignified and appeared fully developed (Fig. 3.5dg; Fig.3.7).

In dxy1, most of the expanding vessels were large, indicating that earlywood was still formed in June. Vessels with small diameters and developing secondary walls occurred near the cambium (arrows in Fig. 3.5df), which indicated that latewood formation was also initiated in June. Xylem deposition appeared completed in October in both 2006 and 2007.

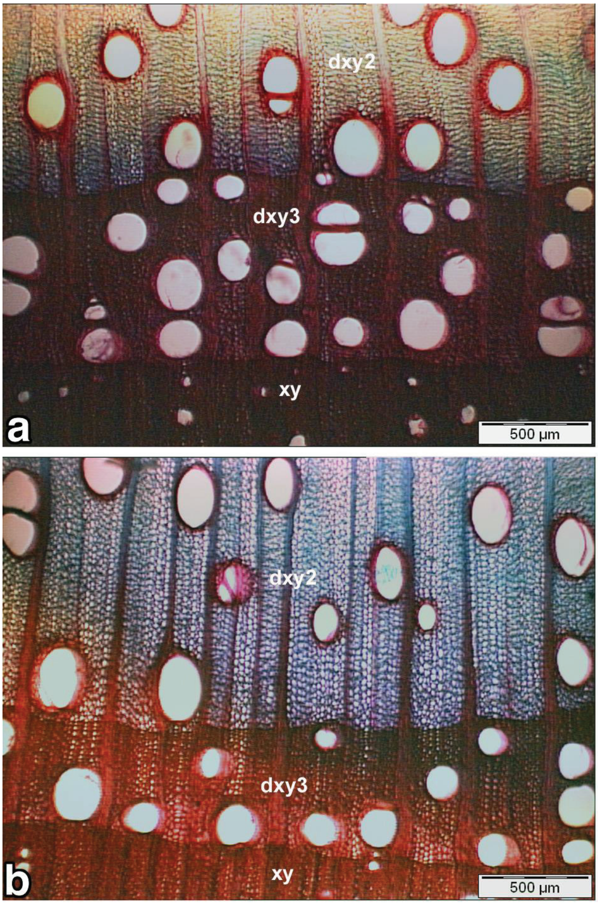


Figure 3.7. June samples of different individuals of teak showing a similar pattern of growth zone formation in the earlywood. Methods: TS and BF. For abbreviations, see list at the legend to Fig. 3.2.

3.2.5. Phloem differentiation

The inner bark of teak consists of alternating layers of sieve tube–companion cell complexes, ray and axial parenchyma cells, and fibre bands (Fig. 3.2 and Fig.3.8). These alternating sclerenchymatic and parenchymatic layers form regularly spaced phloem rings (Fig. 3.8c). The developed sieve tubes and fibres were easily distinguishable with their birefringent cell walls from the parenchymatic tissue and cambium (Figs 3.2d and Fig. 3.5ef). Two or three layers of axial parenchyma occurred at the inner and outer sides of each fibre band (note the dark non birefringent layer of cells between the phloem fibres and sieve elements in Fig. 3.2bd, and the less-stained layers of parenchyma cells in Fig. 3.8a). The axial parenchyma cells adjacent to fibres always contained prismatic crystals (arrows in Fig. 3.8ab).

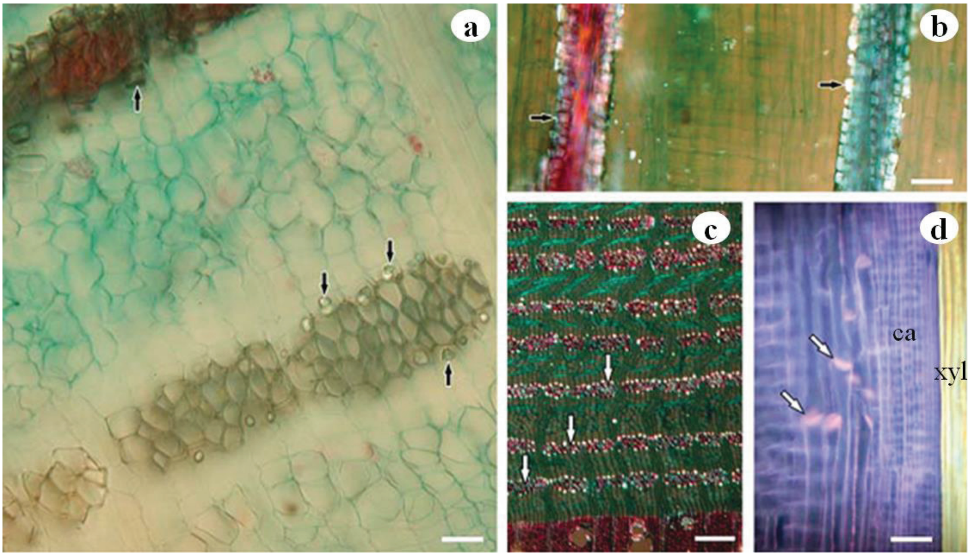


Figure 3.8. Development of phloem fibres of teak: Current-year fibres in June. Red colour indicates cell wall lignification and arrows point to developing crystals (images a, b). The cambium side is towards the bottom in (image a), and to the right in (image

b). Sample in January (image c) with arrows pointing to growth rings in phloem marked by phloem fibres. Sample in February (image d) with arrows pointing to sieve plates with callose. Methods: TS (a, c), RS (b, d), BF (a, b), PL (c), FL (d). Scale bars: (a) = 20 mm, (b) = 50 mm, (c) = 200 mm, (d) = 40 mm. Abbreviations are as in the legend to Fig. 3-2.

In the November-February samples, the sieve elements in all phloem rings contained callose at their sieve plates, which was detected by blue fluorescence (Fig. 3.8d). Callose disappeared from the inner rings during the growing season. Development of new phloem started at the end of February simultaneously with the initiation of the growth of new xylem cells (Fig. 3.2b; Fig. 3.4b). Developing bands of phloem fibres, which mark a growth ring boundary, were firstly seen in the April samples (Fig. 3.2c and Fig. 3.54b). The formation of new phloem was more intensive in May and June when trees were in full leaf at the peak of the rainy season. In the June samples, a second phloem layer was developing despite the fact that not all fibres from the previous phloem ring had completed differentiation (Fig. 3.5e and Fig. 3.8ab; Fig. 3.6c). In Fig. 3.5e, the two developing phloem fibre layers of the current year are indicated with the letters 'df'; note also the occurrence of lignified (Safranin-stained) and non-lignified (unstained) fibres in the first-formed ring of phloem. The size of developing crystals in the parenchyma cells adjacent to fibres was indicative of the stage of fibre development. For example, the small crystals and thin fibre walls in Fig. 3.8a show an early development and undifferentiated fibres of the second phloem ring in June.

3.2.6. Formation of annual xylem growth rings (AXGRs) and xylem growth zones (XGZs)

The transition between earlywood and latewood within AXGRs is characterized by a gradual change of vessel diameter, whereas an abrupt shift in vessel diameter marks annual ring boundaries (Fig. 3.9ab).

Measurements of vessel diameter defined latewood zones with a mean vessel diameter of 110.2+8 mm and earlywood zones with a mean vessel diameter of 212.5+13 mm. These vessel characteristics of the growth increment determine the ring-porous/semi-ring-porous feature of teak wood and the distinct pattern of the annual growth rings. In addition, AXGR boundaries were marked by an abrupt change from thick-walled and flattened terminal fibres at the latewood side of the growth ring boundary to initial axial parenchyma at the earlywood side (Fig. 3.9b; Fig. 3.10aef). In contrast, thin-walled axial parenchyma at the XGZ boundaries was usually not found, or, if present, it was confined to not more than 2–3 layers of cells (Fig. 3.9e;

Fig. 3.10b-d). The AXGR consisted of mostly earlywood and smaller proportions of latewood (Fig. 3.9a).

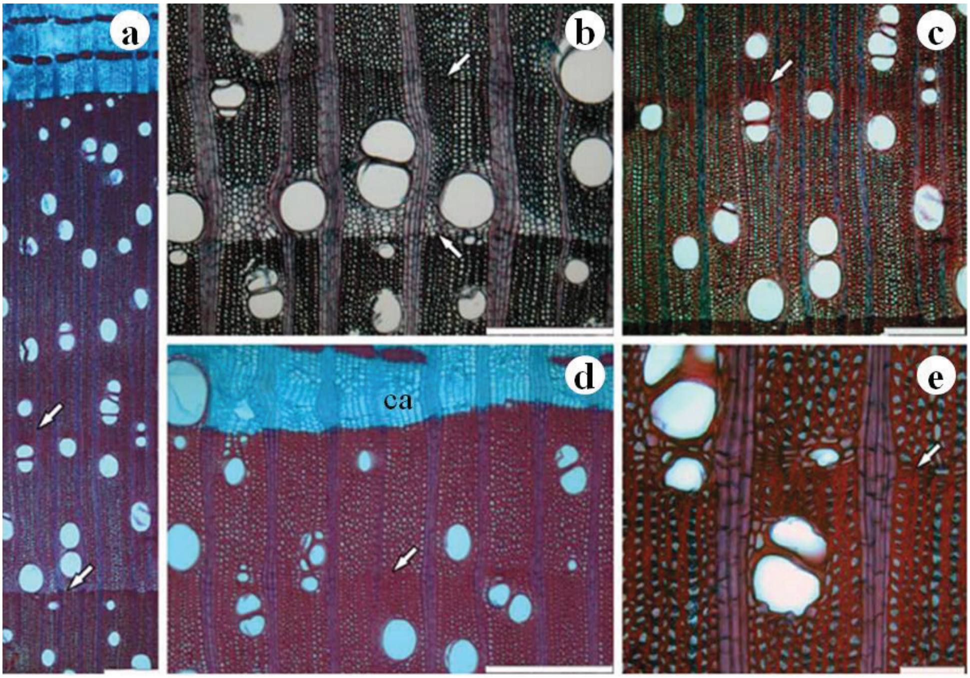


Figure 3.9. Variations in the morphology of xylem growth zones (XGZs) in teak: The current annual xylem growth ring (AXGR) of a sample in December 2007 (image a) with the lower arrow pointing to the previous AXGR boundary and the upper arrow pointing to an indistinct XGZ marked by a variation in the fibre cell wall thickness. Distinct XGZ boundary (upper arrow) in the earlywood of a sample in October 2006 (image b) where the distinct XGZ boundaries are marked by variations in vessel diameter, flattened fibre cells and tangential widening of rays. The lower arrow points to the previous AXGR boundary. Note the difference in structure between the XGZ boundary and the AXGR boundary (for discussion, see text). Image (c) shows an enlarged view of the sample in image (a) showing the indistinct XGZ boundary (arrow). Image (d) shows distinct XGZ boundary (arrow) in the latewood of the previous AXGR of a sample in March 2008. Image (e) shows an enlarged view of the XGZ boundary (arrow) of the sample in (d). Methods: TS and BF. Scale bars: (a-d) = 500 mm, (e) = 100 mm. Abbreviations are as in the legend to Fig. 3.2.

The samples of developing xylem in June showed that most of the AXGR, the entire earlywood plus several cell layers of latewood, was already deposited by the end of June (Fig. 3.5d). In the fully differentiated AXGRs, vessels with small diameters, such as those shown by arrows in Fig. 3.5df, occur near the growth ring boundary within 15 % of the entire width of the annual increment (Fig. 3.9a). This observation indicates that the outer 15 % of the AXGR, which is composed of latewood, is formed in the period July-October.

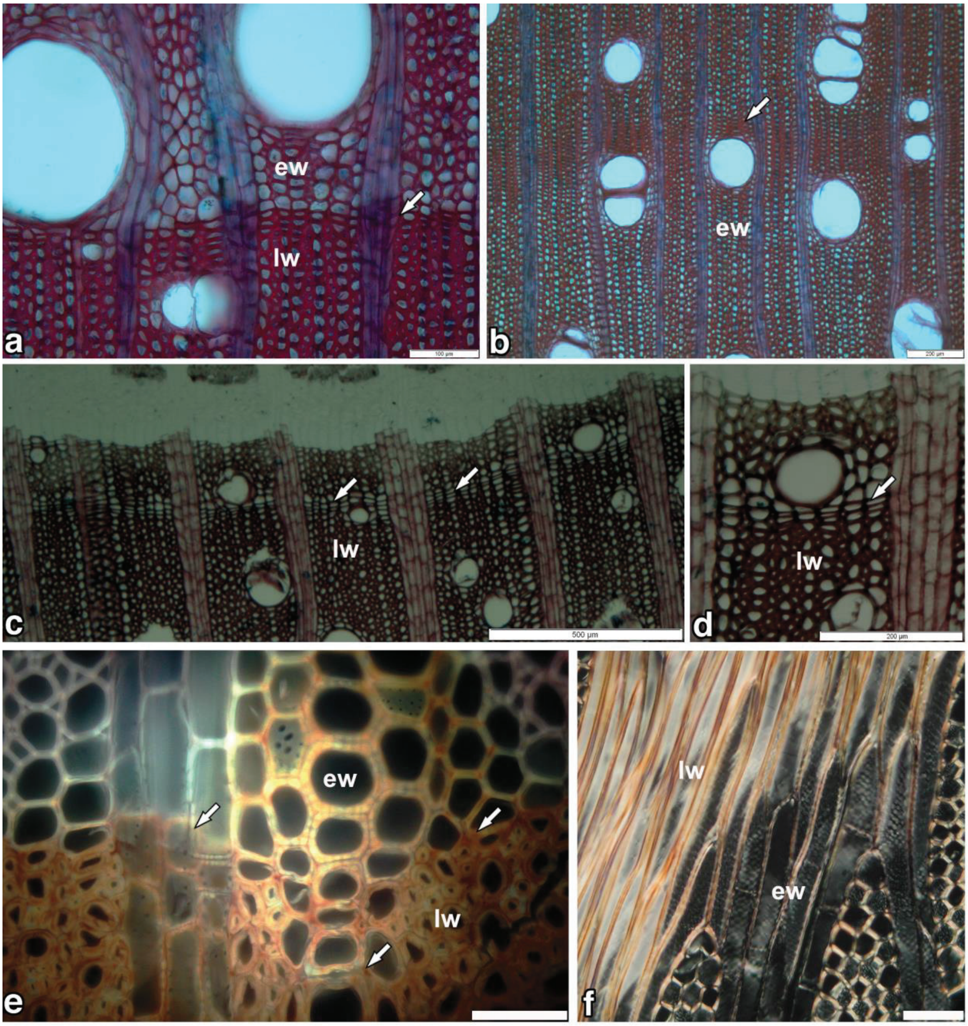


Figure 3.10. Growth zones and growth ring structure in teak: An annual growth ring boundary (arrow) between latewood and earlywood (a). Indistinct growth zone boundary in earlywood (arrow) marked by a variation in fiber cell wall thickness (b). Distinct growth zone boundary (GZB; arrows in images c and d) in latewood where the GZB is marked by flattened terminal fibers and initial layers of axial parenchyma. Image (e) shows the formation of true annual growth ring boundary (arrows) in April. The initial layers of the new annual ring contain axial parenchyma with distinct pits in thickened cell walls. The differentiation of the cells in the middle (marked ew) is advanced (thicker and safranin-stained cell walls) relative to the

cells at the left and right. Image (f) shows an oblique tangential longitudinal section through an annual ring boundary showing latewood fibers (lw) and axial parenchyma (ew). Methods: TS (a through e), TLS (f), BF (a through d), FL (e), PL (f). Bars = 100 µm (a), 200 µm (b, d), 500 µm (c), 50 µm (e, f). For abbreviations, see list at the legend to Fig. 3-2.

A careful observation of dxy3 in all three sampled trees in June (Fig. 3.5dg; Fig. 3.7) revealed a tendency for a decrease of the vessel size from the beginning towards the end of the dx3 zone. The widths of the dxy3 zones as well as the small shift in vessel size were similar to those in the developing xylem in the April and May samples (Fig. 3.5bc), indicating that dxy3 zones were formed prior to May during the development of new leaves. Moreover, dxy3 appeared as separate growth rings because of the different developmental stages of the fibres and different vessel sizes on both sides of the dxy3/dxy2 boundary (see Fig. 3.5d; Fig. 3.7). These growth increments (dxy3) are XGZs and not false annual rings because they were distinct in structure from the true annual rings (for definitions, see the Materials and Methods). The most apparent difference between AXGRs and XGZs was that the vessels at the end of the dxy3 zone were considerably larger than the typical latewood vessels (see xy zone, Figs 3.5d and Fig. 3.9ab; Fig. 3.10a).

Similar XGZs in the initial part of the earlywood in 2007 were found in each of the nine sampled trees after June 2007 (100 % incidence). Distinct XGZs were also seen adjacent to dormant cambium in two trees in December 2006 (Fig. 3.10cd). The occurrence of XGZs was investigated from 2006 back to 1971 in polished stem disks from ten trees of the same plantation. This observation revealed a high frequency of XGZs which were found in each year until the age of 14, and in 64 % of the years after the age 14 (Fig. 3.11). The results also showed that the incidence of XGZs among individuals decreased with age. Up to 14 years of cambial age, 45 % of the total number of annual xylem rings that we investigated had XGZs, and at between 15 and 35 years of cambial age the occurrence of XGZs was 12.4 % (Fig. 3.11).

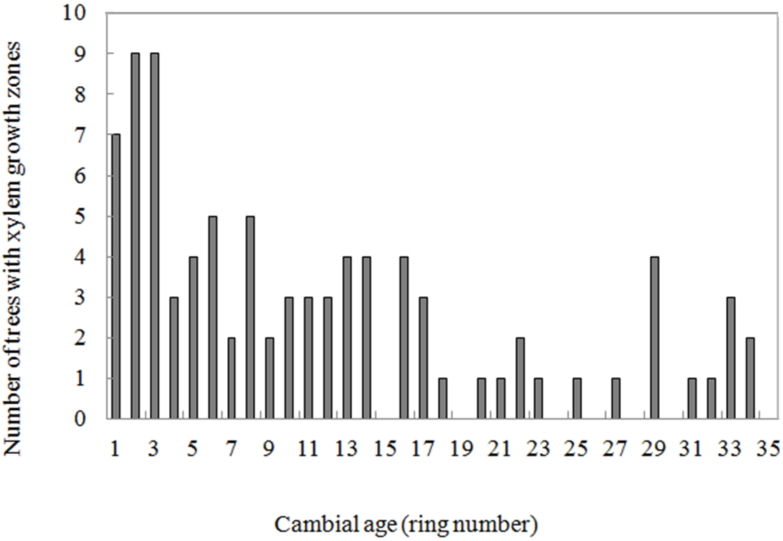


Figure 3.11. Relationship between tree age and the occurrence of intra-annual xylem growth zones (XGZ) in ten 35-year-old teak trees in the Séguié forest. This graph shows that XGZ occurred more in trees juvenile phase (1-14 years).

Unlike the true annual rings, the XGZs were variable in structure and often indistinct. Some XGZs were marked by differences in the wood fibre density (Fig. 3.9ac; Fig. 3.10b), or by several layers of flattened fibre cells (Fig. 3.9b; Fig. 3.10cd), also by slight widening of the rays and differences in vessel diameters in both sides of the growth zone borders (Fig. 3.9bde). The distinctiveness of the XGZs varied between trees and even within the same sample block, therefore, the XGZs sometimes appeared discontinuous. The XGZs were apparent when marked by variation in vessel diameters (Fig. 3.9bd), but could be easily overlooked when marked by variation of the fibre cell wall thickness (Fig. 3.9ac; Fig. 3.10b). However, the XGZs were easily identified in the samples of developing xylem increments because of the distinct developmental stages of the xylem cells on both sides of the growth zone borders (Fig. 3.5d; Fig. 3.7).

3.3. Discussion and conclusion

3.3.1. Seasonal changes of the cambial zone morphology

The occurrence of seasonal fluctuations of cambial activity and morphology has been well studied in temperate trees, but is comparatively little understood in tropical species (Barnett, 1992; Catesson, 1994; Larson, 1994; Worbes, 1995; Frankenstein *et al*., 2005; Rossi *et al*., 2006). Seasonal changes in cambial activity associated with seasonality of the climate have been reported for a number of tropical species in tropical Asia and Latin America (Venugopal & Krishnamurthy, 1987a,b; Fujii *et al*., 1999; Rao & Rajput, 2001; Worbes, 2002; Yáñez-Espinosa *et al*., 2006; Venugopal & Liangkuwang 2007; Marcati *et al*., 2006, 2008; Patel *et al*., 2014) as well as in Africa (Amobi, 1974; Rogers, 1981; Worbes *et al*., 2003; Verheyden *et al*., 2004; Schmitz *et al*., 2008). Studies dealing with teak cambial activity have been restricted to its natural area of distribution (Rao & Dave, 1984; Priya & Bhat, 1999; Rao & Rajput, 1999).

In deciduous teak in India, Rao and Rajput (1999) found 6 cell layers in dormant cambium and 10 or 12 cell layers in the reactivation phase and during the full active phase, respectively. In another study highlighting an effect of moisture conditions, Priya and Bhat (1999) counted 6–10 cells in the dormant cambial zone of irrigated teak, 11–14 cells in the reactivation phase and 15–20 cells in the full active phase. Variations in cambial cell number could be the result of differences in the age of the investigated trees. The reports so far often include young trees, while more research would be needed to reveal the effects of cambial age on the cambial structure. Moreover, our study showed considerable variations in the width of the cambial zone between individual trees of the same age and growing on the same site. The inter-trees variations of the cambial features, we observed, could be attributed to the ability of each tree to detect the restoration of the favourable site conditions and to use the available resources essential to a growth resumption after an environmental cambial quiescence.

Our results showed statistically significant annual fluctuations in the thickness of the cambium (CZ and FC) in teak following the transitions from wet to dry periods. These fluctuations of cambium size could be explained by changes in the mitotic activity and the number of cambial cell layers, and they showed the active and dormant periods of cambial activity. Furthermore, the widest cambial zone occurred simultaneously with the widest zones of differentiating xylem and phloem. Hence, the widest cambial zone in June morphologically represented the most active period for stem diameter growth when most of the current growth ring was deposited (Fig. 3.5de). Independent measurements with dendrometers in this teak plantation also showed the occurrence of a steep increase in the intensity of radial growth in June (Séguié Forest Management Plan, internal document).

Teak grows naturally in monsoonal climates characterized by high precipitation during half of the year and long dry periods during the other half (Suzuki *et al.*, 2007). In contrast to the Asian natural growth sites of teak, the Séguié site experiences a shorter dry season, less cumulative rainfall during the rainy period, and a 1 or 2 month second small dry period. Regardless of the occurrence of the short dry season in August, the growth of the vegetation lasts about 8–9 months from the end of February until October or November. In addition to the rains, the availability of ground moisture is probably substantial (N'Go *et al.*, 2005). It is noteworthy that cambial reactivation started at the end of the dry season in February when precipitation was still low, and xylem and phloem formation had ceased in October when precipitation was still relatively high. These facts are suggestive of a complex physiological and genetic regulation of the duration of radial growth in Séguié teak. Despite the fact that secondary growth had stopped, the cambium in October and November was statistically thicker than the cambium in December and January, which might be an indication that due to favourable moisture conditions the cambium in November was not yet in the resting stage.

As discussed earlier, dendrometer measurements showed that growth activities reach their peak during the precipitation peak, which is in June (for the entire Southern part of the country and our study site location) and in July (for the deciduous forest zone: Central-West of the country). Growth activities stop in September–October. These observations have allowed the establishment of management strategies in teak plantations. Therefore, forest inventories (diameter and height measurements for wood biomass estimate) take place at the onset of the dry season (December) when there seems to be no growth of trees. In this way, the annual growth increment that has started with the onset of rains (March in the case of the Southern part of the country) can be measured (Dr Anatole Kanga, Centre National de Recherches Agronomiques, previously CTFT: Centre Technique Forestier Tropical, pers. comm.).

3.3.2. Xylem growth zone (XGZ) formation and structure

Teak is an interesting model species for studying how growth rings develop in tropical trees because it forms distinct ring porous rings as well as XGZs and variations in xylem structure.

For example, it was found that irrigated trees form diffuse porous rings in the juvenile phase (Priya & Bhat, 1999). The same authors reported that old trees show a shorter duration of annual cambial activity than juvenile trees and suggested that this could explain the absence of pronounced ring porosity in very young trees. The annual nature of the ring porous xylem rings in teak is well documented in Asia (cf. Somaru *et al*., 2008; Managave *et al*., 2011, and references cited therein). However, surprisingly little information is available on the intra-annual pattern of xylem formation.

Priya and Bhat (1998) identified four types of false rings in young teak trees (from 1 to 12 years old) based on anatomy and location within annual rings. The XGZ at the initial part of the AXGR in our study corresponded to variations of the 'false ring types 1, 2, or 3' described by Priya and Bhat (1998). Some of the XGZs that we observed in the latewood were similar to the 'false ring types 3 and 4'. Because the XGZs in our samples were very distinct in structure from the annual rings, we refer to them not as 'false rings' but a 'growth zones' for consistency with the definitions proposed earlier in the Materials and Methods.

Our observations in teak confirmed the results of previous studies of many different species that have shown the vessel elements to be the first cells to expand and form lignified secondary walls, attributed to their importance in water conduction (Suzuki *et al*., 1996; Kitin *et al*., 2003; Marcati et al., 2006) or the pattern of auxin transport (Ridoutt & Sands, 1994). When development of new leaves initiated in March, a partial wall lignification was evident in fully expanded new vessels but not in the surrounding developing fibres (Fig. 3.5a; Fig. 3.6). Therefore, the new xylem in March was not completely functional for water conduction because lignification is necessary for the proper functionality of woody cells (Hacke *et al*., 2001; Plomion *et al*., 2001; Voelker *et al*., 2011). SEM observation of vessel elements with developing secondary walls revealed perforation-partition membranes (Fig. 3.6b), which were not present in fully developed vessels. Fibres close to vessels iniated the secondary wall development earlier than those further away, similarly to the results of Ridoutt and Sands (1994) in eucalypts. It is possible that these early lignified fibres can assist vessels in their function of hydraulic conductance.

Formation of XGZs at the beginning of the growing season clearly coincided with the period of leaf growth, and these XGZs were fully developed at full leaf before the most intensive radial growth. It was previously proposed that insufficient rainfall soon after the onset of cambial activity might be the reason for intra-annual rings within earlywood (Priya & Bhat, 1998;

Palakit *et al.*, 2012). However, the monthly rainfalls in the Séguié teak plantation during the course of our study were typical for the region (increasing from February to May in each of the 3 study years) and sufficient for growth. Therefore, we propose that the XGZs at the start of the annual rings in our sampled trees might be a physiological response to the new foliage growth and to an increased demand for xylem water transport. In the same samples, tyloses were observed in the previous-year xylem, suggesting that older xylem rings were not fully functional. The early maturation of the XGZs in June (dxy3 in Fig. 3.5) may indicate that new functional xylem is needed to provide the water transport at an accelerated transpiration rate and diameter growth in full leaf. Similarly, in temperate ring-porous woods, early development of new functional xylem takes place before the full-leaf phenological phase of the seasonal development (Funada *et al.*, 2001; Kitin *et al.*, 2003). Xylem with ring-porous growth rings is compartmentalized structurally and physiologically, which is regarded as an advanced safety feature for water transport in climates with distinct seasonality of moisture availability (Tyree and Zimmermann, 2002; Kitin *et al.*, 2004; Ellmore *et al.*, 2006).

As described earlier, the wood formation in May was slow, which was not related to a decrease in the moisture availability because monthly precipitation was in fact increasing from February to May in each of the study years. New leaves were growing in May, which may have diverted photosynthetic assimilates toward foliage development at the expense of radial growth. In contrast, a sharp increase in the rate of wood deposition was observed from the end of May to June, after the new foliage was fully developed. Our microscopic observations were in accordance with results from several years of dendrometer measurements in the same plantation which have shown significant increases in the rates of diameter growth after the trees develop full leaf (Séguié Forest Management Plan, internal document).

Formation of distinct XGZs was frequently observed in young trees. During the first 3 years of cambial age, XGZs were present in almost all growth rings of the investigated trees (Fig. 3.11). Similarly, Priya and Bhat (1998) observed that 73 % of 8-year-old teak trees displayed intra-annual growth rings in their second annual increment. In another sample of nine 12-year-old trees, the maximum numbers of intra-annual rings were found in the second and third annual rings (Priya & Bhat, 1998). It is generally agreed that physical factors, such as drought during the growing season, which may disturb the normal activity of cambium, may also trigger formation of false rings. Priya and Bhat (1998) showed that induced drought during the growing period, as well as transplanting, causes formation of false rings in 1-year-old seedlings. Younger trees are more likely to be influenced by physical disturbances which could explain why the frequency of XGZs was negatively correlated with cambial age (Fig. 3.11). In addition to direct physical factors, the developing xylem in young tree stems is strongly influenced by hormonal signals from the leaves (Aloni, 2010).

The XGZs in the earlywood were easily observed in the June samples of developing wood because of the distinct differentiation stages of the wood increments before and after May (dxy2 and dxy3 in Fig. 3.5 and Fig. 3.7). The XGZ boundaries can become indistinct in fully developed annual rings, but through careful observations we were able to detect them in the earlywood zone in all other trees during the study years 2006 and 2007 (Fig. 3.9a-c; Figs 3.7 and Fig. 3.10b). In our study, as well as in previous reports (Priya & Bhat, 1998), XGZs were observed in the latewood of teak. Compared with the XGZs in the earlywood, those in the latewood were always distinct and easier to detect in microscope slides or disks (Fig. 3-9de; Fig. 3.10cd). In two of our samples from December 2006, the occurrence of XGZs at the end of the annual rings might be related to a temporal interruption of the cambial activity due to the exceptional drought in August 2006 (10 mm monthly precipitations). However, the response to drought is either varied among individuals or the XGZs form incomplete rings, because the other sampled trees in 2007 and 2008 did not display XGZs in the latewood of 2006.

Growth anomalies resulting in the formation of xylem growth zones and false rings affected trees more and most often during the juvenile growth phase (1-14 years; see Fig. 3.11). The occurrence of these anatomical structures seem to reflect the ecophysiological flexibility of trees juvenility

3.3.3. Differentiating phloem

The phloem structure in teak is characterized by distinct phloem growth increments that have relatively equal thickness. Our observations, together with investigations in different locations in India, indicate that secondary phloem and xylem differentiation initiate simultaneously or within a month after the emergence of new leaves (Venugopal & Krishnamurthy, 1987b; Priya & Bhat, 1999; Rao & Rajput, 1999). Similar phloem differentiation patterns in relation to the phenology were reported for other tropical species in seasonal climates (Rao & Rajput, 2001; Marcati *et al*., 2008). In addition, our study showed that teak trees form at least two growth increments of phloem during one growing season. Therefore, the last two or three phloem growth increments always contain relatively new phloem with non-collapsed sieve elements. An interesting observation which would need additional investigation was the occurrence of callose in all phloem rings during the dormant period but not in the inner phloem rings during the growing period. A characteristic of teak phloem is the consistent occurrence of crystals in the adjacent-to-fibres parenchyma cells. The dimensions of those crystals together with the thickness of the fibre cell walls vary during the growing season and indicate the stage of development of the corresponding phloem increment. We also observed the occurrence of callose in all phloem rings during the dormant period but not in the inner phloem rings during the growing period. Further focus should be given to this observation.

Conclusion

This study confirmed the annual nature of growth rings in teak, showing their potential for analysis of tree age, carbon sequestration and reconstructions of forest growth dynamics and climate. The most active cambium and radial growth occurred during the peak of the rainy season in June. Phloem formation took place simultaneously with the formation of xylem. At least two growth rings of phloem, marked by alternating layers of sieve tubes and sclerenchyma bands, were formed during one growing season. Morphometric features of cambial development, such as cambial zone width, number of tangential cell layers and width of the xylem differentiation zone, were strongly correlated with each other and showed a linear relationship with monthly precipitation.

Xylem growth zones were formed within earlywood or latewood of true annual rings. The annual xylem increments started with XGZs that were formed while new leaves of the semi-deciduous trees were developing and moisture conditions were favourable. When the trees achieved full leaf and radial growth rate accelerated, these XGZs were fully differentiated. The cause of the XGZ formation in earlywood remains to be experimentally identified. We propose that XGZs functional for water transport must be developed early in the growing season in order to supply sufficient water for increased transpiration, photosynthesis and radial growth when teak trees achieve full foliage. These XGZs can be easily detected in differentiating xylem, but their boundaries are structurally less distinct and may appear discontinuous in mature xylem. The XGZs are morphologically different from the true annual rings and represent a potential feature for intra-annual tree ring analysis.

Box 3.2. Supplementary data and relevant information complementary to chapter 3

The below information is obtained from additional observations carried out while investigating the wood formation in teak. The results thereof can contribute to have an insight into the physiological and structural changes occurring in the cambial zone along the vegetative season. We first focus on the presence of crystals in the monthly cambial samples in order to establish a correlation between crystals seasonality and cambium periodicity. Crystals seasonal appearance in the cambial zone has shortly been addressed in earlier studies carried out on teak and gmelina, two Verbenaceae species (Rao & Dave, 1984). Secondly we also examined the vessel walls pitting. As a highly climate sensitive species like teak reacts strongly to the site water availability. Vessels, as conductive elements, assure water uptake and its ascent through the stem to supply the functional organs. The features (lumen diameter, walls pitting and pit size variation) of these conductive elements represent a key to understand the mechanism through which a species can adapt to water deficit and prevent xylem cavitation. Inspite the amount of literature available on teakwood, the vessels anatomy and specifically vessels wall pitting has not been clearly addressed.

1. Seasonal presence of crystals and druses in the cambial zone

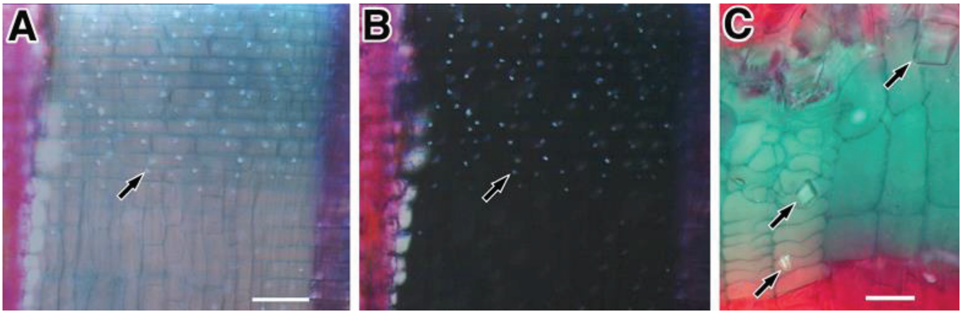
Both the transversal and radial sections showed scarcity or absence of crystals in the cambial cells by the onset of the dormant phase, ie in October-November (Supplementary table below: ST).

Table ST. Seasonal presence of crystals in teak cambial zone and in the differentiating tissues.

	October	November	December	January	February	March	April	May	June
Crystals	-	-	+ (fc-rc-dt)	++ (fc-rc-dt)	+ (cr)	++ (fc-rc-dt)	+ (dt)	++ (rc)	++ (rc)

- : absence ; +: presence/trace; ++: abundance; dt: differentiating tissues (xylem and phloem; rc: initials of the xylem ray; fc: fusiform cambial cells.

At the beginning of the dormant phase, crystals were stored in differentiating tissues (phloem and xylem) and not in the cambial fusiform cells. Few crystals were observed in December and they appeared abundant in the middle of the dry season (January) in the cambial zone, differentiating tissues and in the rays initials (see Table ST and Supplementary Fig. 1 below: S1).



S1. Crystals location and shape during the dry season (December) indicated by the arrows: radial and transversal views under conventional light (A and C) and radial view under fluorescence (B). Scale bars: A and B (100µm) and C (20µm).

At the onset of the mitotic activities (cambial reactivation), crystals appear in the cambial cells (February and March). They became rare and even absent in the cambial zone but are, rather, present in the differentiating tissues during the intensive growth activities.

Beside the anatomical changes occurring in the cambial zone, we observed a seasonal pattern in the crystals. At the onset of the dry season (October and November), the cambial zone was crystals free. Crystals appear in December and are abundant in January in the cambial initials as well as in the ray initials and in the differentiating xylem and phloem adjacent to the cambium. They were still visibles at the onset of the cambial reactivation and absent in the cambium during the active and full active phases. When they were present during the active phase, these crystals were observed only in the differentiation tissues.

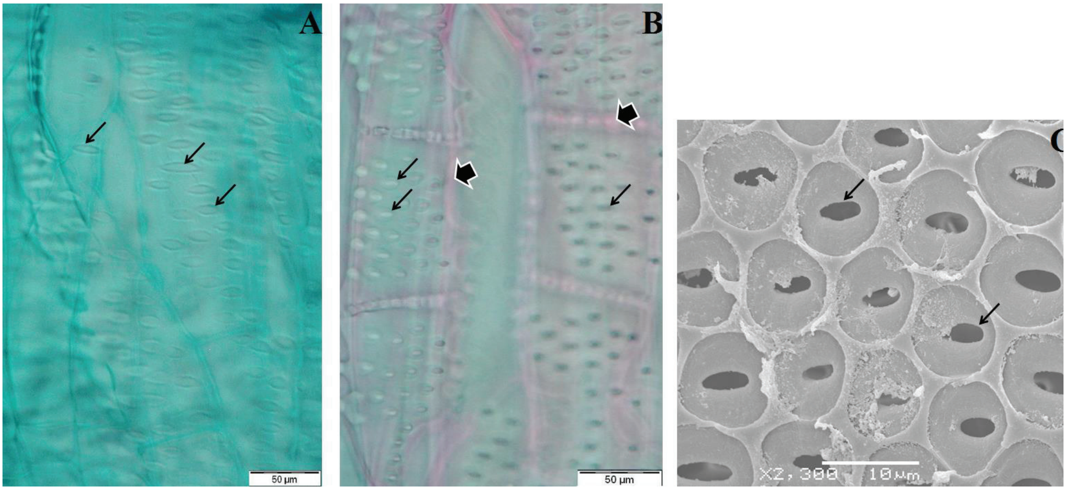
Previous works, dealing with crystals seasonal presence in *Tectona grandis* and *Gmelina arborea* (Rao and Dave, 1984), are similar to our observations. Other authors reported similar results in *Terminalia crenulata*, *Tectona grandis*, *Gmelina arborea* and *Citharexylum myrianthum* in different sites or countries (Venugopal & Krishnamurthy, 1987; Marcati & Angyalossy, 2005). All these studies are in agreement with Rao and Dave (1984) on the seasonal pattern of crystals in the cambial zone.

This preliminary study was not dealing with the discussion on the genesis, the development, distribution, and role of the crystals in teak cambial zone in Ivory Coast. However, our results (table in the above text box), in accordance with the previous ones, suggest that the minerals, resulting from a high cell metabolism, are sequestered in the form of crystals. In this way, crystals represent, an internal reserve that will be mobilized during the following vegetative season and used to support cell divisions and differention (Hepler, 1994; Fromm, 2011). This may be the physiological role of the crystals found in teak cambium which were previously identified as calcium oxalate and considered as the by-products of the species high metabolism (Rao & Dave, 1984). The crystallization of these minerals seems to help plants in preventing a cytosolic toxicity due to excessive mineral concentration (Bush, 1993; Marcati & Angyalossy, 2005). This, probably, explain crystals scarcity or absence in teak cambial zone during the reactivation, active and full active phases and their presence during the dry months.

On the other hand, crystals presence in the diffentiating tissues, at all the growth stages, indicates their role in the cell differentiation process, i.e, during the formation of the perforations plates (Hepler, 1994). Whereas crystals storage in phloem fibres indicates their contribution in the cell (fibres) wall hardening, in order to enhance the protective role of tree bark (Webb, 1999). This explains, probably, the relation between the crystals size and the differentiation stage of the corresponding phloem fibres (Fig. 3.8 in Chapter 3).

2. Wall pit size evolution and vessel maturation

Light microscopy and SEM observations provided details on the vessel wall structure development (Fig. S2). More stretched vessels pits were found on the primary wall with a tangential diameter of 15-25 µm (Fig. S2A) before the secondary wall deposition. The pit diameter decreased to 10 µm (Supplementary figure S2B), at the beginning of the wall lignification (indicated by thick arrows in Fig. S2B) and reached its final size (3-4 µm) in mature xylem (Fig. S2C).



S2. Different stages of xylem vessel pits diameter: Diameter of the elongated vessel pits before the secondary wall deposition (A: thin arrows), pits with reduced tangential diameter indicated by the tin arrows (B) observed during the lignification stage (B, thick arrows) and final pits diameter on mature vessels (C). Scale bars: A and B (50 µm) and C (10µm; x 2 300).

Teak vessels pitting has not yet been reported. The above illustrative description may indicate that the dimension and shape of the wall pits can reflect the developmental stage of the vessel maturation. This paragraph shows potential importance of teak vessel pitting. Further studies will be needed to examine the evolution of pits membrane and diameter of the functional vessels throughout the vegetative season. This approach can help to understand how teak, as a ring-porous species, can resist and cope under water limited conditions.

Chapter 4: Tree rings show a different climatic response in a thinned and a non-thinned plantation of teak (*Tectona grandis* L.f.) in West Africa

This chapter is based on the following paper:

Dié A., De Ridder M., Cherubini P., Verheyden A., Kitin P., Toirambe B.B., Van den Bulcke J., Van Acker J., Beeckman H, 2015. Tree-ring shows evidence of differences in climate response between a managed and non-managed plantation teak (*Tectona grandis* L.f.) in West Africa. IAWA J. 36(4): 409-427, DOI: 10.1163/22941932-20150111.

Abstract

Establishing large-scale plantations of teak could reduce the pressure on natural forests and sequester atmospheric carbon into durable wood. Understanding the growth dynamics of this species in plantations, outside its natural distribution area, is crucial for forest management. Stem discs of teak were collected in Ivory Coast at two sites, a non-managed plantation (Gagnoa) and a managed plantation (Séguié). All stem discs were processed using the standard dendrochronological methods in order to unravel the relationships between growth and climate.

Results showed that growth is slower in Gagnoa compared to the Séguié plantation that is being thinned regularly. In Gagnoa, trees responded positively to April rainfall, i.e., during the early stage of tree-ring formation, and negatively to September-October rainfall, i.e., during the short dry period. In Séguié, trees responded positively to July rainfall, i.e., during latewood formation, under decreasing rainfall. At both sites, tree growth was influenced by sea-surface temperature anomalies during the summer in the Gulf of Guinea. Teak growth in Séguié could be additionally linked to El Niño events, specifically during three major episodes (1976-77, 1982-83 and 1997-98).

Introduction

Teak (*Tectona grandis* L.f.), a fast-growing tree native to South-East Asia, which produces high-value timber, is one of the most widely planted hardwood species in the world, occupying 75% of the world tropical planted forests for high quality wood (Pillai *et al*., 2014). Teak is, to date, the most important precious wood species used in reforestation. It has become the most important source of high quality wood in Ivory Coast, a country ranked as the first teakwood producer outside Asia, in terms of exported volume (Koné *et al*., 2010). It is intensively grown in areas of dry forest (Bamoro), deciduous to semi-deciduous forest (Téné) and in semi-deciduous to evergreen forest (Mopri, Séguié) and in zones with diffent climate conditions (Dupuy *et al*., 1999; Kouadio *et al*., 2003). Having being used in intensive afforestation programs, to mitigate deforestation processes, teak plantations currently occupy almost half of the planted forests in Ivory Coast (Koné *et al*., 2010).

The climate in West-Africa, including Ivory Coast, is driven by the seasonal latitudinal displacement of the complex formed by the West-African Monsoon and the Inter-Tropical Convergence Zone (ITCZ). This displacement generates short-term and long-term rainfall anomalies between the Gulf of Guinea and the Sahel (Rodriguez-Fonseca *et al*., 2011). The ITCZ is, in turn, influenced by the teleconnection between sea surface temperatures (SSTs) of the Gulf of Guinea and the El Nino-Southern Oscillation (ENSO) (Kouadio *et al*. 2003; Balas *et al*., 2007; Joly *et al*., 2007).

As the first tree species used for tree-ring analysis, i.e., dendrochronology, in the tropics (Coster 1927; Berlage 1931; Pumijumnong 1995), teak has been proven to contain a strong climatic signal. Dendrochronological studies of teak resulted in tree-ring chronologies containing reliable information on local and global climate (Ram *et al*. 2011; Pumijumnong, 2012). Series of earlywood vessels of teak, also, revealed the effect of intra-annual climate influence on tree-growth (Pumijumnong & Park, 1999). In Ivory Coast, ongoing climatic changes are expected to affect teak growth at inter- and intra-annual levels.

Examining climate-growth patterns can, therefore, provide accurate knowledge on the short-term radial growth responses to climate. Information on growth dynamics of young trees can help the management of plantations subjected to short rotations or short lifespan (Dupuy *et al*. 1999). These plantations are becoming important since they represent a major timber source which satisfies the increasing demand of teakwood on the international market (Kollert & Cherubini 2012).

Tree-ring analysis of teak can also provide guidance for forest management, in terms of site selection for reforestation.

Our study is focussing on two sites, a non-managed plantation in a semi-deciduous forest area with rather stable annual precipitation and a managed plantation in a zone where the vegetation is, gradually, shifting from evergreen to semi-deciduous forest, with more fluctuating annual precipitation. We addressed the following questions:

(i) How does the variability in precipitation influence tree growth in the two plantations?

(ii) Is there a large-scale climatic signal in the tree-ring width in addition to the local precipitation signal? How are the sea surface temperatures (SST) and El Niño episodes influencing teak tree-growth?

(iii) What are the effects of thinnings on the tree ring patterns and climate responses?

4.1. Material and methods

4.1.1. Sampling sites and sample procedure

All study sites belong to the Guineo-Congolian regional centre of endemism (White, 1983) and they are situated in vegetation belts classified as semi-deciduous forest in Gagnoa and as evergreen moist rainforest in Séguié (Kouamé & Zoro Bi, 2010). The Gagnoa site is part of a teak plantation of the Centre National de Recherches Agronomiques (CNRA) in Central-West of Ivory Coast (Fig. 4.1). The plantation was established in 1966 on a sandy soil with poor water retention but with a superficial water table (N'Cho, 2001) with an initial stand density of 2500 stumps.ha^{-1}.

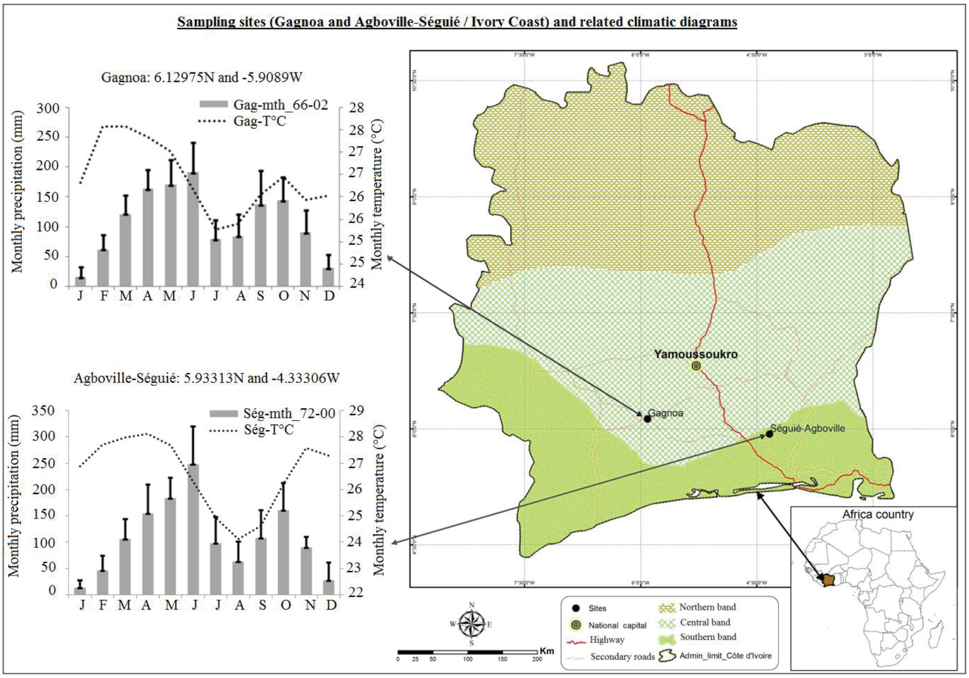


Figure 4.1. Localisation of the study sites within the different climatic zones with the respective climatic diagrams where the grey bars indicate the monthly precipitations with their intervals of confidence and the dotted lines, the temperature: Gagnoa (1966-2003) and Agboville-Séguié (1972-2000). Source: Kouadio *et al*. (2003) and Kouamé & Zoro Bi (2010).

The second plantation is situated in the Séguié forest in the Agboville province (South-East Ivory Coast). Trees grow on a hydromorphic soil mainly consisting of sand and clay (N'Go *et al*. 2005). The plantation was established in 1971 as part of the Séguié Forest Reserve (Forêt Classée de Séguié: FC-Séguié) and is under permanent sylvicultural management (thinnings and pruning) by the state forest company SODEFOR. Repeated thinnings (every 5 years) reduced the stand density from 2500-3000 stumps.ha^{-1} (initial density) to 79 trees.ha^{-1} (harvest time).

At both sites, trees were randomly sampled. Stem discs were taken at 50-70 cm above ground level from stumps of trees felled in August 2002 (Gagnoa) and August-September 2006 (Séguié) during logging campaigns. Thirty-four stem discs were obtained: 18 from Gagnoa and 16 from Séguié. All discs are accessible at the Xylarium of the Royal Museum for Central Africa in Tervuren (Belgium), with the exception of six, which are stored in the Laboratory of Botany of Cocody University (Abidjan, Ivory Coast).

4.1.2. Ring-width measurements and cross-dating

Stem discs were dried and polished using sand paper with a grit size of 60 up to 1200. Tree-ring widths were measured along four to eight radii per stem disc to cope with the irregular shape of most of the discs and measurements were taken to the nearest 0.01 mm under a stereomicroscope using the TSAPWin 0.55 software (Rinntech, Heidelberg, Germany).

Before measurement, all tree ring borders were marked with pencil under a stereomicroscope and every fifth ring was followed along the circumference in order to detect growth anomalies such as wedging rings and intra-annual growth zones that could mislead tree-ring delineation. When present, the growth anomaly was followed along the circumference and was identified as such through visual crossdating. These anomalies were archived and were, later, considered in the correction procedure during the subsequent ring analysis.

Crossdating ensures that each individual tree ring is assigned to the exact year of its formation. Visual crossdating was performed by matching patterns of wide and narrow rings between radii from the same stem disc and between trees from the same site. Successful cross-dating of several trees indicates the presence of a common external growth controlling factor (Cook & Kairiukstis 1990).

Two criteria were used to confirm the visual crossdating: The percentage of parallel run (p.p.r.), a non statistical parameter, which measures the year-to-year agreement of growth fluctuations. The t-value of Baillie-Pilcher (Baillie & Pilcher 1973), expressing the mediumwave year-to-year growth affinity between two time-series, was also used. The thresholds adopted by Trouet *et al.* (2010) for tropical species (i.e., ppr ≥ 60% and t-values ≥ 2) were considered in the present work, to conclude on the success of the crossdating.

The cubic smoothing spline was applied to detrend (remove the natural age trend) and to standardize the tree ring series (Cook *et al.* 1990). The mean sensitivity (ms) of these standardized series represents the extent to which the calculated chronology reflects local climate variations for each individual ring series. For each site chronology, the expressed population signal (EPS), which quantifies the degree to which the constructed chronology portrays the population chronology, was determined (Haneca *et al.* 2005; Wigley *et al.* 1984). An EPS value of 0.85 is considered as a reasonable limit for a reliable chronology and allows climatic influence analysis (Wigley *et al.* 1984).

4.1.3. Climate description

Rainfall data covering the periods 1966-2002 for Gagnoa (National Oceanic and Atmospheric Administration: NOAA) and 1972-2000 for Séguié (Société de Développement et d'Exploitation Aéronautique et Météorologique: SODEXAM-Ivory Coast) were used. Both sites show a similar pattern of yearly rainfall distribution with a major wet season (GW), extending from March to June, followed by the minor dry season (sd) of July-August. There is a minor wet season (sws) of September-November, preceding the major dry season (DS) of end November to February.

The minimal and maximum annual precipitations were recorded in 1992 and 1984 at Gagnoa (MinPrec. = 954 mm and MaxPrec = 1789 mm) and in 1983 and 1989 at Séguié (AnnPrec. = 773 mm and MaxPrec = 1928 mm). Gagnoa experienced severe drought in November 1972 and February 1980, leading to the dessication of the river passing through the teak plantation. Mean monthly relative air moisture content was 82 % in Gagnoa and 80 % in Séguié. A minimum of 77% and 60 % is recorded in February at Gagnoa and in December at Séguié.

4.1.4. Climate-growth relationship

The sylvicultural management has been a realistic option to sustain sustainable forest management and especially teak forestry in Ivory Coast. The present work intended to know how the applied sylviculture influences the species growth responses to the precipitation fluctuations in Ivory Coast. Because precipitation disturbances prevailing in the country are described as driven by the seasonal latitudinal displacement of the West African Monsoon and the Inter-Tropical Convergence Zone (Kouadio *et al*., 2003). Our research was not prompted by the need to study a detrimental effect of climate to teak growth in Ivory Coast. It rather aims (1) to provide tools to examine the species growth under predicted future climate change (IPCC, 2007) and (2) to assess the efficiency of the sylviculture in teak forestry in the country.

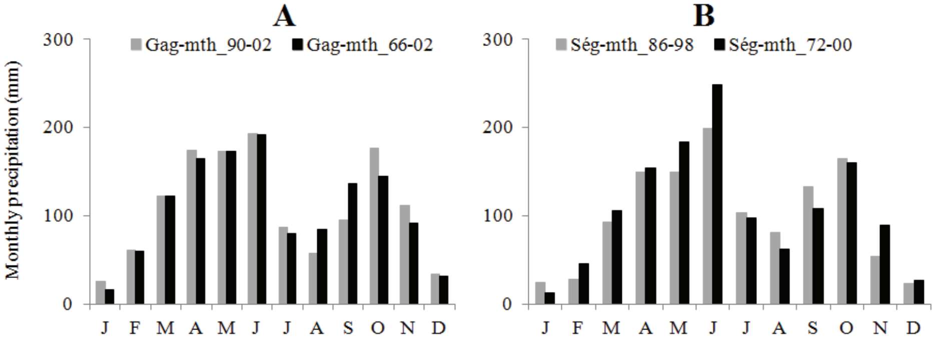
In order to consider the thinnings as the plausible factor explaining the differences in growth and climate sensitivity of teak between the two study sites, it seemed essential to show that these sites experience similar precipitation variables and site-index. A pairwise comparison test (ANOVA, $p < 0.05$) performed showed no inter-site difference in these variables (see figure S4.2 in Supplementary document 1 below). Previous research dealing with teak growth and productivity also indicated similar inter-sites precipitation conditions and site-index which represent the two main factor explaining teak growth and productivity in Ivory Coast (Dupuy *et al*., 1999).

The climatic influence on tree growth was, first, examined at the local level (study site) through correlations between monthly, seasonal and annual rainfall and the site chronologies. Then, the effect of the interaction between large-scale climate and local rainfall on tree growth was investigated. For that purpose, SST anomalies in the Gulf of Guinea were extracted from the KNMI explorer (Van Oldenborgh & Burgers 2005; Trouet & 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). Spatial correlation maps were calculated (over the period from 1970 onwards) between the annual Niño 3.4 index and gridded 1°x1°monthly and seasonal precipitation fields (CRU T.S3.0; Mitchell & Jones 2005). The close link between SST and El Niño indices explains the need to investigate a potential influence of each of these climate variables on site rainfall and tree growth. ENSO events were defined by 5-month running means of SST anomalies in the El Nino 3.4 region (51N-51S, 1201-1701W) exceeding +0.4 °C for 6 or more consecutive months (El Nino years) (Trenberth 1997). The correlations were studied, using DendroClim2002+ (Biondi & Waiku 2004).

Box 4.1. Supplementary information relevant for a reliable interpretation of the climate-growth responses of a thinned Teak stand

1. Meteorological data collection and inter-site climate comparison

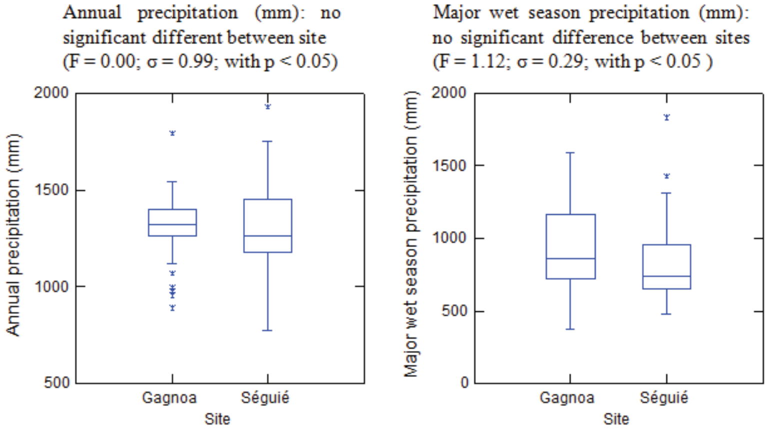
Rainfall data were first collected from the meteorological station of each forest site and covered the periods of 1990-2002 for Gagnoa (Gag-mth_90-02) and 1986-1998 for Séguié (Ség-mth_86-98). These short data sets (covering a shorter period of time) could not be used in DendroClim+2002 to analyze the influence of climate change on tree growth (Biondi & Waikul, 2004). Therefore, relative longer data sets were extracted from the broad scale climate sites namely the National Oceanic and Atmospheric Administration (NOAA) for Gagnoa and the Société de Développement et d'Exploitation Aéronautique et Météorologique of Ivory (SODEXAM) for Séguié. The longer data sets covered the periods of 1966-2003 for Gagnoa (Gag-mth_66-02) and 1972-2000 for Séguié (Ség-mth_72-00). Both data sets of each site showed a similar amount and similar pattern of monthly precipitation (Supplementary figure S4.1).



S4.1. Patterns of monthly precipitations variation between long and short datasets in Gagnoa (Gag-mth_66-02 and Gag-mth_90-02) and Séguié (Ség-mth_72-00 and Ség-mth_86-98).

A significant correlation was found between the shorter and longer data sets in each site ($p < 0.005$): $r = 0.786$ (Gagnoa) and $r = 0.736$ (Séguié). The below climate description and analysis are, therefore, based on the use of the longer precipitation data sets.

Annual rainfall was 1296 ± 204 mm in Gagnoa, located almost 300 km apart from the Atlantic coast and 1298 ± 249 mm in Séguié, situated at less than 100 km away from the coast. Gagnoa and Séguié respectively showed an average monthly rainfall of 167 ± 33 mm and 171 ± 37 mm during the major wet season (GW). Both sites experience two wet periods (GW and post wet season: September-November) and one major dry season of less than 5 months. Minimal annual rainfall of 954 mm and 773 mm was observed in 1992 at Gagnoa and in 1983 at Séguié. Maximal annual rainfall of 1789 mm and 1928 mm was recorded in 1984 (Gagnoa) and 1989 (Séguié). Furthermore, figure S4-2 shows no significant differences in the total annual and major wet season precipitation between the two sites.



Annual precipitation (mm): no significant different between site ($F = 0.00$; $\sigma = 0.99$; with $p < 0.05$)

Major wet season precipitation (mm): no significant difference between sites ($F = 1.12$; $\sigma = 0.29$; with $p < 0.05$)

S4.2. Comparison of the annual and major wet season precipitation between Gagnoa and Séguié (ANOVA): $F_{statistics}$ (F), observed probability (σ) and theorical or population probability (p).

2. Forest type and site index

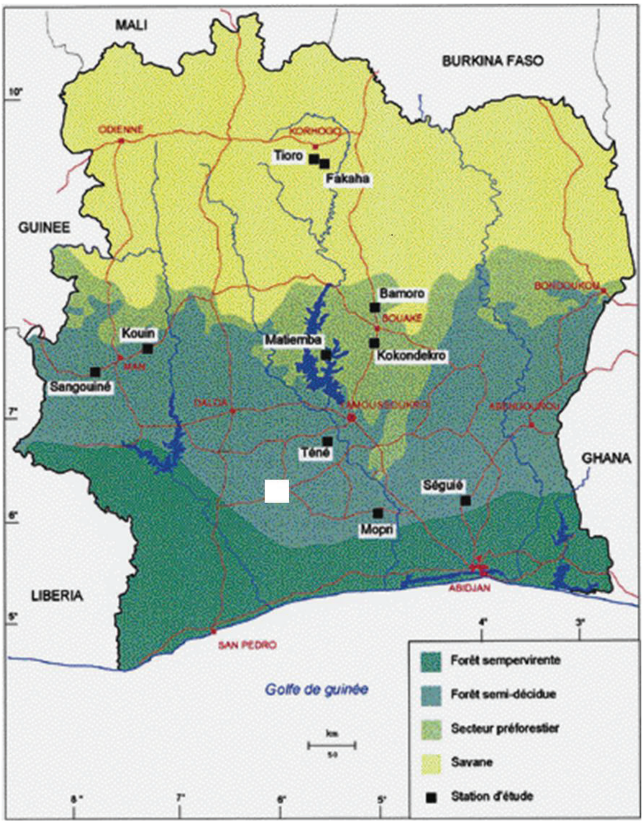
The present study mainly aimed to examine the growth rate and variations of teak and the effects of growth variations on wood structure in Ivory Coast. For that purpose, we selected the Forest Division of Séguié (Forêt classée de Séguié: FC-Séguié), situated in the south of the country, as a study site. FC-Séguié shelters the second largest teak forest next to that of Téné (Maldonado, 1999). FC-Séguié belongs to – and thus represents – the geographic zone where the species is said to show its best growth performances (Dupuy *et al*., 1999). Séguié teak stands received sylvicultural interventions (mainly thinnings) on the basis of 4-5 year interval. All the samples used in the present work to address the research objectives were, therefore, collected from the FC-Séguié.

At first, we intended to sample in a non-thinned stand in Séguié near by the thinned one, in order to assess the climate-growth responses of teak under sylvicultural treatments through a comparative tree-ring analysis. Unfortunately that intention could not be fulfilled, since all the teak stands of FC-Séguié are under sylviculture. We therefore opted for the Gagnoa teak plantation – a non-thinned stand – as a reference site. Gagnoa teak received no sylvicultural treatment since the plantation was established.

According to previous studies on teak growth and productivity, both Gagnoa and Séguié belong to the dense forest zone reputed to be the most appropriate for the species (see below figure S4.3 taken from Dupuy *et al*., 1999). Although a recent publication seemed to present the Gagnoa vegetation as semi-deciduous and that of Séguié as evergreen (Kouamé & Zoro Bi, 2010). We described our study sites vegetation based on this recent publication.

In their research, Dupuy and co-authors (1999) defined the dense forest zone as a vegetation experiencing:

- A total annual rainfall amount higher than 1200 mm/yr
- Two wet seasons
- One dry season of less than 5 months
- A water deficit less than 600 mm/yr



S4.3. Phytogeographical subdivisions of the Ivorian vegetation in relation to teak growth (Dupuy *et al*., 1999). The white square represents the Gagnoa province.

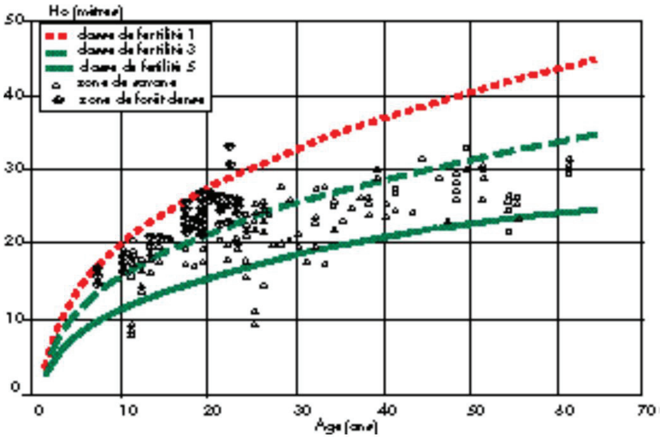
In regard to our climate description, the two study sites belong to this same dense forest zone characterized by the site index presented below (productivity in relation to soil fertility: Supplementary figure S4.4).

Yellow area: Sudano-Guinean savanna

Light-green area: Preforest zone

Blue and dark-green area: Dense forest

The annotations of this figure remain in French as they appear in Dupuy *et al*. (1999) because the map is not the result of my own data processing. This is also the case of figure S4.4.



S4.4. Distribution of the dominant height in relation to tree age and to forest type (Dupuy *et al*., 1999)

From the vegetation map (figure S4.3) and the distribution of teak productivity in relation to soil fertility (figure S4.4), Gagnoa and Séguié are considered as showing a similar site index typical of the dense forest zone, although no sampling was specifically made in the Gagnoa stand.

3. Take home message on the climate-sylviculture-growth related remark

As a conclusion, the two sampling areas show a similar (but certainly not identical) site index and climate which represent the two main parameters essential to teak growth and productivity in Ivory Coast (Dupuy *et al*., 1999). In such a case where the two sites experience similar growth conditions, we can admit that the sylvicultural treatments (thinnings in our case) remain the only major factor that can explain differences in ring widths variations, growth synchronicity and growth sensitivity to climate between Gagnoa (non-thinned stand) and Séguié (thinned stand).

4.2. Results

4.2.1. Tree-ring characteristics and growth anomalies

At both sites, teak formed distinct annual growth rings and shows (semi-) ring porosity (Fig. 4-2AB). The growth boundary is marked by a parenchyma band and by a sharp transition between previous ring latewood (average vessel diameter of 110 µm) to the current ring earlywood (average vessel diameter of 212 µm). The ring border is also marked by locally expanded xylem rays. Almost all trees exhibited diffuse-porous wood in the first five growth rings (around the pith) with small vessels regularly distributed from the earlywood to the latewood with sparse axial parenchyma. Wood structure of these most juvenile rings made the ring delineation somewhat difficult. The visual crossdating, therefore, helped in accurate ring demarcation.

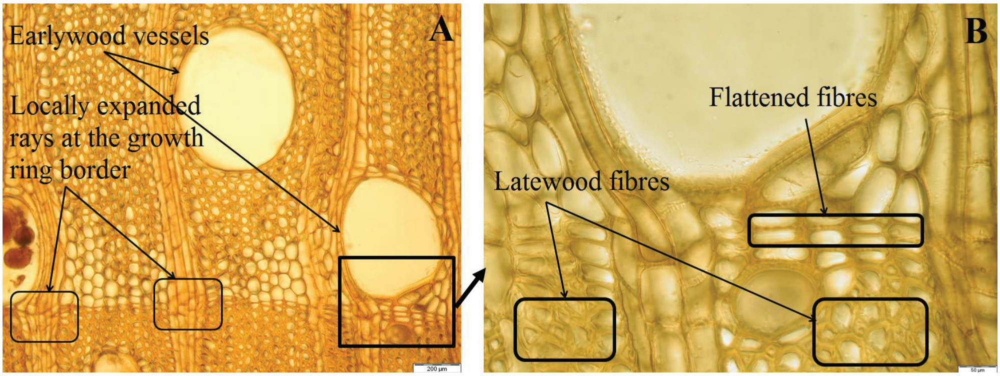


Figure 4.2. Anatomical structure of a tree-ring boundary. Both panels show rays distension and wide diameter earlywood vessels in plantation teak from Ivory Coast. Low magnification of the growth boundary (A). High magnification showing the thick-walled fibres in the latewood of the previous ring (B). Scale bars: 200µm (A) and 50µm (B).

The total number of tree-rings of each site corresponded to the age of the related plantation. At the sampling dates (August 2002 for Gagnoa and September 2006 for Séguié), the last growth ring of the current year was in an advanced stage of its formation. This is due to the fact that the teak cambium is reactivated with the onset of the major wet season (Dié *et al.*, 2012)

Gagnoa samples displayed more frequently wedging rings in comparison to Séguié where trees mostly exhibited intra-annual xylem growth zones (XGZ) morphologically different from the true annual ring (Fig. 4-3). The wedging ring refers to a true annual ring. Its limit appears on some growth segments around the pith and is locally absent in other segment(s). In the XGZ the axial parenchyma, surrounding the true ring boundary, is usually sparse or absent.

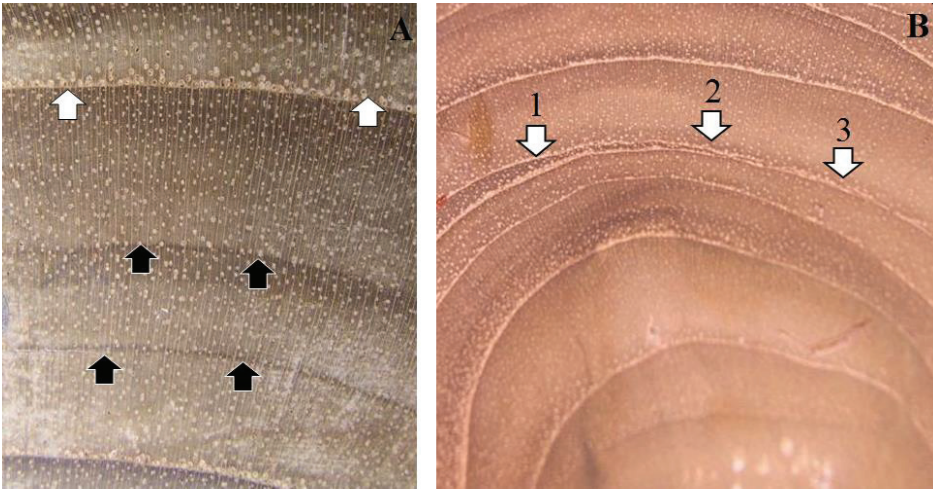


Figure 4.3. True tee-ring characteristics and ring anomalies under the stereomicroscope. The dark arrows point at the borders of the intra-annual xylem growth zones (XGZ in A) and the white arrows indicate the true growth boundary (A). White arrows of panel B show the merging of two true ring limits resulting in the phenomenon of wedging/missing ring (B) and finally merged ring boundaries (arrow 3). A (5 mm), B (1 mm) and C (500 µm).

4.2.2. Radial growth and crossdating

More noticeable inter-annual variability in the raw ring-width data was observed at the Séguié site (CV = 67%) compared to the Gagnoa site (CV = 43%). As in the mean raw ring-width series (Fig. 4.4A), higher magnitudes of variation were detected in the year-to-year tree-ring index chronology of Séguié compared to Gagnoa (Fig. 4.4B). The Tukey multiple mean comparison showed a significantly higher mean ring width at Séguié than at Gagnoa ($p < 0.05$). The widest rings, of 9.2 and 20.2 mm, were formed during the early stages of the trees' life, i.e., in 1970 and 1972, corresponding to the 5th and 2nd growth years at Gagnoa and at Séguié, respectively. The narrowest rings were observed, not in the most mature stem part, but in the 16th and 13th years, i.e., in 1980 at Gagnoa in 1983 at Séguié. In addition, the tree growth was reduced at both sites in the following years: 1977, 1983, 1990-1995, 1998 and 2000.

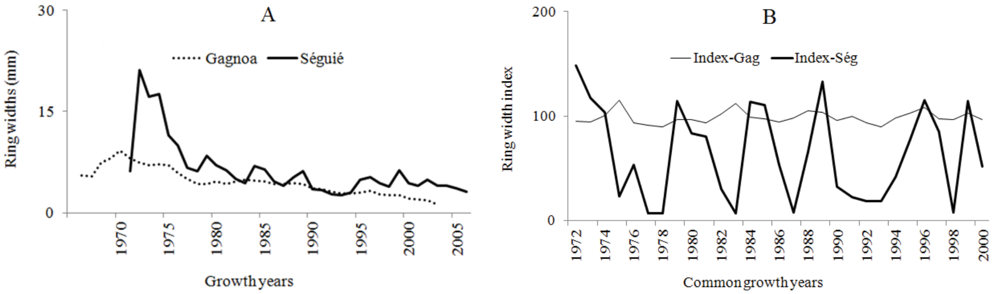


Figure 4.4. Mean raw ring-width series (A). Site chronologies (B). Dotted line represents growth parameters in Gagnoa and the solid line indicates those of Séguié in both figures. The most juvenile rings (first 5 and first 2 rings for Gagnoa and Séguié, respectively) included when estimating the wood production (A) were excluded from the chronologies (B) for the climatic analysis purpose.

A strong tree age effect, reflecting the natural biological declining growth trend, was observed in the raw ring-width at both sites (Fig. 4.4A) and confirmed by the high values of autocorrelation (AC) before standardisation (table 4.1). In addition to the age effect, a periodicity in growth recovery is detectable, every 4-5 years, in the Séguié site chronology from the 5th growth year.

Table 4.1. Results of cross-dating and standardization (mean values from each parameter). The ppr and $T_{v\text{-}BP}$ are the averaged values obtained from all possible pairs of comparisons.

	p.p.r. (%)	$T_{v\text{-}BP}$	Mean	Stdev	ac (1)	EPS	ms
Gagnoa	63	2.5	0.99	0.28	-0.08 (0.58)	0.32 (0.82)	0.26 (0.29)
Séguié	74	4	0.99	0.29	- 0.063 (0.65)	0.90 (0.84)	0.32 (0.35)

p.p.r.: Percent of parallel run; Tv-BP: t-value of Baillie and Pilcher (1973); Mean and Stdev: arithmetic mean of ring widths and their standard deviation; ac(1): first order autocorrelation; EPS: expressed population signal and ms: mean sensitivity. Values into brackets are obtained before standardization.

The values of Tv-BP, p.p.r., EPS and ms were lower in the non-managed trees (Gagnoa site) compared to the managed trees at Séguié (table 4.1). The cross-dating and standardisation values of table 1 are based on tree-ring series after the removal of the most juvenile rings (first five and first two growth rings for Gagnoa and Séguié, respectively) from the tree-ring series.

Without this removal, values of Tv-BP and p.p.r. were below the thresholds for acceptable crossdating.

4.2.3. Growth responses to the local rainfall

Dry years are associated with the formation of narrow rings in either the same year (mostly at Séguié) or in the following one (frequently at Gagnoa). The narrowest ring was formed at Gagnoa in 1980 under the lowest total annual rainfall, a year that corresponds also to the second severe drought period at Gagnoa. Séguié trees formed their narrowest growth ring in 1983, corresponding to the site lowest rainfall.

In Gagnoa, the site chronology correlated significantly only with precipitation of the major wet season ($r = 0.60$; $p < 0.05$) and not with the total annual rainfall. The Séguié site chronology showed a significant correlation with both the annual precipitation and precipitation of the major wet season ($r = 0.50$ and $r = 0.38$; $p < 0.05$). Growth response to the major and minor dry seasons rainfall was insignificant at both sites.

The Gagnoa site chronology correlated significantly and positively with April rainfall ($r = 0.32$; $p < 0.05$) and negatively with September and October rainfall ($r = -0.33$ and $r = -0.37$; $p < 0.05$). The Séguié site chronology gave a significant positive correlation with July rainfall ($r = 0.55$; $p < 0.05$, see also Fig. 4.5).

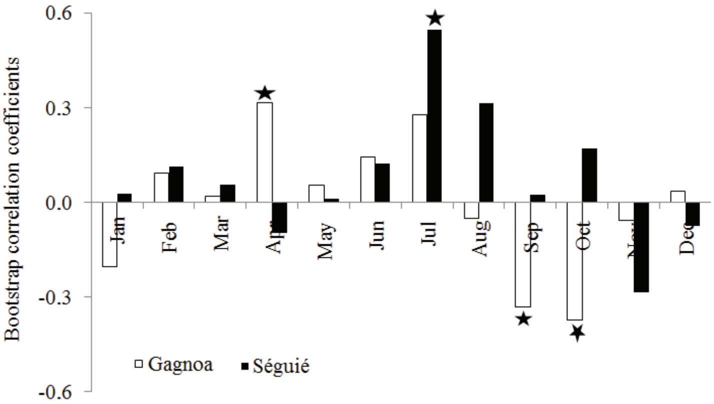


Figure 4.5. Relationship between monthly precipitation and site chronologies from Gagnoa (grey bars) and Séguié (white bars). Analysis was performed with Dendroclim2002+ over the period 1971-2001 for Gagnoa and 1972-2000 for Séguié. The black stars indicate significant correlations ($p < 0.05$).

4.2.4. Regional and global climate influence on tree growth: Sea Surface Temperature (SST) and El Niño

SSTs anomalies of the Gulf of Guinea gave a significant and positive correlation with annual precipitation in January and March at Gagnoa and in January, April, June, July and August at Séguié (Fig. 4.6A). In addition to their effect on annual precipitation, SSTs anomalies significantly correlated positively with the site chronologies in July-August at Gagnoa and in June-July at Séguié (Fig. 4.6B). On average, the influence of SSTs anomalies on tree growth was observed with a lag of one month in Gagnoa compared to Séguié.

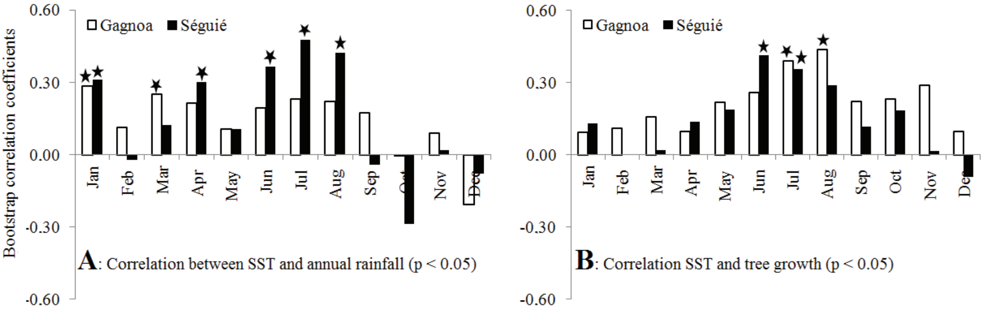


Figure 4.6. Influence of anomalies in monthly sea surface temperatures on growth and precipitation in Ivory Coast. Relation between monthly sea surface temperatures of the Gulf of Guinea and annual precipitation (A). Relation between monthly sea surface temperatures of the Gulf of Guinea and site growth chronologies (B). The correlation is performed under Dendroclim2002+ ($p < 0.05$). White bars represent data for Gagnoa and dark bars, data for Séguié. Black stars indicate significant correlations values ($p < 0.05$).

Over the growth period common to both sites (1972-2000), the first highest value of the ENSO index (index = 39) was observed in 1983 corresponding to the year of the lowest annual precipitation in Séguié (773 mm). This site experienced a continuous decrease in precipitation from 1990 to 1994, i.e., during the prolonged period of high ENSO values (from 1991 to 1998) where annual precipitation reached its lowest value (954 mm) also at Gagnoa (i.e., in 1992). Several years of decrease in precipitation coincided with high ENSO index values.

At the global scale, no significant correlation was found between ENSO index and annual precipitation in Gagnoa and Séguié over the whole study period. No relation was found between the Gagnoa site chronology and the ENSO index. At Séguié, the ring width indices correlated negatively and significantly with ENSO index only over the period 1976-2000 ($r = -0.55$; $p < 0.05$) and not over the trees' total lifespan ($r = -0.30$; $p>0.05$).

Growth pointer years (GPY), corresponding to years of decrease in precipitation, fall within the period of high ENSO indices at both study sites and within drought episodes in the study sites (local scale), in West Africa (sub-regional scale) and in Africa (regional scale) (table 4.2).

Table 4.2. Chronological similarities between rainfall variability, drought periods and pointer years in teak growth at the local scale (study site and country) and global level (West-Africa, Africa, and surface Atlantic ocean).

Decades	GPY		SRR		CRR	WRR/ WAD	ADp	ENSO events
	Gagnoa	Séguié	Gagnoa	Séguié				
1960 - 1970			1967 1969		1966 1969	1968	1968	1965-66 1969-70
1970 - 1980	1976-77	1973 1975 1977-78	1972 1976 1977-78	1973 1977	1975 1977-78	1972 – 73 1976 1979	1976	1972 – 1973 1976-1977 1979
1980 - 1990	1980 1983 1988	1982-83 1987	1980 1983 1986	1980-81 1983 1986 1988	1980-81 1982-84 1986 1988	1980 1982-84 1986-87	1980 1983 1987	1982-83 1986-87
1990 - 2000	1990-95 1998 2000	1990-95 1997-98 2000	1991-94 1997-98 2000	1990 1992-94 1997-98 2000	1990-95 1997-98 2000-01	1991-92 1997-98	1990-95 1997-98	1990-95 1997-98
2000 - 2010		2001 2003	2002		2000-01			

GPY: growth pointer years
SRR: site rainfall reduction corresponding to the formation of narrow rings at the site level
CRR: rainfall reduction at the country level
WRR/WAD: West-African drought episodes
ADp: African drought episodes
ENSO: El Nino Southern Oscillation events
Sources: Gopinathan (1997); Janicot (1997); Latif *et al*. (1999); Mahé *et al*. (2001); Kouadio *et al* (2003); Dai *et al*. (2004); N'Go et al. (2005); Goula *et al*. (2006); (Kouassi *et al*., 2013); Gebrekirstos *et al*. (2008); Deepak *et al*. (2010).

4.3. Discussion

4.3.1. Tree-ring characteristics

In both plantations, teak showed tree-ring distinctiveness and porosity typical for this species (Pumijumnong & Park 1999). In addition to this teakwood structure, the study trees exhibited wedging rings and intra-annual growth zones (XGZ). Wedging rings in teak are reported to be mostly induced by the formation of buttresses at the base of the stem or to pith eccentricity, similar to recent observations (Akachuku & Abolarin 1989; Kumar *et al*. 2002; Sousa *et al*., 2012). There were no thinnings in the Gagnoa plantation resulting in a clear stratification of the stand with dominant trees and dominated trees. We observed more ring wedging in the smaller, dominated trees. This phenomenon was also observed by Worbes (2002) in ring profiles from trees growing in the understory with scarce light conditions.

The XGZ formation, rather, results from a growth interruption caused by significant decrease in soil moisture (due to precipitation decrease) and followed by a growth recovery triggered by significant precipitation resumption within the same vegetative season (Priya & Bhat 1998; Campelo *et al*. 2006; Palakit *et al*. 2012). Novak *et al*. (2013) related the formation of XGZ to lower temperature and high precipitation occurring in autumn. Dié *et al*. (2012) suggested that XGZ formed in the earlywood resulted from a growth interruption due to the development of new foliage. The allocation of carbohydrates towards new leaves growth may have mobilized the largest part of photosynthates and induced a slowdown or interruption of the mitotic activities. In this previous cambial histological analysis, we observed a steady increase in the monthly precipitation during the earlywood formation, i.e., from February of the current growing season through June (Feb: 55 mm; Mar: 88 mm; Ap: 121 mm; My: 137 mm; Jn: 157 mm). The growth interruption – resulting in the earlywood XGZ formation – could, therefore, not be ascribed to water deficit. Furthermore, during the same period, there was no flowering or fruit setting that could act as intra-seasonal sinks for photosynthetic assimilates.

Given the impact of wedging rings and XGZ on tree-ring delineation and their relevance for the analysis of intra-annual climate-growth responses (Battipaglia *et al*., 2014), their accurate characterization appears essential.

4.3.2. Radial growth and ring width variations in managed and non-managed trees

Our results showed that Séguié trees formed wider ring-widths compared to Gagnoa. This difference could be considered as the result of thinnings applied in Séguié. These thinnings resulted in reducing the stand density from 2500-3000 stumps.ha^{-1} (initial density) to 79 trees.ha^{-1} (at the harvest time). Reducing the stand density makes more resources available for a reduced number of trees and contributes to enhance the growth rate, through the formation of wider growth rings. Similar results were, previously, obtained in oaks and pines (Canellas *et al.* 2004; Gea-Izquierdo *et al.* 2009; Zhang *et al.* 2013). In addition, thinnings applied in this site may explain the apparent periodicity observed in the growth recovery in the Séguié site chronology every 3-6 years from the 4th year of trees lifespan (Fig. 4.4B). Thinnings start from the 4th year after the plantation is installed and they are repeated every 3-6 years depending on tree age, in high productive sites (see teak production table of Ivory Coast in Maître 1983).

On the contrary, the lack of treatment in Gagnoa resulted in a gradual reduction of available growth resources for each tree and may have led to the stratification of trees into dominant and codominant and suppressed individuals. In that close canopy, with a high stand density (initial density = 2500 seedlings.ha^{-1}), growth is limited in the lower stories, due to competition for growth resources. This results in reducing the averaged ring width at the trees population level in Gagnoa, as it was observed in *Quercus ilex* and *Pinus halepensis*to (Gea-Izquierdo *et al.* 2009; Moreno-Gutiérrez *et al.* 2012).

4.3.3. Growth synchronicity in managed and non-managed stands

The cross-dating thresholds were exceeded in both Gagnoa and Séguié, after the removal of the most juvenile rings. Next to the presence of these rings, the loss of stem cylindricity can result in uneven growth dynamics around the entire circumference (Akachuku & Abolarin 1989) and can, thus, lead to the loss of growth synchronicity. The typical ring pattern around the pith, driven by an internal rhythm, is among the main causes of the low growth synchronization between trees and can also explain the weak crossdating at the stand level.

On average, the values of standardization and crossdating were higher in Séguié compared to Gagnoa. The difference in crossdating values between these two sites can be attributed to the lack of sylvicultural treatment in Gagnoa. Thinnings and pruning applied in Séguié, apparently, led to a strong growth synchronizing effect at the stand level, resulting in more common (uniform) growth responses between trees (high EPS value). In the non-managed plantation of Gagnoa, this effect is lacking.

The ms obtained in Gagnoa and Séguié is higher than that reported in Western and Central Indian teak (Deepak *et al.* 2010; Ram *et al.* 2011) and in Ivorian limba (De Ridder *et al.*, 2013). This is indicative of the high sensitivity of our study trees to climate. However, the ms recorded in our study sites is lower than that observed in *Brachystegia spiciformis* (Trouet *et al.* 2006). This discrepancy can be site-related and reflects the degree of both the climate seasonality and the vegetation deciduousness (Borchert 1999). The results of Trouet and co-authors (Trouet *et al.* 2006) were obtained from the Miombo woodland which, obviously, experiences drier climate compared to our two sites.

4.3.4. Local climate influence: precipitation vs. Growth

At both sites, the narrow ring formation matches with a decrease in annual precipitation in the same year, which was the case in Séguié or a year after, as was the case at Gagnoa. A one-year lag in the effect of annual precipitation on deciduous trees growth was, recently, observed in teak (Deepak *et al.* 2010; Sousa *et al.* 2012) and in *Acacia* species and *Balanites aegyptiaca* (Gebrekirstos *et al.* 2008). The lag in the effect of water deficit can indicate that, in deciduous forest, the decrease in annual precipitation affects tree growth in the following growing season, if the latter experiences rainfall not substantial enough to supply the soil water reserve and sustain growth activities.

Quantitative analysis showed that tree growth in Gagnoa correlated with April precipitation, i.e., during the early stage of the tree-ring formation (Dié *et al.* 2012) when the largest portion of the ring is being formed. Teak reaction to wet season precipitation, in deciduous forests as is the case in Gagnoa, was, previously, observed (Pumijumnong *et al.* 1995; Deepak *et al.*, 2010). Our results concord with the typical growth responses of tropical deciduous trees to precipitation (Borchert, 1999). In addition to their reaction to wet season precipitation, Gagnoa trees formed the narrowest growth ring in the year with severe drought (1980) that started in February corresponding to the beginning of the major wet season and the onset of cell divisions in teak (Dié *et al.* 2012). This shows that a pronounced decrease in precipitation, occurring at the onset of the mitotic activities, can generate a water deficit which affects radial growth.

The significant responses of Séguié teak growth to July precipitation – during the latewood formation (Dié *et al.* 2012) – show that trees did not respond with reduced cambial activity to the decreased precipitation in July due, probably, to a substantial water availability throughout the vegetative season (Wagner *et al.* 2014). Our analysis is supported by the results of N'Go and co-authors (2005) who observed that the annual precipitation exceeded the evapotranspiration over the study period (precipitation - evapotranspiration > 0); indicative of positive soil water balance. In addition, tree growth at Séguié was also sensitive to annual precipitation, similar to the climate-growth relation of evergreen species, and to wet season precipitation as in the case of deciduous species (Worbes, 1999; Gebrekirstos *et al.*, 2008). Séguié tree growth showed significant correlation with monthly precipitation only in July which is even not the wettest month of the study period. Second, shallow rooted species, as teak (Nidavani *et al.*, 2013), have access only to subsurface soil water resulting from precipitation (Enquist & Leffler, 2001). In such conditions, a significant decrease in rainfall (from June = 249 mm to July = 98 mm) was expected to impact on tree growth. Since the water availability (precipitation) appears as the main driver of tree growth for tropical regions, although growth can be influenced by additional factors (Wagner *et al.*, 2012 and 2014). We admit that the significant relation between tree growth and annual precipitation cannot be considered as the cumulation of the correlations between growth and monthly precipitation. Since the latter showed almost no correlation with tree growth during the months preceding July (Fig. 4 . 5). Precipitation of the preceding months, supplying the soil hydraulic reserve, rather resulted in maintaining positive soil water balances which were efficient to sustain tree growth throughout the rest of the growing season. The relationship between the water availability and the complex growth dynamics, observed in the Séguié site, is supported by a recent study of the cambial activity and could explain the prolonged period of the mitotic activities over 9 months (Dié *et al.*, 2012). Complex growth periodicity patterns, in relation to water availability have recently been reported for *Cedrela odorata* (Costa *et al.*, 2013).

Future investigations would help to determine the threshold of water deficit inducing the onset of growth interruption in trees and clarify the relationship between teak growth responses and moisture conditions.

Second, previous research revealed that precipitation accounts for 83% of water infiltration at Séguié (N'Go *et al.*, 2005). In addition, thinnings increase the availability of water and other resources for individual trees, which in turn may explain the low sensitivity of trees to a decrease in precipitation in the thinned teak stand.

Thinned are consistently reported for their positive effect on tree climate-growth responses in other species (Gea-Izquierdo *et al.*, 2009; Martin-Benito *et al.*, 2010; Moreno-Gutierrez *et al.*, 2012; Zhang *et al.*, 2013). Bréda and co-authors (1995) performed a monitoring of soil water content resulting from rainfall over two consecutive years in a thinned and non thinned stands of *Quercus petraea*, a hardwood and ring-porous species like teak. They recorded higher relative extractable water – an improvement of soil water availability – in the soil of the thinned stand as a result of decrease in crown interception and transpiration due to thinnings. And they concluded that thinnings improve water availability for tree growth. Gea-Izquierdo and co-authors (2009) also analyzed the effect of thinnings on long-term climate-growth responses of *Quercus ilex*. They observed a higher sensitivity of trees in low density stand and concluded that tree climate sensitivity can partly be modified by management. Martin-Benito and co-authors (2010) found similar results while examining the effect of thinnings on climate-growth responses in *Pinus nigra*.

On the other hand, the Séguié site experienced dry conditions in the 1980s. Considering that water is the limiting factor at the site, one should expect tree growth in Séguié to show a stronger relation with annual precipitation than Gagnoa during these years (Principle of limiting factor, see Fritts & Swetnam, 1989). And this impact could be significant enough to persist during the rest of the study period.

4.3.5. Regional and global climate effects on local precipitation and teak growth

Anomalies of SSTs showed a significant influence on annual precipitation, but this influence was lower (moderately low correlation) and less prolonged (over few months) in Gagnoa compared to Séguié. This indicates that precipitation is less affected by the global climate changes in Gagnoa site, typical for the central belt of Ivory Coast (Kouadio *et al.*, 2003). According to these authors, this zone is protected by the northern belt counteracting the effect of the Sahelian dry climate and by the southern belt which mitigates the direct influence of the Gulf of Guinea's SSTs. The vicinity of the Gulf of Guinea, relative to Séguié, explains its higher influence on precipitations in this site (high fluctuations) compared to Gagnoa.

Teak growth responded to SSTs of the Gulf of Guinea in June-July at Séguié (close to the Atlantic coast), similar to the climate-growth relationship recorded in the North-East of the country (close to the Sahelian region, see Schöngart *et al.*, 2006). While at Gagnoa, tree growth reacted significantly to SSTs in July-August with a month lag compared to Séguié. This lag could be attributed to the weaker influence of the Atlantic ocean, which may also be the cause of the weak relation (non significant correlation) between the annual precipitation and the ENSO in Gagnoa.

At Séguié, the influence of the Gulf of Guinea seems to explain the stronger relationship between tree growth and ENSO. The ENSO and drought years are associated with narrow rings formation in Séguié trees (i.e., growth pointer years; table 4.2). This supports the formation of the narrowest ring in 1983, a year where the ENSO index reached its first highest value over the study period. The most severe drought of West-Africa, also, occurred that same year (N'go *et al.*, 2005; Fauset *et al.*, 2012).

In addition, Séguié annual precipitation and growth were related to three of the major El Niño events (1982-'83, 1990-'95 and 1997-'98) occurring after the 1970s at the global scale (Trenberth & Hoar, 1996; Gopinathan 1997; Janicot *et al.*, 1998; Mahé *et al.*, 2001; Dai *et al.*, 2004; Ummenhofer *et al.*, 2013). The SSTs-precipitation and ENSO-precipitation relationships, added to the effect of SSTs and ENSO on tree growth, (i) give evidence of the interconnection between global climate phenomena and local precipitation and (ii) show how global climatic events can influence tree growth through narrow ring formation, at the local level. This also shows that tree-ring analysis of climate-sensitive species can contribute to unravel the complexity of the West-African Monsoon, a system including the oceanic and continental surface processes.

Conclusion

Our study showed a higher growth rate in the managed plantation (Séguié) compared to the non-managed stand (Gagnoa). Both plantations responded differently to varying precipitation, except for a common influence of the wet season on tree growth. The study also showed that global climatic events influence growth responses at the site level. Sylvicultural treatments resulted in accelerating radial growth rate and inducing a growth synchronizing effect in trees. Management techniques, such as thinnings and pruning, appear to enable trees to better cope with the water deficit during the growing season.

On the other hand, notwithstanding their short length, which is below the 40 years appropriate for dendrochronological studies (Fritts, 1976), both sites chronologies showed cross-dating and standardisation values comparable to those of older trees. In addition, the two sites exhibited climate-growth response patterns similar to those of older teak. This shows the potential of young trees in dendroclimatological studies in areas with depleting natural old forests.

The climate-related growth of teak under sylvicultural management found in the present work has not been studied yet. For that purpose, we suggest future studies on tree-ring analysis in combination with monitoring the time-intervals between thinnings. This could define and document appropriate thinning regimes for teak in Ivory Coast and elsewhere in tropical regions.

For a better understanding of thinnings effects on tree growth and their role in assisting trees to buffer water deficit effect, future tree-ring analysis should also include leaf area and potential evapotranspiration analyses, in addition to the combined use of local and global climatic variables, as they were used in this study.

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Box 4.2. Appendix to Chapter 4: Explanatory information on ring widths standardisation

1. Parametric and non parametric tests used for ring widths synchronization

a- Percentage of parallel run (p.p.r.). The p.p.r. is a non statistical parameter, which measures the year-to-year agreement of growth fluctuations and is calculated as follows:

$$p.p.r. = G_{(x,y)} = \frac{100}{n-1}\sum_{i=1}^{n-1}\left|G_{ix} + G_{iy}\right|$$

G = Gleichläufigkei, n = number of ring widths, x and y being the 2 ring widhs series to be tested.

b- The t-value of Baillie-Pilcher (Baillie & Pilcher, 1973), expressing the mediumwave year-to-year growth affinity between two time-series, was also used.

$$t = r\frac{\sqrt{n-2}}{\sqrt{1-r}}$$

(n: number of measured growth rings, r: Pearson correlation coefficient).

The thresholds adopted by Trouet and co-authors (2010) for tropical species (i.e., ppr ≥ 60% and t-values ≥ 2) were considered in the present work, to conclude on the success of the crossdating.

c- Mean sensitivity

$$MS = \frac{1}{n-1}\sum_{i=1}^{n-1}\left|S_i + 1\right| \text{ where } S_i = \frac{2(x_i - x_{i-1})}{(x_i + x_{i-1})}$$

n is the number of growth rings at a given time, Si, the sensitivity in the interval i, *x*i, the ring width measured the current year (i) and *x*i-1, the ring width of the preceding year (i-1).

d- EPS

$$EPS(t) = \frac{n\bar{r}_{bt}}{n\bar{r}_{bt} + (1-\bar{r}_{bt})}$$

rbt is the averaged correlation of all the individual series of ring widths and n, the number of the series that correlated.

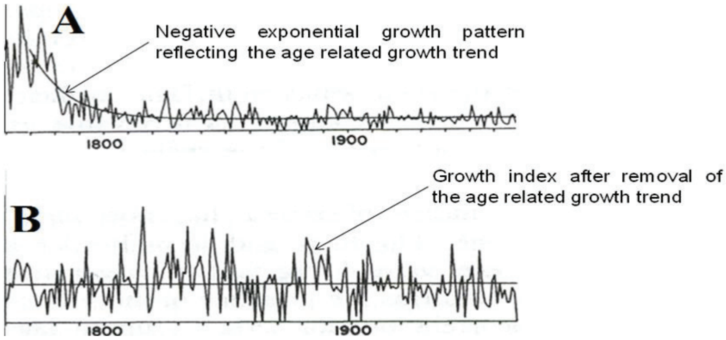
2. Role of the auto-regression method

The autoregressive method applied to standardize the ring width profiles allows to remove the long-term (multi-annual or multi-decadal) variations also called low and medium frequencies signals. The variations of the remaining ring widths profile reflect the inter- or intra-annual fluctuations of the main growth factor. These fluctuations are well described by a polynomial regression and can be observed through the sinusoidal shape of the standardized ring widths profile (Supplementary Fig. 1A: S1A).

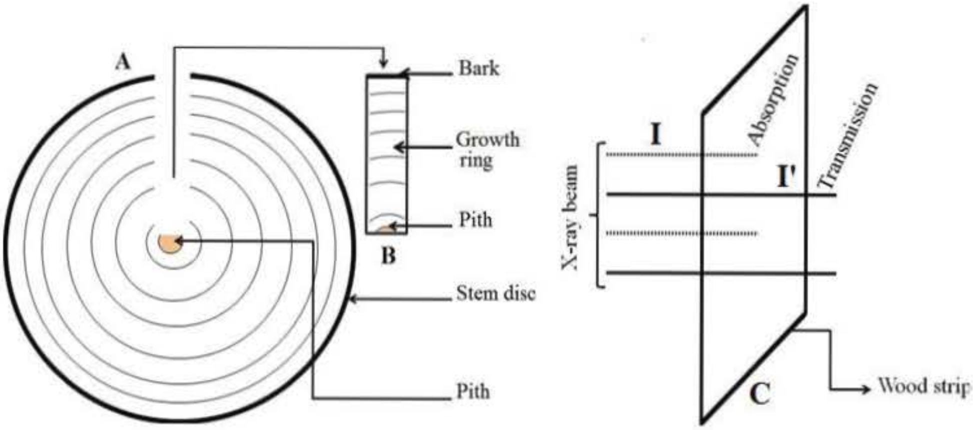
The low frequencies signal represents a growth factor with long-term effects (at a multi-decadal scale). These slow and continuous disturbances may result from the effect of age, silvicultural operations and other environmental conditions with low and slow fluctuations. Age effect, which represents the main source of long-term variations, imposes a continuous negative exponential growth trend to the ring widths profile (Supplementary Figure S1A).

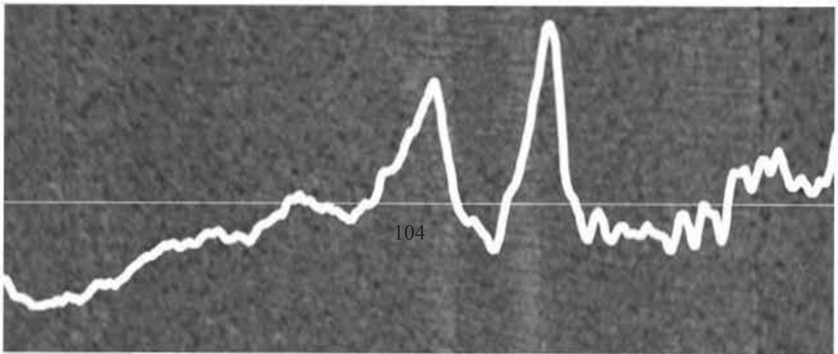
The medium frequencies signal corresponds to perturbations with decadal scale effects, i.e. growth disturbances likely caused by repetitive droughts, intensive thinning, dieback of trees due to fungal or insect attack. The effect of these disturbances occurs, in general, over a period of 5 to 30 years (Merian, 2012) and is reflected into periodic peaks and/or drops in ring widths, which can be observed on the site chronology.

High-frequencies signals refer to growth factors with annual or intra-annual variations such as the environmental conditions, namely the climate, which represents the main growth limiting factor. When the low and medium frequencies signals are extracted from the ring widths, the variations of the resulting dimensionless growth index (Figure S1B) reflect essentially the climate fluctuations.



S1A. Growth chronology (ring widths index) building (B) after the removal of the age trend observed through the negative exponential (A).


A
Bark
Growth ring
Pith
B
Stem disc
Pith
I
Absorption
Transmission
I'
X-ray beam
C
Wood strip



Chapter 5: Assessing wood density variability of *Tectona grandis* L.f. (Lamiaceae) through microdensitometrical profiling shows latewood sensitivity to climate

This chapter is based on the following paper:

A. Dié, J. Van den Buclke, P. kitin, H. Beeckman and J. Van Acker. Microdensitometrical profiling of *Tectona grandis* L. reveals latewood sensitivity to climate. Under revision by Dendrochronologia.

Abstract

Tectona grandis is a tropical species with high natural durability, planted worldwide for valuable timber and also showing high potential for carbon sequestration. Wood density is an important property for the evaluation of tree growth performance and wood mechanics. The density of xylem is variable within a tree and it is therefore essential to investigate the causes of its variability. We measured wood density in Ivorian planted teak on pith-to-bark strips using high-resolution helical X-ray Computer Tomography scanning. Cell wall thickness and lumen diameter of fibres were measured on microtome cross-sections for a better understanding of within-ring density fluctuations. The relationships between density and rainfall and cambial age were also examined.

The results showed that density is more variable between trees than within a tree and evidenced the close link between wood density and xylem anatomy within the ring. Total ring density is mainly attributed to the latewood density ($r = 0.93$; $p < 0.001$) and the latewood percentage ($r = 0.51$; $p < 0.05$) but it was also significantly correlated with earlywood density ($r = 0.79$; $p < 0.05$). Total ring density significantly correlated with October rainfall ($r = 0.37$; $p < 0.05$). Latewood density also showed high correlation with October and the post wet-season rainfall ($r = 0.47$; < 0.05 and $r = 0.41$; $p < 0.05$, respectively). In addition, latewood proportion significantly correlated with June rainfall ($r = 0.43$; $p < 0.05$).

The study revealed thus a clear rainfall – xylem density relationship mainly explained by the strong sensitivity of the latewood to climate. In summary, the study gives evidence for the clear potential of latewood density in teak for climatic analyses.

Introduction

Reforestation programs – using fast growing species – aim to ensure high quality and homogeneous wood production and reduce atmospheric carbon emissions while satisfying the local and international demands for wood. In both hard- and softwoods, wood density is the best indicator of wood physico-mechanical and chemical properties. In teak (*Tectona grandis*), a tropical Asian ring-porous timber tree, density represents the fundamental feature of high dimensional stability, ease of drying, stiffness, natural durability and resistance to biodegrading agents such as termites (Moya *et al*., 2009; Izekor *et al*., 2010; Shanbhag & Sundararaj, 2013; Wanneng *et al*., 2014). Wood density is also the key parameter for forest productivity assessment through wood biomass calculation. However, notwithstanding its role for the wood quality, density can exhibit significant variations likely to affect the above wood properties and biomass estimate. It is therefore needful to investigate the factors driving wood density fluctuations.

Most of the wood products derived from teak thinnings are used in local carpentry and also serve as outdoor furniture (stakes, poles and posts) at an early age (5-15 years). Such usages require hard, dense and homogeneous wood, i.e, wood with less fluctuating density (Echols, 1973) in order to stand the biodegrading agents. For that reason, it seems essential to know the extent to which growth factors such as the cambial age could influence wood density in trees within a stand. We first pointed at the age effect because most of the studies dealing with teakwood generally attributed its density variations to tree's age, i;e younger trees form less dense wood compared to older individuals. This could hold true for wood samples from different age classes and species. We, therefore, sought (i) to understand how variable wood density could be within a single-species planted stand like the Séguié plantation where trees are from the same age and grow under uniform soil and climate conditions and (ii) to identify the factor that influences wood density the most in such an environment.

Earlier research considered tree growth rate – reflected in the ring widths – as the main cause of wood density variability in ring-porous species (Fukazawa, 1984). However, the fact remains obvious that wood density is the result of ecophysiological processes (Zobel & van Buijtenen, 1989), namely cell production and secondary cell wall deposition (Plomion *et al*., 2001). This indicates that density variations originate from physiological changes occurring within the tree and are thus determined by parameters such as the xylem anatomy and the transition from earlywood to latewood (Zobel & van Buijtenen, 1989; Knapic *et al*., 2011; Michelot *et al*., 2012; Zieminska *et al*., 2013). Those parameters are, in turn, influenced by environmental factors, such as the climate, that control the cambial functioning during the vegetative season. As such, climate variables, with in particular precipitation as factor, are likely to cause wood density fluctuations within the tree at both the short-term (intra-seasonal) and long-term (annual) levels (Xiang *et al*., 2014). In addition, studies addressing the within-tree density in hardwood species consistently identified the latewood as an important source of variations. More specifically, latewood density is described as the best representative of the total ring density in regard to the strong correlation between the former and the latter densities (Knapic *et al*., 2008, 2011; Kumar *et al*. 2014). This is also because latewood width is the key parameter of the growth ring (Knapic *et al*., 2011; Genet *et al*., 2012; Michelot *et al*., 2012; Kumar *et al*., 2014). Latewood is thus more likely to record changes occurring in the growth conditions such as the climate during the vegetative season. While analyzing tree-ring proxies of pedunculate oak, Kern and co-authors (2013) pointed out the high climatic potential of the latewood width. The aforementioned literature review indicates that (i) fluctuations of ring width and ring density can be imputed to latewood and that (ii) the responses of tree growth and wood density to climate can be traced back to the latewood sensitivity to climate.

Teak growth rings are proven highly sensitive to moisture conditions (Ram *et al*., 2011). This is because teak cambium functioning is strongly driven by precipitation (Priya & Bhat, 1999; Dié *et al*., 2012). Second, the species is planted beyond its natural distribution area under variable climates such as in Ivory Coast where teak represents the main source of high quality timber (Koné *et al*., 2010). The current and predicted climate change and its effect on forest cover and tree productivity in West-Africa (Hulme *et al*., 2001; Kouadio *et al*., 2003; Heubes *et al*., 2011; Fauset *et al*., 2012) demands to understand the implications of the growth climate sensitivity on the density variability for a climate sensitive species such as teak. This approach can help to assess the effect of the climatic fluctuations on teakwood density at the annual and sub-annual time scales and to develop possible adaptative strategies for the species to buffer the effects of the changing environmental conditions.

Studies dealing with teakwood density variations have not yet addressed the role of climate variability and a detailed analysis of earlywood and latewood. The present work, therefore, aims to assess if there exists a main factor explaining the within-tree fluctuations of wood density in teak having a higher impact than the commonly investigated sources such as cambial age, growth ring width, and provenance. Then, we examine the relationship between wood density and climate, more specifically precipitation as growth controlling factor in the tropics (Wagner *et al*., 2012, 2014). Using teak trees from Ivory Coast, this study aims:

(i) To assess the degree of density variability through microdensitometrical profiling using X-ray CT scanning (Van den Bulcke *et al*., 2014);

(ii) To identify the main force driving density changes within the tree;

(iii) To clarify the climate-density link in relation to xylem anatomy and

(iv) To examine latewood sensitivity to climate.

5.1. Material and methods

5.1.1. Study site and material

The study material is sampled from the Forêt Classée of Séguié, the second largest teak plantation of Ivory Coast, located in Agboville province and resting on a hydromorphic soil (N'Go et al., 2005). The site experienced a mean annual rainfall of 1298 mm from 1972 to 2000 (SODEXAM/Ivory Coast). The great wet season (GW) extends from March to June, followed by the small dry season (sd: July-August) which precedes the small wet season (sws: September-November) and the great dry season (DS: end November to February). The monthly mean temperature is 26.6 °C (minimum in August, 24 °C and maximum in February-April, 28 °C).

The study material consisted of six stem discs (one disc per tree) which were not planed nor sanded, in order to avoid any error in X-ray attenuation due to sanding particles. All discs are being conserved at the Xylarium of the Royal Museum for Central Africa (Tervuren/Belgium), and are accessible by their Tw number (Tervuren wood): Tw59769, Tw59770, Tw59771, Tw59772, Tw60583 and Tw60586.

5.1.2. X-ray microdensitometry

5.1.2.1. Sample preparation and scanning

In order to obtain unbiased density values and accurately address the objectives, we implement a ring density profiling based on the state-of-the art helical X-ray tomography combined with ring and fibre angle correction in 3D (Van den Bulcke et al., 2014). X-ray computed tomography is used to measure wood density. For that purpose, a radial (pith-to-bark) wood strip with a tangential-section measuring 1 x 1 cm² was cut from each stem disc. The strip was taken radially from each stem disc on which the growth rings were correctly demarcated, except for specimen Tw60583 which showed a reduced growth from the 22nd ring onward. The strip was sampled as perpendicular to the stem axis as possible in order to obtain an actual pith-to-bark radius containing all the growth rings, starting from the first ring near the pith to the last one under the bark.

All pith-to-bark strips were scanned in helix mode using the Nanowood scanner at Woodlab-UGent (Dierick *et al*., 2014), a system developed at the Ghent University Centre for X-ray Tomography (UGCT). Reconstruction is performed with Octopus, a tomography reconstruction package for parallel, cone-beam and helical geometry as well as phase correction and retrieval

(Vlassenbroeck *et al.*, 2007). Beam hardening correction was applied, both by hard- as well as software filtering. The obtained approximate voxel pitch was 40 µm.

5.1.2.2. Converting grey values to absolute densities

All strips were inserted in a sample holder which consists of a reference material with an absolute density of 1.4 g cm^{-3} which is close to wood cell wall density. By using the density of the sample holder and the average grey level of air (considered zero density), the 16-bit grey values of the reconstructed wood strips are directly converted to absolute densities or X-ray density (ρ_{wood}) calculated as follows:

ρ_{wood} ($g.m^{-3}$) = $\rho_{holder} \times (G_{wood} - G_{air}) / (G_{holder} - G_{air})$

ρ_{holder}: absolute density of the sample holder (1.4 $g.cm^{-3}$);

G: grey values of wood, air and sample holder respectively.

More information on this procedure and the calibration can be found in De Ridder and co-authors (2011).

5.1.2.3. Microdensitometrical profiling

Growth rings were often not concentric, leading to non-parallel ring boundaries on the transversal plane (Fig. 5.1). Such rings show spiral grain which results in skewed fibres on the radial plane. As a consequence, the obtained average density of a tangential plane from pith-to-bark on the border of a growth ring is an average across more than one ring. This can lead to misinterpreting the derived density in terms of intra-ring and inter-ring density variations. Volumes were re-interpolated, in order to avoid this bias and to obtain density values representative for each growth ring. The re-interpolation procedure (Van den Bulcke *et al.*, 2014) resulted in obtaining a new density profile which reflects the fluctuations that actually occur within each growth ring (Fig. 5.1). The re-interpolated volumes were used to extract all separate ring density profiles using ImageJ (Dubin-Thaler *et al.*, 2004).

The X-ray derived density was then compared to the density measured using the water displacement method (WDD). The WDD was determined on unwrapped samples using a procedure similar to that described in Maniatis and co-authors (2011). The method consists of weighing the oven dried sample, immersing it in water and reweighing it when removed from the water. Reweighing the sample aims to correct any liquid absorption. The samples used for WDD determination, consisted of the growth rings obtained from splitting the same strip used for X-ray densitometry. The rings were cut following the ring boundaries such that each sample contained only the material of a single ring.

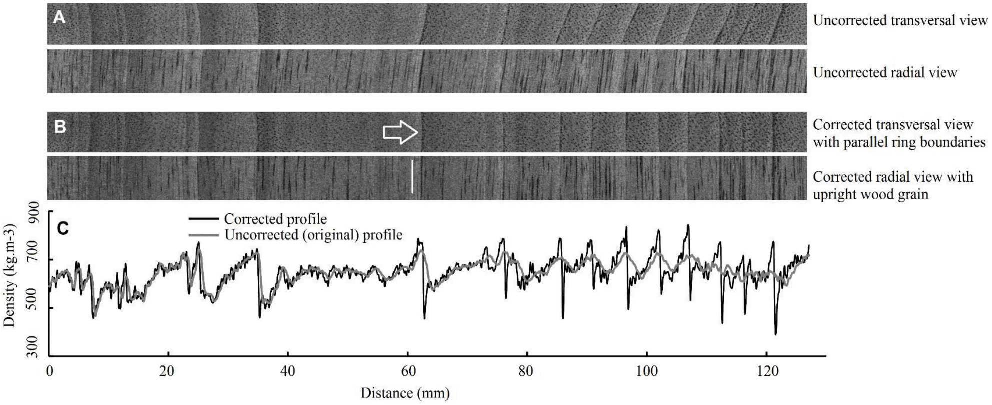


Figure 5.1. Transversal and radial cross section of the uncorrected (A) and corrected (B) teak volume as well as their microdensitometrical profile (C). The arrow points at the ring boundary and the vertical white line indicates the wood grain (B).

5.1.3. Ring density

The X-ray derived density of each growth ring was subdivided into earlywood density and latewood density using the Segmented Regression method "SegReg" (Muggeo & Adelfio, 2011). The density profile of each growth ring was also visually assessed to support the SegReg results. Based on the transition point, the proportion of earlywood and latewood was also calculated as the ratio of earlywood or latewood width on the total ring width. The measurements of earlywood and latewood width were performed on the X-ray scans. SegReg was also applied to analyze the radial variation of density in order to assess the potential of microdensimotrical profiling for juvenile wood demarcation (Bhat *et al*., 2001; Medzegue *et al*., 2007)

5.1.4. Intra-ring xylem anatomy

Intra-ring xylem anatomy variations were analysed by examining the distribution of vessel lumen diameter and vessel density as well as fibre wall thickness and fibre lumen diameter within the selected growth rings. On each wood strip, samples were taken according to 4 different positions: the portion near the pith (growth ring 3 or short R3), the inner heartwood

(R11), the middle heartwood (R18) and the outer heartwood (R29). Each of these 4 rings has the same age in all the sample strips. The terminology used for the strip portions, can be found in Niamké (2010).

5.1.4.1. Fibre wall thickness and lumen diameter

Fibre wall thickness and lumen diameter were measured on microsections approximately 18 µm thick. The mean wall thickness was determined by measuring the two opposite tangential walls and the mean lumen is the average of the radial and tangential lumen diameter. Then, the fibre ratio (wall thickness/lumen diameter) is calculated as the best parameter for fibre wall thickness and lumen diameter characterization (IAWA, 1989). Finally, a mean fibre ratio comparison was performed using ANOVA ($p = 0.05$) to check whether fibre wall thickness and lumen diameter are similar in all the growth ring zones.

5.1.4.2. Vessel characterization

Vessel diameter was measured on 20 µm microsections in a series of successive grids of 1 mm^2. All anatomical measurements were carried out, successively at different positions within the investigated growth rings:

- Earlywood (Ew) and outer earlywood (Ewzone) of the true growth ring;
- Inner and terminal latewood (Lwzone and Lw) of the true growth ring.

The same measurements were performed at the boundary of each intra-annual xylem growth zone (XGZ) when this latter was present:

- Latewood of the intra-annual xylem growth zone (Lwlike);
- Earlywood of the intra-annual xylem growth zone (Ewlike).

XGZ's are formed intra-annually as a consequence of growth interruption and recovery within the true growth ring and due to fluctuations in growth factors. This can cause intra-ring density changes (Campelo et al., 2006). Xylem anatomy before the boundary of the XGZ is characterized by latewood like cells and is therefore called latewood like (Lwlike). The anatomy after the boundary is marked by earlywood like cells and is called earlywood like (Ewlike).

5.1.5. Statiscal analysis

The coefficient of variation (CV) was used to assess radial density variations in each ring/tree. A CV lower than 10 % was considered indicative for a uniform density profile over the entire growth period, based on previous studies (Quilhó & Pereira, 2000; Kokutsé, 2002). Tukey multiple comparisons are used to test differences between all density types (total ring density, earlywood and latewood densities). The total ring density was correlated to earlywood and latewood features (width and density), using Pearson correlation analysis.

Density fluctuations were related to vessel diameter and fibre wall thickness in different locations within the growth ring: Ew, Ewzone, Lwzone, Lw and on both sides of the boundary of each XGZ). We examined the relationship between ring components (total ring density, earlywood and latewood width and density) and the climatic variables. All statistical analyses were run in SYSTAT 11.5 and XLSTAT 2012.

5.2. Results

5.2.1. Comparison between X-ray derived and water immersion measured densities

Two density sets were obtained for each sample tree (wood strip): the water displacement density calculated density (WDD) and the X-ray attenuation based CT-Scan derived density (X-rayD). We recorded a deviation (percentage of ring-to-ring difference in density) of 1.6% between WDD and X-rayD. The correlation between the two densities sets (X-rayD and WDD) was positive and highly significant ($r = 0.77$; $p < 0.0001$). The two density sets did not differ significantly (ANOVA: $F = 2$; $p < 0.0001$).

5.2.2. Inter and intra-ring density variations in relation to microdensitometric components

We recorded a non significant ring-to-ring density variation of 8% (CV = 8%; $p < 0.05$) between all the six examined trees and a non significant variation of 5% between the six mean density values. From the six individuals, only one sample (Tw60586) showed a significantly higher mean density (745.15 kg.m^{-3}) as revealed by the Tukey comparisons test (ANOVA: $F = 26$; $p < 0.0001$). All the five other trees showed no significant differences in ring density ($F = 13$; $p < 0.0001$).

Over the entire growth period, the total ring density (TotrD), earlywood density (EwD) and latewood density (LwD) reached mean values of 683 kg.m^{-3} ± 24; 634 kg.m^{-3} ± 24 and 710 kg.m^{-3} ± 26, respectively.

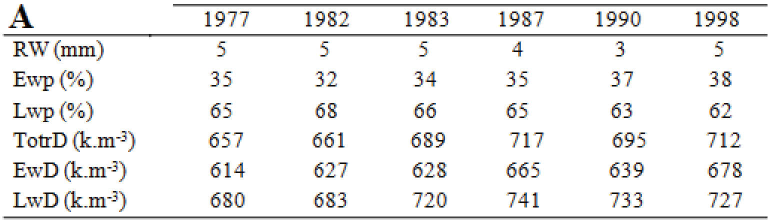
The Tukey multiple comparisons test showed significant differences between these three densities ($F = 84$; $p < 0.0001$), with latewood having the highest density (710 kg.m^{-3} ± 26) followed by the total ring (683 kg.m^{-3} ± 24) and earlywood density (634 kg.m^{-3} ± 24). Despite these differences, LwD was, on average, 1.12 times higher than EwD for all the studied trees (LwD/EwD < 1.12 with $n = 190$ growth rings). Results also indicated small differences between EwD and LwD for all rings: overall difference represented 12 % (LwD - EwD = 76 kg.m^{-3} = 12 %).

TotrD gave a positive and significant correlation with EwD ($r = 0.79$; $p < 0.001$) and LwD ($r = 0.93$; $p < 0.001$).

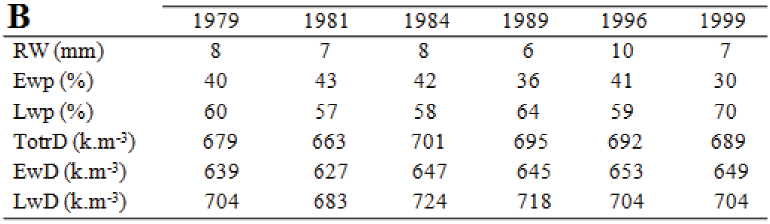
Wider rings had higher LwD and contained a higher proportion of latewood (table 5.1) which occupied an overall mean percentage of 62% of the annual ring width. Over the growth period, latewood percentage correlated positively with EwD ($r = 0.43$; $p < 0.05$) and with TotrD ($r =$

0.51; $p < 0.05$). While the latter showed a reciprocal correlation with earlywood percentage ($r = -0.51$; $p < 0.05$).

Table 5.1. Total ring width (RW) and density (TotrD) as well as the proportion and density of earlywood (Ewp and EwD) and of the latewood (Lwp and LwD) measured in the narrower (A) and the wider (B) rings.



A	1977	1982	1983	1987	1990	1998
RW (mm)	5	5	5	4	3	5
Ewp (%)	35	32	34	35	37	38
Lwp (%)	65	68	66	65	63	62
TotrD ($k.m^{-3}$)	657	661	689	717	695	712
EwD ($k.m^{-3}$)	614	627	628	665	639	678
LwD ($k.m^{-3}$)	680	683	720	741	733	727



B	1979	1981	1984	1989	1996	1999
RW (mm)	8	7	8	6	10	7
Ewp (%)	40	43	42	36	41	30
Lwp (%)	60	57	58	64	59	70
TotrD ($k.m^{-3}$)	679	663	701	695	692	689
EwD ($k.m^{-3}$)	639	627	647	645	653	649
LwD ($k.m^{-3}$)	704	683	724	718	704	704

5.2.3. Density variations in relation to cambial age

A significant logarithmic regression model was constructed between cambial age and both the total ring and latewood densities ($R^2 = 0.38$ and $R^2 = 0.51$ respectively) over the growth period, while such model was not significant when using the earlywood density ($R^2 = 0.24$).

In addition, the tree's age positively correlated with both the TotrD ($r = 0.55$; $p < 0.005$) and the LwD ($r = 0.49$; $p<0.05$), while it showed no significant correlation with EwD ($r= 0.26$ $p > 0.05$). The Segmented Regression (SegReg) applied for juvenile wood demarcation revealed that the cambial age explained 68.2% and 75.5% of density variations in the total ring (TotrD) and in the latewood (LwD) densities respectively ($p < 0.05$). The Breakpoint of the SegReg – which represents the transition age – was found at the cambial age of 13 years for LwD and 14 years for TotrD.

TotrD gave a highly significant and positive correlation with LwD ($r = 0.88$; $p < 0.0001$) in both the juvenile and mature wood parts, correlation between TotrD and EwD decreased when shifting from the juvenile ($r = 0.85$; $p < 0.0005$) to the mature phase ($r = 0.67$; $p < 0.001$). However, TotrD exhibited a very small increase (approx. 5%) from the juvenile to the mature wood, despite the significant demarcation of the juvenile wood and the subsequent correlations.

LwD showed an identical density increase as the TotrD (approx. 5%) from juvenile to mature wood while EwD showed no significant increase.

5.2.4. Intra-ring density variations in relation to rainfall

Annual rainfall showed no significant correlation with total ring, earlywood and latewood density. Likewise, no correlation was found between all the three density types and rainfall of the major dry and wet seasons and the minor dry season. However, rainfall of the small wet season (post-wet season) significantly correlated with LwD ($r = 0.47$; $p < 0.05$). October rainfall showed a significant correlation with TotrD ($r = 0.37$; $p < 0.05$) and with LwD ($r = 0.41$; $p < 0.05$). Monthly rain of May and June gave a similar and moderately high but however not significant correlation with the EwD ($r = 0.34$; $p > 0.05$). Finally, latewood width also correlated significantly with June rainfall ($r = 0.43$; $p < 0.05$).

When the monthy rainfall distribution followed a pattern typical of the study zone (monthly distribution with no significant fluctuations) as it was the case of the year 1989 (Fig. 5.2), trees showed a pattern of gradually increasing density from earlywood to latewood (Fig. 5.3).

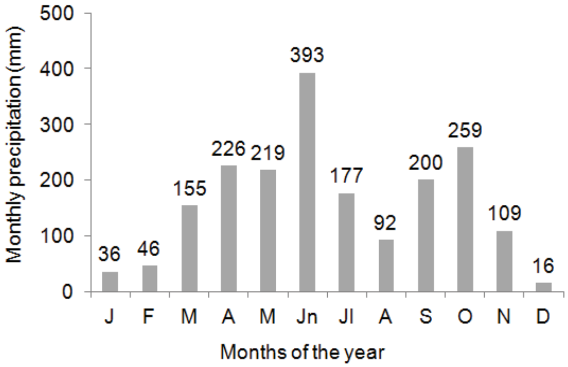


Figure 5.2. Distribution of monthly precipitations in the year of above normal anuual rainfall (1989).

Figure 5.3 shows the density profile of ring 19 formed in 1989 where the density profiles exhibited no significant variations ($CV \leq 10\%$; $p < 0.05$) in all trees, except for sample Tw60583 ($CV = 11\%$).

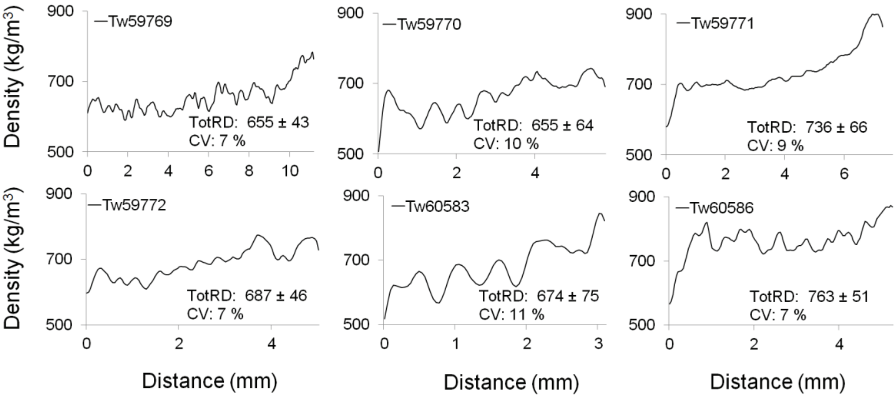


Figure 5.3. Intra-ring density profiles showing variations with low magnitudes except in specimen Tw60583 which shows a CV = 11%. TotRD: Total ring density and CV: coefficient of variations.

5.2.5. Intra-ring density variations in relation to xylem anatomy

In the studied trees, two typical anatomical features marked the transition between the latewood of one growth ring and the earlywood of the following one (Fig. 5.4):

(i) An abrupt increase in vessel diameter from 110.2+8.0 mm (latewood) to 212.5+13.0 mm (earlywood) and

(ii) A sharp change in fibre characteristics i.e., from thin-walled (earlywood) and wide lumen to thick-walled and narrowed lumen fibres (latewood).

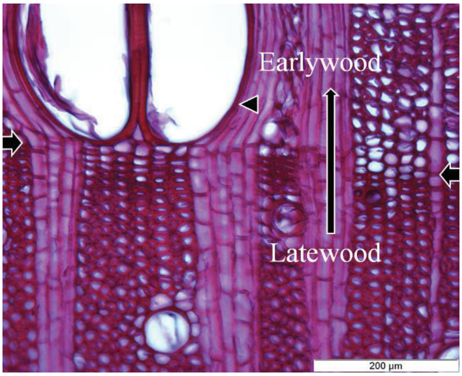


Figure 5.4. Sharp transition from latewood of growth ring 10 characterised by thick-walled fibres and small vessels to the earlywood of ring 11 characterised by thin-walled fibres and larger vessels (arrow head) in sample tree Tw59771. The horizontal arrows point at the growth ring boundary and the vertical one indicates the latewood to earlywood gradient. Scale bar: 200 µm.

The interrelation between rainfall, xylem anatomy and density is well illustrated in Figure 5.5. Figure 5.5A (right) shows an abnormal decrease in precipitation during the first part of the major wet season (April) i.e., in the early stage of the growing season (earlywood formation). The decrease in precipitation corresponds to a growth anomaly that led to changes in the ring structure (Fig. 5.5B) which are also reflected in wood density fluctuations (Fig. 5.5C). Results also indicated variations in the xylem anatomy (Fig. 5.5D) corresponding to those density changes at the same position within the ring.

A detailed observation of the X-ray scans provided evidence of a close relation between the ring structure, xylem anatomy and wood density (Fig. 5.5B-C-D). In all the studied rings, small diameter vessels were associated with thick-walled and narrow lumen fibres (higher fibre ratio) in the latewood. And wood density increases with an increasing fibre ratio and decreases with increasing vessel diameter and fibre lumen. The intra-ring density profile in Figure 5.5 (left) clearly illustrates these relations between xylem anatomy and wood density. This figure shows a ring zone with a density increase to a first peak value (XGZ1) which corresponds, simultaneously, to the first peak of the fibre ratio and the first decrease of vessel diameter. The zone with the peak in density and similar to true latewood is, thus, called first latewood like zone (Lwlike1). Then follows a decrease in density, which is associated with a decrease in fibre ratio and an increase in vessel diameter as in a true earlywood zone. This zone, called earlywood like (Ewlike1), precedes a second density peak (XGZ2) in a second latewood like region (Lwlike2) which is followed by another earlywood like zone (Ewlike2).

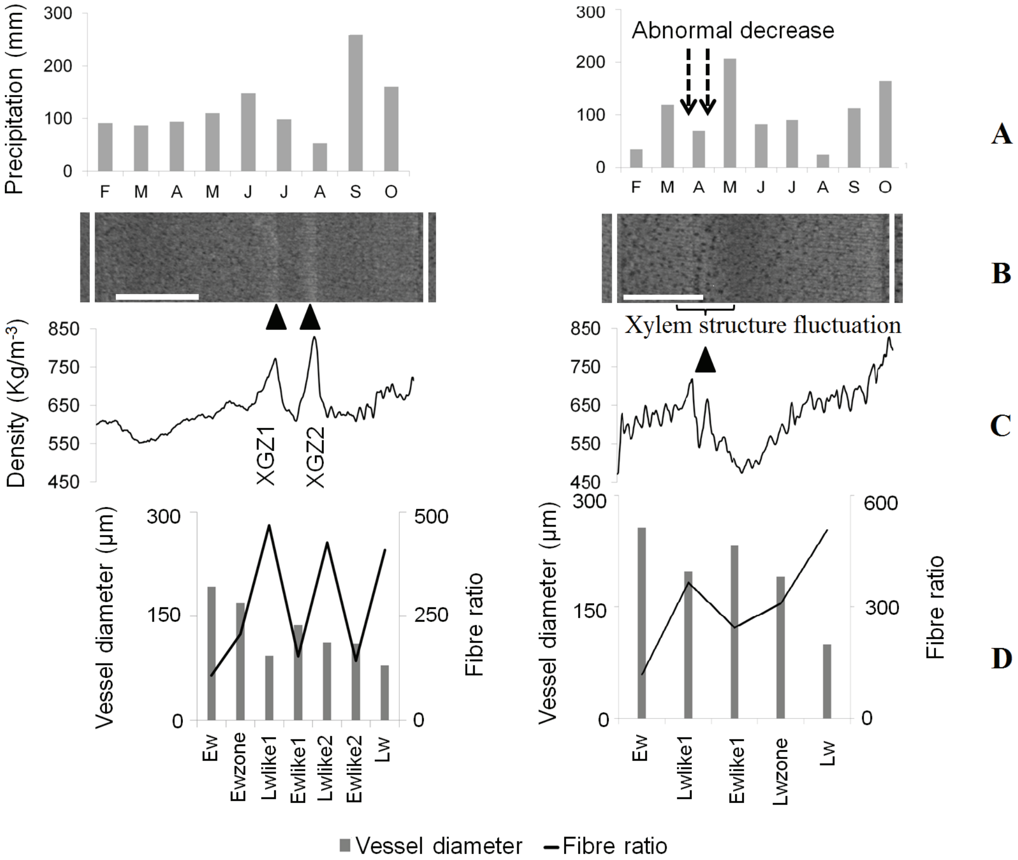


Figure 5.5. Illustration of the relationship between monthly precipitation (A), ring structure (B), wood density (C) and the corresponding xylem anatomy (D). Arrow heads point at the intra-annual xylem growth zone boundaries. The effective vegetative period lasts from February through October (cambial activity; Dié *et al*. 2012). Vertical lines (B) indicate growth boundaries of true ring number 3 of sample Tw59772 (left) and ring number 11 of sample Tw59771 (right). Scale bars (horizontal white lines in B): 500 µm.

Moreover, a high but not significant correlation is found between wood density and fibre ratio (positive) and vessel diameter (negative) within the rings that showed pronounced fluctuations in the xylem anatomy from earlywood to latewood. Such is the case for sample Tw9771 ring 11 in which the density gave a correlation of $r = 0.64$ and $r = -0.66$ ($p > 0.05$) with fibre ratio and vessel diameter respectively. This relation between ring structure, xylem anatomy and wood density was observed in all the studied rings. The methodology applied to establish the correspondence between the growing year rainfall and the wood features (macrostructure, anatomy and density) of the related rings is fully explained in the text box 5.1 below.

Box 5.1. Supplementary information usefull to the interpretation of figure 5.5

Methodological approach used to obtain Fig. 5.5

We measured the anatomical features (vessels and fibres lumen diameter and fibres wall thickness) at different positions within each investigated growth ring:

- Earlywood (Ew) and outer earlywood (Ewzone) of the true growth ring
- Inner and terminal latewood (Lwzone and Lw) of the true growth ring
- Latewood of the intra-annual xylem growth zone (Lwlike)
- Earlywood of the intra-annual xylem growth zone (Ewlike)

We then matched these quantitative anatomical data (Fig. 5.5D) with the density profiles of the corresponding growth ring (Fig. 5.5C) and its xylem macrostructure (Fig. 5.5B).

Discussion

During the cambial activity analysis (Dié *et al*., 2012), we recorded highly significant correlation between cambial fluctuations and monthly precipitation distribution and between the latter and cell differentiation. The precipitation controlled cell maturation showed that wide lumen and thin-walled cells are formed under substantial rainfall whilst narrow lumen and thick-walled cells are formed under decreasing rainfall.

Second, in the current chapter dealing with microdensity profiling, we observed an increase in wood density along with an increase in fibre wall thickness and a narrowing of vessel diameter. While density decreased with a decrease in fibre wall thickness and an increase in vessel diameter. This relationship explains the straightforward correlation between wood density and xylem anatomy. In addition, wood density significantly correlated with monthly precipitation.

In consideration to the above correlations and the subsequent analyses, we matched the wood features (macrostructure, anatomy and density) of rings R3 and R11 formed in 1973 and 1981 with the monthly rainfall of the corresponding vegetative periods. Growth rings R3 of tree Tw59772 (left) and R11 of tree Tw59771 (right) were selected for illustration in figure 5.5. This interrelationship could be observed in the same rings (with R3 and R11) of other trees, although somewhat inter-trees differences could exist (see supplementary figures in Appendix 5.4 in the present manuscript).

The inter-trees differences can be attributed to (i) the capacity of each tree to detect a change (improvement/degradation) in the growth conditions and (ii) to the growth rate (reflected by the ring width). The cambium may not respond immediately to a precipitation reduction/resumption. Precipitation induced growth interruption/recovery can occur days or weeks later. It is also worth noting that XGZ formed in ring 3 showed sharper boundary (in more trees) compared to XGZ formed in ring 11 (see supplementary figures in Appendix 5.4).

Based on the analysis of the cambial activity and the microdensity profiling, we deduce that the precipitation related cambial fluctuations appear as the plausible explanation of the precipitation-anatomy-density interrelation established in figure 5.5. And that the corresponding rings were, thereby, formed from February through October of the current year. This assumption is plausible because the cambium is reactivated in February and cell divisions cease in October (Dié *et al*., 2012); which explains the temporal length of the rainfall graph used in figure 5.5A.
Owing to the climate-cambium relationship, we conclude that the pronounced precipitation decrease occurring within the vegetative period (July-August: Fig. 5.5 left and April: Fig. 5.5 right) has caused growth cessation with the formation of latewood like cells. The subsequent resumption of precipitation has induced growth recovery with earlywood like cells formation. This xylem anatomy fluctuations – resulting in intra-annual xylem growth zones (XGZ) – is consistent with previous and recent investigations on rainfall related false rings formation in teak (Priya & Bhat, 1998; Palakit *et al*., 2012).

Conclusion

The overlapping of the different parts of figure 5.5 is not a comparative result of a day-to-day monitoring of wood formation and xylem anatomy changes in relation to daily rainfall variability. Some days or even weeks lag can be observed between the precipitation onset and the start of cell divisions and differentiation. Nevertheless, the present work provides evidence of precipitation induced wood density variability in teak.
The lack of documented density-rainfall correlation of teak is probably due to the fact that previous authors considered the total annual rainfall while wood density appears more sensitive to the intra-seasonal climate. We therefore suggest to combine a day-to-day monitoring of wood formation with density fluctuations in relation to daily precipitation collection (from the forest meteorological station). This approach is fundamental to assess teakwood density changes and growth dynamics under future more variable climate.

5.3. Discussion

5.3.1. Comparing the two study methods

A linear correlation and no significant difference were found between the X-ray derived density and the oven dried density obtained with the water displacement method. The little discrepancy between the two densities can be attributed to inaccuracies in both the X-ray and the immersion method. Therefore, future immersion density determination should consider the water absorption of the wood samples due to the wide vessels pores as well as the errors in the moisture content estimation. The tomography method is based on the attenuation of X-rays. As a consequence, the derived density is not only due to the wood structure (cell wall) but it also reflects the wood mineral composition (Lindgren, 1991; Knapic *et al.*, 2008). Because components such as crystals that fill cell cavities (Fig. 5.6) can increase X-ray absorption, this can give rise to an increase in density (Vansteenkiste *et al.*, 2007).

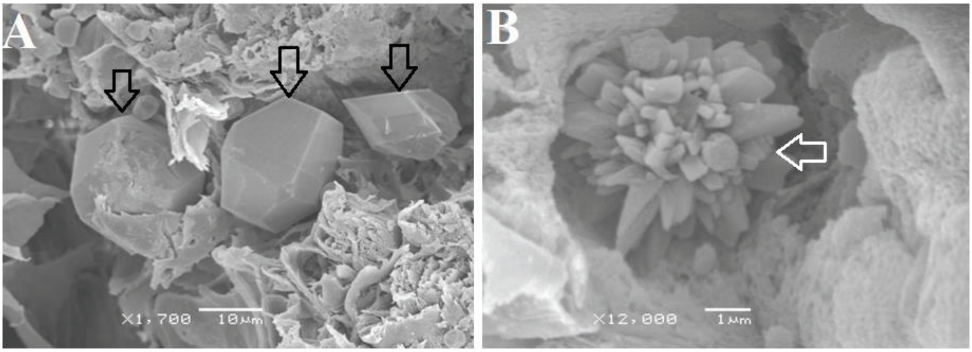


Figure 5-6. Solitary crystals (black arrows, A) and druses (white arrow, B) filling the lumens of differentiating xylem cells. Scale bars (white lines): 10 µm (A) and 1 µm (B).

Nevertheless, the average deviation (1.6 %) between the two densities, determined in this work, is lower than the 9 % obtained in *Terminalia ivorensis* (De Ridder *et al.*, 2011). This suggests that X-ray derived density is a sufficiently accurate estimator of the real wood density in *Tectona grandis*.

5.3.2. Main factor of density variability

5.3.2.1. Effect of the cambial age and ring components

Ring wood density highly correlated with earlywood and latewood densities over the growth period. This indicates that wood density variations are mainly generated by the variations occurring in the ring components features, namely earlywood and latewood content and densities, rather than by the cambial age.

Moreover, a small difference and an almost linear positive correlation were found between the total ring wood density and that of the latewood; although the former was statistically lower than the latter. In addition, total ring density positively correlated with latewood content which accounted for 62% of the ring width and wider rings contained higher latewood percentage. Second, total ring and latewood density both showed a very small increase from the juvenile to the mature wood (5 %), indicating that the total ring density increase is driven by that of latewood density. We also noticed that the correlation between total ring and latewood density remained constant in both the juvenile and mature part of the wood. Similarly to our result, high latewood content was obtained in Indian teak rings (Kumar *et al*., 2014). These relationships and the moderately low correlation between TotrD and EwD (this study), give evidence that latewood features (content and density) remain the main factors of wood density variations within the tree in teak.

Identical observations were also obtained in other hardwood species. In fact, a linear correlation was recorded between latewood and ring wood density in *Quercus faginea* where the latewood portion accounted for 66% of the total ring width (Knapic *et al*. (2011). Similar high latewood content was reported in the growth ring of *Quercus petraea* (Michelot *et al*., 2012).

Earlywood content was negatively correlated with total ring wood density, showing that a prolonged earlywood formation leads to a delay in the latewood initiation. This can (i) result in low latewood content as evidenced by a recent cambial activity (Dié *et al*., 2012) and (ii) cause, consequently, a decrease in total ring density due to the positive link between the latter and the latewood content. Furthermore we found a positive correlation between the earlywood density and the latewood proportion. This may suggest that environmental growth conditions triggering and sustaining latewood formation can contribute to an increase in earlywood density.

Radial variations of the intra-ring density also showed a significant effect of the cambial age on latewood percentage and density while no significant age trend was noticed in earlywood density variations over the growth period. Earlywood content (percentage) is being reported as a constant intra-ring and intra-tree parameter in teak (Priya & Bhat, 1999; Kumar *et al*., 2014) and other hardwoods such as European oaks (Degron & Nepveu, 1996; Knapic *et al*., 2011; Michelot *et al*., 2012). Fewer studies, dealing with hardwood density variations, addressed the age effect on earlywood features. The plausible reason can be that earlywood of hardwood species is more inherent to the tree rather than being controlled by the age, as it has been reported for softwood species (Gaspar *et al*., 2008). However, further study of cambial activity, combined with density heritability, is needed to explain the lack of correlation between earlywood density and cambial age as observed in the present study.

5.3.2.2. Effect of xylem anatomy variations

The present study demonstrated that wood density increased with increasing fibre ratio (wall thickness/lumen diameter) whereas it decreased with increasing vessel lumen diameter. The small number of position sampled within each of the examined growth-rings did not allow to prove significance of the above correlations, although they showed high values. Moya and co-authors (2009) observed an increase in teakwood density with an increase in fibre wall thickness in the latewood, although they did not perform a correlation analysis between xylem anatomy and wood density. Kumar and co-authors (2014) also recorded a wood density increase in the latewood. Our results confirm the close link between xylem anatomy and wood density for teak as it has been evidenced in other hardwood species (Guilley, 2000; Zieminska *et al*., 2013; Fortunel *et al*., 2014).

This influence of xylem anatomy explains the low values of wood density observed in the earlywood and earlywood like zones in this study. Results also showed wide lumen and thin-walled fibres in these earlywood zones which correspond to the early stage of teak cambial activity under substantial soil water availability (Dié *et al*., 2012; Palakit *et al*., 2012). Such fibres possibly assist earlywood vessels in capillary water storage (Zieminska *et al*., 2013), particularly in xylem containing low parenchyma content (Hao *et al*., 2013) such as is the case in teak (Bhat & Pryia, 2004). In spite of their ecophysiological role, the formation of such fibres can lower the wood density in earlywood region.

Similar xylem anatomy influence on wood density has been reported in low and middle dense wood species (Découx *et al*., 2004; Moya & Tomazello, 2007). More specifically, Moya and Tomazello (2007) evidenced that 76 to 96% of density variations observed within the ring were generated by the xylem anatomy fluctuations. Thus, examining xylem variations still point at the fact that latewood remains the main intra-ring driver of wood density.

5.3.3. Climate influence on wood density

The cambial activity studies consistently give evidence of the indirect effect of rainfall on wood density through its influence on xylem cell properties (Dié *et al*., 2012; Wang *et al*., 2013; Patel *et al*., 2014). During a growing season with no significant intra-seasonal rainfall variations the cambial functioning results in a steadily decrease in cell lumen diameter associated to a steadily increase in cell wall thickness from earlywood to latewood (see Fig. 5.4). This gradual distribution of xylem anatomy leads to an increasing density along the earlywood-to-latewood gradient due to the close anatomy-density link.

Most of the scarce studies, available on wood density sensitivity to rainfall in tropical trees, generally use the mean tree density (a.o. Yeboh *et al*., 2014). Only few investigate the annual and intra-annual density fluctuations in relation to climate e.g., in *Tectona grandis* (Moya *et al*., 2009; Nocetti *et al*., 2011). Nocetti *et al*. (2011) found no local rainfall influence on teakwood density, while the results of Moya and co-authors (2009) somehow suggested a link between the two variables in Costa Rica. However, our results confirmed the interrelation between rainfall, xylem anatomy and wood density and provided a direct link between wood density and rainfall of the post-wet season of the current growing year.

The occurrence of a severe water shortage – due to a significant decrease in rainfall at any stage of the growing season – can induce an onset of the cambium environmental quiescence characterized by the formation of latewood like cells. When rainfall resumes significantly, this triggers growth recovery through the production of earlywood like cells. This fluctuation in xylem anatomy results in the occurrence of intra-annual xylem growth zones (XGZ) in the current ring (Palakit *et al*., 2012; Battipaglia *et al*., 2014; De Micco *et al*. 2014) as it is observed in our study (Fig. 5.5). High wood density values are observed with an abrupt narrowing of vessel diameter at the inward border of these XGZ (Lwlike zone) then density decreases with the formation of wide lumen vessels and fibres (Ewlike zone). This fluctuating xylem anatomy, in response to significantly varying moisture conditions, reflects the physiological adjustments of trees to environmental constraints (Gea-Izquierdo *et al*., 2012); a process through which trees reduce their vessels diameter in order to prevent cavitation risks and maintain efficient water uptake and transport (Hacke *et al.,* 2001; Ziaco *et al*., 2014).

Accurate description of the above XGZ can provide an insight in the climatic characteristics having caused their occurrence. Wider diameter vessels are reported to form under high moisture availability (Kitin *et al*., 2003; Marcati *et al*., 2006; Dié *et al*., 2012; Patel *et al*., 2014).

5.3.4. Latewood sensitivity to climate

Our results clearly gave an insightful understanding of the climatic signal in the ring wood density variations that can be traced back to the high sensitivity of latewood features (width and

density) to the post-wet season rainfall. Environmental factors influencing variations of latewood features also cause changes in the wood density, as the latter is strongly dependent on the former ones.
Previous studies consistently reported the sensitivity of latewood features to climate variability in other species (Zhang, 1997, Vanstone *et al*, 2010; Alla & Camarero, 2012; Chen *et al*., 2012; An *et al*., 2013). Theses authors revealed latewood responses to climate during the late part of the growing season, similar to our results and to previous investigations of the xylogenesis in teak (Dié *et al*., 2012). In those investigations, latewood formation extended from June through November (post-wet season) of the current growing season. This explains the significant correlation of latewood features with rainfall variables during that period. It also indicates that climatic events remain the main factor controlling latewood formation. Previous works, on intra-annual growth variations, also concluded on the limitation of latewood formation by the water shortage rather than by carbohydrates availability (Mirjam *et al*., 2005) or by the indole-3-acetic acid concentration (Uggla *et al*., 2001).

Earlywood formation, rather, seems subjected to the availability of growth hormones and carbohydrates stored during the preceding growing season (Rao & Dave, 1983; Latt *et al*., 2001; Mirjam *et al*., 2005; Simard *et al*., 2013). Dié *et al*. (2012) observed starch accumulation in the quiescent cambium samples used for teak xylogenesis study. They also noticed an earlywood initiation under monthly rainfall equal to that of the onset of the dry season. These facts show the complexity of the factors controlling earlywood formation. This complexity, in turn, can justify the insignificant correlation between earlywood features and all precipitation variables found in the present study.

Conclusion

Teakwood density variability was examined through microdensitometrical profiling. Wood density was highly variable within the tree, more than between trees. All 6 trees examined were collected from the same plantation and show a similar trend of inter-ring density profile. Inter- and intra-annual wood density fluctuations were, mainly, ascribed to the variations of the latewood features. The small difference in density between earlywood and latewood (12%) can represent an advantage for teakwood. Because the earlywood formation, that seems to be inherent and low in variability, can buffer the impact of latewood density fluctuations and thus stabilize the overall tree wood density under fluctuating climatic episodes.

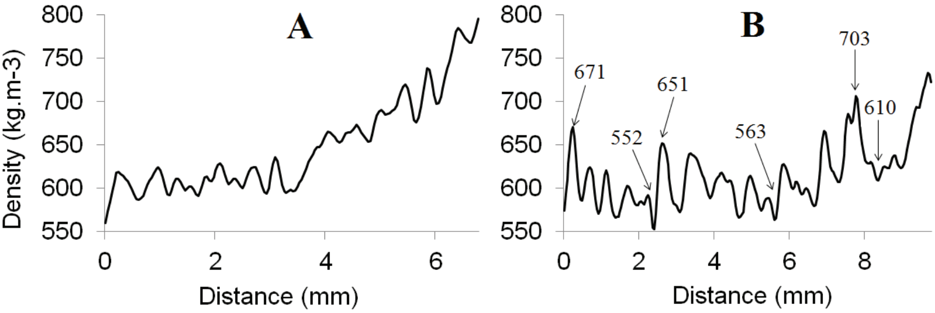
Climate-wood density responses are mainly related to the high sensitivity of the latewood features to the post-wet season rainfall. All density types (ring, earlywood and latewood density) did not significantly respond to long-term climate change (annual rainfall and major wet season rainfall). This suggests that intra-ring density components are appropriate proxies to study short scale climate variability. Further studies, using X-ray computed tomography, should also focus on vessel frequency and other climatological relevant structures such as parenchyma. The current microdensitometrical profiling showed clear climatic potential of the latewood as a proxy for further forest ecophysiological studies.

Box 5-2. Additional data to chapter 5

1. Trends and patterns of ring density profiles within the trees

The width and density of both earlywood and latewood ring components are becoming promising proxies in the analysis of the intra-seasonal influence on both the tree growth and wood density. For that reason, it is necessary to accurately measure the extent of the earlywood or latewood zone in order to determine the related wood density.

Clearly it is of interest to discuss the use of intra-ring density variations in the growth ring delineation. The existing ring limits demarcation, using the tomography method (X-ray CT scnning), is based on the general observation that the lowest density values are found in the earlywood zone and that the highest density values characterize the latewood. The presence of another intra-ring density fluctuations pattern may affect the reliability of both the ring delineation and the estimate of earlywood and latewood width. Therefore radial (intra-ring) variations of the density profiles were carefully examined in order to define the fluctuation trends. This section is intended to present and discuss the different trends of density variations that can be found within a growth ring. Assessing the density fluctuations pattern within the ring is usefull for two major reasons, (i) the determination of the transition between earlywood and latewood, and (ii) the radial variations of wood density.



S5-3. Intra-ring density variations showing the trend of increasing or ID (A) and the trend of alternating density or AD (B) from earlywood to latewood. Note the magnitudes of the density fluctuations (AD) from the earlywood to the latewood in the graph B corresponding to the density profile of the growth ring 29 of sample Tw59772.

The determined density profiles gave two clear earlywood-to-latewood density trends in all trees: a steadily increasing density (ID) and a significantly fluctuating or alternating pattern of density (AD) along the earlywood-latewood gradient.

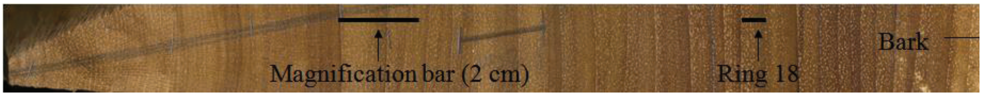
Diverse methods, based on density threshold values and considering the ID as the general trend of intra-ring density variations, were developed in order to determine the transition between earlywood and latewood (Koubaa et al., 2002; Découx et al. 2004; Knapic et al., 2007). While the clear occurrence of the alternating pattern of density fluctuations pattern (AD), described in our study implies that the highest density values are not always found in the true latewood. The presence of a significant AD can compromise the application of the methods using the density threshold values to determine the earlywood-latewood transition for species that exhibit intra-ring wood density fluctuations as significant as those observed in our study. It can also affect the use of density for accurate growth rings delineation in the stem portions exhibiting such pattern.

Due to these implications of the occurrence of AD, it is essential to develop an appropriate methodological approach which integrates such density fluctuations trend. This will enhance the robustness of the use of earlywood and latewood widths in dendroclimatic analysis at the intra-annual scales. The presence of one of the density pattenrs (ID or AD) as such can also be an indication for different seasonal climatic patterns of the corresponding growth years.

2. Radial variations of fibre length

2.1. Methods

Ten stem discs (one disc per tree) were used in order to assess the radial variations of fibre length (FL). For that purpose, a pith-to-bark wood strip (Fig. S5-4) was cut off from each stem disc or tree. The strip was then split into 35 small wood blocks following the growth rings boundaries under the stereomicroscope. As a result, each wood block corresponds to one growth ring.



S5-4: Pith-to-bark wood strip of tree sample Tw59769 scanned at a resolution of 2400dpi and showing the growth ring 18 used to illustrate the intra-ring fibre length sampling.

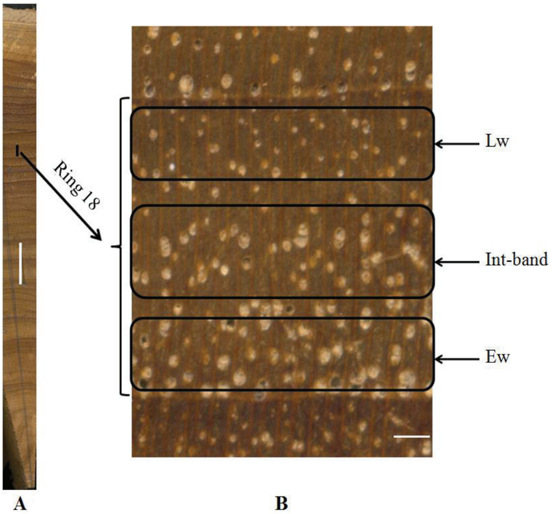
The radial variations of the FL were examined at both the within-tree and intra-ring levels.

- Inter-rings (pith-to-bark) FL variations

We sampled in the middle of each growth ring according to IAWA (1989) recommendations for growth rings with clearly visible boundaries. Each growth ring was divided into 3 parts (Fig. S5-2). The middle part (intermediate band) was split into small sticks that were soaked in the maceration solution prepared according to Franklin's method (Ruzin, 1999). All relevant informations concerning the wood sample were reported on the bottle containing the maceration and the immersed wood piece. The container is then left in the oven (50°) over days and taken out when the wood sticks were whitish. The latter (sticks) were rinsed in running water for 10-15 minutes and left in water overnight. Only one twig was taken from each container and was dissociated into individual fibres that were stained in Safranin O (Merck), dehydrated in 100% ethanol and mounted in Euparal (Art. 7356.1; Carl Roth Gmbh + Co. KG., Karlsruhe/Germany) on permanent slides. Fifty individual fibres per slide were measured in order to calculate the mean FL per ring. The radial distribution of the set of 35 values of mean FL (for the 35 used rings) was analyzed to describe the pith-to-bark FL variations and define the extent of wood juvenile phase.

- Intra-ring FL variations

Five trees were used to analyze the intra-ring or earlywood-to-latewood variations of the FL in both the juvenile and mature. For that purpose we sampled wood sticks in fives positions per tree. These positions are represented by 5 growth rings: near the pith (R3), inner heartwood (R11), middle heartwood (R18), outer heartwood (R26) and one growth ring (R30) in the sapwood. Each of these growth rings is divided into three parts: earlywood (Ew), middle part or intermediate band (Int-band) and latewood (Lw, see Fig S5-5). The small wood sticks of of each ring zone were macerated following the same procedure as in the case of the inter-ring FL variations analysis. This method was applied to all the randomly selected five trees. The mean FL was the average of fifty fibres measured from each microslide representing each ring zone.



S5-5. Wood strip (A) with a detailed view of the sampled ring zones (B). The black bar on figure (A) represents the growth ring 18 of tree Tw59769. Image shows the detailed sampled ring zones: Ew = earlywood, Int-band = intermediate band and Lw = latewood. Scale bars: 2 cm (A, vertical white bar) and 1 mm (B, horizontal white bar).

Basic statistics (coefficient of variation: CV) were used to characterize the inter-rings and intra-rings fibre length variations. A CV value below 10% indicated homogenous (non significantly variable) distribution; which characterizes the mature wood (Quilhó & Pereira, 2000; Kokutsé, 2002). A Segmented Regression (SegReg) was applied to the pith-to-bark set of FL in order to define the transition age between juvenile and mature wood based on the radial FL variations.

For each ring zone (Ew, Int-band and Lw), a FL comparison was performed between the five selected trees; aiming to find out if the intra-ring FL variation was similar between all studied trees. In the Tukey HSD multiple comparisons, displaying the pairwise similarity probabilities, the FL was considered as dependent variable and the different zones within the growth ring (Ew, Inter-band and Lw) as factor. We also investigated the intra-ring variation of FL in order to know whether the intra-ring FL distribution also reflects trees juvenility. We obtained the following results:

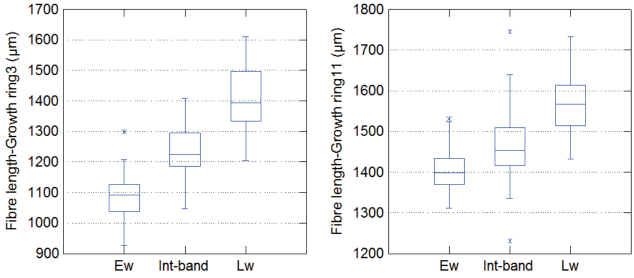
2.1. Results and discussion

- Pith-to-bark FL variations with regard to IAWA and juvenile wood demarcation

Fl increased from 626 µm (ring 1) to 1892 µm (ring 31) with a mean value of 1615 ± 241µm. The study trees form long fibres (FL = 1604.43µm) – according to IAWA description – at the cambial age 11. However, the Segmented Regression (SegReg) showed a significant breakpoint or transition age between the growth rings R7 and R8 (Breakpoint value =7.35), with the cambial age explaining 94% of the FL variation ($p < 0.05$). At this transition age (R8), the FL reached a mean value of 1554.68µm. From R8, the Fl variations significantly decreased (R1-R8: CV = 20 % and R8-R35: CV = 6 %). Our study trees showed a transition between the juvenile and mature wood at the cambial age of 8 years, later than the transition age (5 years) found in Teak growing in a humid tropical climate site of Costa Rica (Moya *et al.*, 2009).

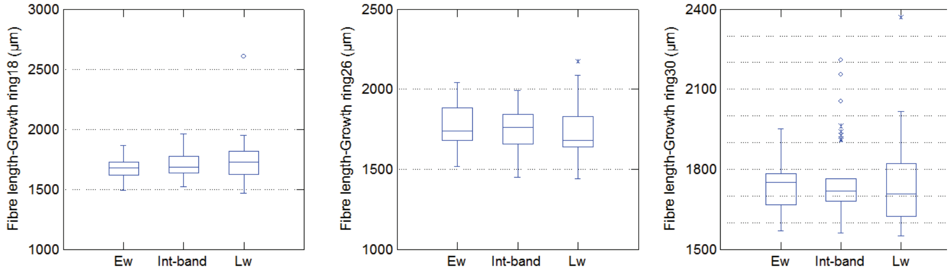
- Earlywood-to-latewood FL variations

The FL was highly variable near the pith (R3: r^2: 0.69; F-ratio: 99.23 with p: 0.000) and in the inner heartwood (R11: $r^2 = 0.43$; F-ratio = 35.49 with p = 0.000, see also Fig S5-6)



S5-6. Earlywood-to-latewood variation in the FL near the pith (Ring 3) and in the inner heartwood (Ring 11).

While from the middle heartwood (R18) to the sapwood (R30) the FL showed no significant variations from earlywood to latewood (Fig S5-7).

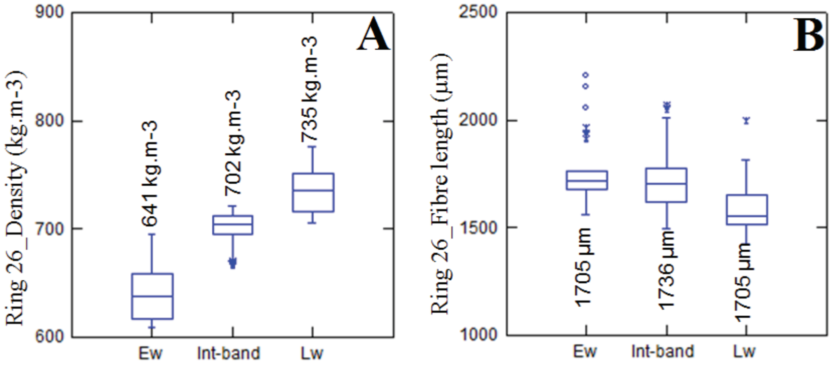


S5-7. Earlywood-to-latewood FL variations in the middle heartwood (R18), outer heartwood (R26) and in the sapwood (R30).

3. Comparing radial variations of wood density and fibre length in juvenile wood demarcation

We can somehow indicate that the Fl exhibits an earlier mature phase (from the 7th year) compared to wood density which reached its mature phase at the age of 14 years.
A ring-to-ring comparison of Fl and density distribution within the ring indicated high variations in both variables along the Ew-Lw gradient near the pith (R3) and in the inner heartwood, although wood density showed pronounced fluctuations rate compared to FL. In R3, the Tukey test gave the following statistics: $F = 47$ and $F = 1265$ at $p < 0.0001$ for FL and wood density, respectively. In R11, we obtained $F = 35$ and $F = 79$ ($p < 0.0001$) for Fl and density.

In the middle heartwood (R18) the mean FL was found significantly similar in both the Ew, Int-band and Lw (F: 0.06; $p < 0.0001$) while wood density still fluctuated ($F = 10$; $p < 0.0001$). In the outer heartwood (R26), Fl was significantly homogenous in both ring zones ($F = 0.38$; $p < 0.0001$). On the contrary, density still exhibited significant fluctuations between Ew, Inter-band and Lw (F: 963; $p < 0.0001$, see Fig S5-8) in the outer heartwood (R26).

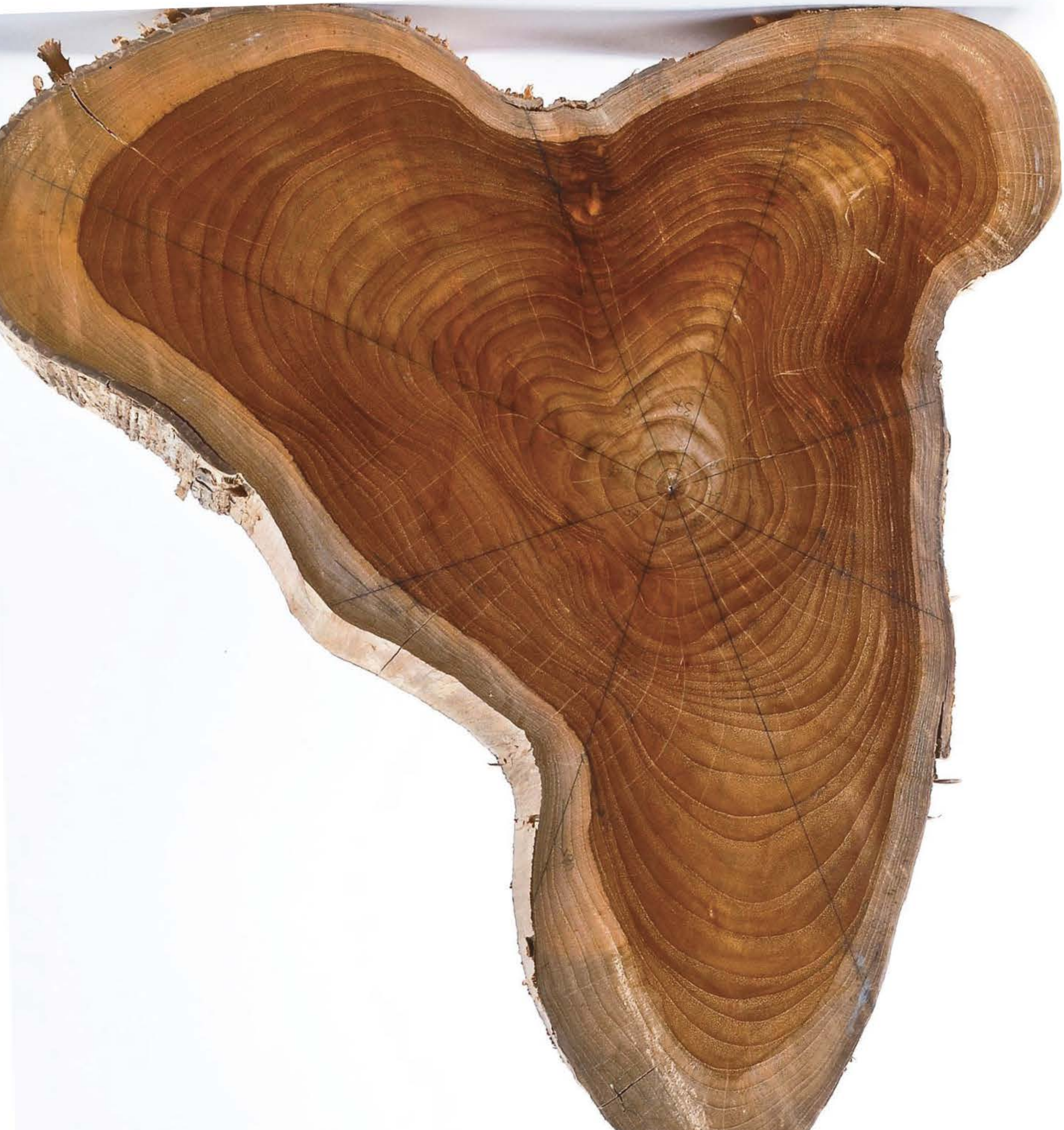


S5-8. Comparison of earlywood-to-latewood variations of wood density (left) and fibre length (right) in the outer heartwood (R26). Note the highly significant differences in density between Ew, Int-band and Lw zones (F: 963; $p< 0.0001$) while the fibre length showed no difference (F: 0.46; $p< 0.001$).

From the above results comparison, it is worth noting that wood density appeared highly variable at the different growth stages in trees: near the pith (R3), in the inner, middle, outer heartwoods (R11, R18 and R26). From this result and in accordance with Izekor *et al.* (2010), we conclude that density, representing the fundamental estimator of wood properties (Moya *et al*., 2009; Izekor *et al*., 2010; Shanbha & Sundararaj, 2013; Wanneng *et al*., 2014), remains the key parameter explaining wood homogeneity/heterogeneity.

As a reforestation species, thinnings implemented in the Ivorian Teak plantations provide wood products at an early age (5-15 years). These products are used for interior capentry as well as for outdoor applications (Voui Bi, 2008). For these solid utilizations, it is important to have an homogenous wood material, i;e, in which the density is less variable (Echols, 1973).

In the present study, we obtained a juvenile phase covering the 14 years of trees lifespan based on the radial density variations. This transition age between the juvenile and mature falls within the interval of 5-15 years of the products derived from thinnings.



Chapter 6: Conclusions, outcome impact and implementation

Reforestation programs play a vital role in contributing to restore the degraded lands. The management of both natural and man-made forests, on a sustainable basis, represents a challenge when reliable and useful data are not available. The success of these forest/plantations necessitates information on the relationship between site conditions and growth characteristics of the tree species used. For instance, the knowledge of the long-term diameter increment of trees as well as the growth responses to climate is essential for a sound sylvicultural management, aiming to enhance high quality wood production. Integrating different research methodologies to study the diverse growth influencing factors related to anatomical, dendrometric and ecophysiological components represent an efficient attempt to gain insight into tree growth dynamics under climate change.

In Ivory Coast, the reforestation programs preferred teak to other exotic and local species because of its high growth performance and wood quality. Due to the increasing international demand for teakwood, logs from short rotations of 20 years are now preferred (Kollert & Cherubini, 2012) to the traditional long rotations of 50-80 years, which were previously used in the country (Tariel, 1966). Reducing the plantations rotations raises the concern about the age related dynamics of wood properties like density. Evaluating wood density variability holds, therefore, a noticeable importance for timber quality. Because wood density – described as key indicator of general wood properties (Moya *et al*., 2009; Izekor *et al*., 2010; Shanbha & Sundararaj, 2013; Wanneng *et al*., 2014) – is said to be mainly controlled by trees juvenility and also by intra-annual growth fluctuations.

The present work first examined (i) the climate-growth responses of teak under sylviculture and (ii) evaluated the effect of growth influencing factors on wood density. We intended to study the effect of the climate on growth because climate and particularly precipitation has been identified as the main tree growth controlling factor in tropical regions (Wagner *et al*., 2012; 2014).

The current level of climate change is not yet detrimental to teak growth and productivity in Ivory Coast. At this stage of their development, the Ivorian teak plantations do not suffer a significant water deficit – induced by a decrease in precipitation – likely to hinder tree growth. Our work, nevertheless, aims to provide methodological tools on how to accurately evaluate growth rate and sensitivity to water deficit in these planted forests under sylvicultural management and under the predicted future precipitation decrease due to global warming (IPCC 2007). For that purpose, we first presented xylem vessels and we addressed a possible vessel conductivity failure due to water deficit (Chapter 2). Because vessels represent the most relevant cells of the tree functional anatomy involved in tree's ecophysiology (water transport for growth activity). We then analyzed growth periodicity and responses in relation to climate and finally evaluated the effect of growth fluctuations on wood fibres and density in a single-species forest stand such as teak plantations.

In the current ending chapter, we (i) highlight the methodological approaches applied and (ii) consider important to provide few additional information relevant to better explain and support the important aspects developed in this study and useful for a sound forest management.

6.1. Cambial sampling, tree-ring analysis and microdensity profiling as tools to accurately analyze growth responses and evaluate wood variability

Growth responses analysis necessitates the knowledge of growth periodicity and sensitivity to the environmental factors. To that effect, the monthly cambial sampling implemented during one and half years (Chapter 3) is an efficient strategy to (i) monitor the cambial activity and (ii) determine and relate the cambial periodicity to the climate seasonality. Our investigations allowed to observe successive structural changes in the cambial zone resulting in the formation of one growth ring per year. Furthermore, relating the morphometric features of the cambial development (cambial zone width, cambial cells number and width of the differentiating xylem zone) each to another and establishing a straightforward correlation between these features and monthly rainfall provides a biological explanation to the statistical analysis of the climate-growth relationship.

The rainfall related intra-seasonal cambial fluctuations resulted in the formation of the intra-annual xylem growth zones (XGZs) accompanied by fluctuations in the xylem anatomy. XGZs formation is mainly induced by a pronounced decrease in rainfall (during cell divisions) followed by the resumption of substantial precipitation during the same vegetative period. XGZs, morphologically different from the true annual rings, show considerable potential to (i) study the influence of intra-annual climate fluctuations on tree growth and (ii) to evaluate the effect of the subsequent anatomical fluctuations on wood density.

The self-regenerative capacity of the cambium, observed in this work, is essential for tree recovery and tissues regeneration after cambial wounding or an attack by biotic agents such as insects or fungi such as *Fomes lignosus*. This fungus is known as the main pest affecting teak growth and productivity and can induce trees dieback in West Africa (Maillet *et al*., 1985; Ganglo & Lejoly, 1999), particularly in Ivory Coast (Dr. Coulibaly of the Centre National de Recherches Agronomiques of Cocody: CNRA, pers. Com.). The result of these cambium wounding and attacks can be observed in the annual ring in the form of narrow rings (low productivity) and false rings which has a negative effect on wood density.

The annually formed wood layer (annual ring width) is the cumulation of the influence of several growth factors both endogenous (tree age and genetics) and exogenous (climate, soil, sylviculture, insects and/or fungi attacks, fire). In a climate-growth responses analysis, it appears essential to statistically eliminate the other influencing factors, through the ring widths standardisation in order to highlight the climate effect (Mérian, 2012).
In our study case where both plantations showed no attack from insects, fungi or fire, the autoregressive method – using the Cubic smoothing Spline (Cook *et al.*, 1990) – was applied to the series of the ring widths accurately measured under a stereomicroscope using the TSAPWin 0.55 software. This standardisation function (Cubic smoothing Spline) aims to detrend (remove the year-to-year cambial age effect) from the ring widths time series. We, later, calculated the different growth parameters (see text box 4.2 of Chapter 4), to decide whether the ring widths series could be used to examine the climate influence. The significant values of crossdating and standardisation indicated the effect of an external factor, namely the climate, that influenced growth dynamics during trees lifespan.

It was said that younger trees – with an age below 40 years – are not appropriate for tree-ring analysis or dendrochronology (Fritts, 1976). The ring widths series of such trees give low values of crossdating resulting from weak growth synchronicity. These short ring widths time-series are also not appropriate for climate-growth analysis. In spite of their young age, however, the two ring width time-series of both the Séguié (35 years) and the Gagnoa plantation (37 years) gave significant crossdating and standardisation values comparable to those of older teak from natural forest. Furthermore, the two sites showed climate-growth response patterns similar to those of older trees. This shows the potential of young trees for dendroclimatological studies.

Most of the studies dealing with teakwood density variations based their investigations on the mean tree density and attributed the density changes mainly to the tree age. Research carried out mostly on temperate trees (Découx *et al.*, 2004; Bouriaud *et al.*, 2005) complemented to the findings of Moya and Tomazello-Filho (2007) on Gmelina *arborea*, clearly indicates that the within-tree variations – largely generated by the xylem cells structure and proportions, the earlywood-to-latewood transition, the widths and densities of earlywood and latewood – account for more in wood density fluctuations (Zobel & van Buijtenen, 1989; Knapic *et al.*, 2011; Zieminska *et al.*, 2013).

The Ivorian teak plantations provide wood for multiple utilizations at an early age. To encourage the use of this wood for solid timber applications – carpentry and outdoor furniture, for instance – it appears essential to assess the extent of its homogeneity, i.e., the degree of wood density variability (Echols, 1973). The methodology, aiming to fulfil this objective, should integrate all possible sources of density variability such as the external growth factors, tree age, xylem anatomy as well as the earlywood-to-latewood transition. For that reason, we performed a microdensitometrical profiling using the state-of-the-art helical X-ray tomography combined with ring and fibre angle corrections (Van den Bulcke *et al*., 2014) in 3D, in order to obtain unbiased ring density values. The analysis of the derived density profiles, combined with xylem anatomy description, led to important results such as the juvenile wood phase demarcation and the determination of the main density influencing factors within a single-species tree stand such as the teak plantations.

6.2. Integrating cambial activity, tree-ring and wood density for sustainable forest management and carbon sequestration under future climate

6.2.1. Relevance of growth periodicity determination

The cambial monitoring (Chapter 3) and tree-ring analysis (Chapter 4) both confirmed the annual nature of growth rings in teak growing in both study sites as it has been documented in the natural Asian forests. The cambium formed one growth ring per year and the number of the delimited growth rings (during tree-ring analysis) corresponded to the age of the studied plantation. This indicates that both applied methods were successful. Future studies should combine visual and statistical crossdating underpinned by cambial monitoring for accurate determination of ring boundaries especially in tropical species showing diffuse-porous wood. Accurate ring delimitation is essential because annual growth rings hold a considerable potential for:

- **Tree age determination**: The age determination can help to know (i) the forest age, an important data which is still missing for more natural forests in the tropical regions and (ii) the biological rotation age. Applying the current methodology (cambial sampling) to local tree species in the neighboring natural forest stands will contribute to overcome this lack of information. The knowledge of tree age also helps in demarcating the juvenile growth phase likely to influence both the growth rate, xylem anatomy and wood properties.

- **Tree growth dynamics evaluation**: The annual nature of the growth rings can help to calculate relevant parameters such as mean annual/current volume increment useful for sustainable forest management. This wood productivity parameter is fundamental for biomass calculation. Integrating the forest inventories and the combined cambium-ring analysis will represent an efficient approach leading (i) to a reliable determination of these management concepts and (ii) to assess their temporal variations.

Furthermore, the knowledge of the onset and the timing of the cambium activity in relation to seasonal precipitation variations added to the climate-ring width relation can help (i) understanding how trees respond to climate changes and (ii) estimating biomass productivity under future significant climate change. While integrating wood formation, tree-ring analysis and high-resolution ring density determination represents a perfect experimental setup for accurate calculation and prediction of trees biomass productivity and carbon storage capacity under changing environment. Most of the existing methods commonly use the mean tree wood density for these calculations; which may overestimate the carbon content and may lead to biased predictions (De Ridder, 2013). Because wood density is shown here (Chapter 5) to be more variable within the tree and especially at the intra-ring level.

6.2.2. Importance of characterizing growth and wood juvenile phase

Tree-ring analysis (Chapter 4) revealed a significant age effect on tree growth, leading to the demarcation of the growth juvenile phase (covering the first 13 years). In addition, during the microdensity profiling (Chapter 5) performed on wood strips extracted from the stem discs used in tree-ring analysis, we obtained accurate absolute density values that served to construct the pith-to-bark density profiles. The correlation and regression analysis thereof led to obtain a juvenile wood density phase covering the first 13 or 14 years using the latewood or total ring density, respectively. Furthermore, the fibre length (Fl) measurements also gave a short juvenile phase of 11 years based on the intra-rings Fl variations (see supplementary figure S5.6 in Chapter 5). Our study trees from the thinned stand (in regard to the above results) exhibited a shorter juvenile phase compared to the results found in East Timor and Indian teak (Bhat *et al*., 2001; Sousa *et al*., 2012; Kumar *et al*., 2014).

The simultaneous observation of cambial activity, fibre length measurements and wood density profiles gives evidence that the juvenile phase is more affected by growth anomalies resulting in the formation of intra-annual xylem growth zones (Fig.3.11 of Chapter 3 and section 5.2.5 of Chapter 5).

Juvenile wood properties have been described in Indian teak (Bhat *et al*., 2001) by applying the Segmented Regression to the measurements of differents wood properties. The present work is the first one providing results from integrated research approaches (cambial activity, wood anatomy, tree-ring analysis and wood density profiling). The structural changes occurring in the cambial zone and their possible causes (Chapter 3) provide further data to strengthen the statistical analysis applied for juvenile wood demarcation based on the use of radial variations of wood properties.

Based on the combined results of tree-ring analysis, fibre length measurements and density profiling, we found that the sylvicultural treatments, aiming to optimize growth performances, did not result in prolonging the formation of juvenile wood in trees. This is an interesting observation indicating that the intensification of sylvicultural treatments during the juvenile phase will accelerate wood productivity and may not be significantly detrimental to wood density in the mature part of trees trunk.

The juvenile phase characterization holds a noticeable importance for a sound sylvicultural management of our study species because trees juvenility is said to mask the expression of the indicators of growth (tree height and diameter) and wood properties (knots and buds index, and wood physico-mechanical properties) in teak (Verhaegen *et al*., 2010; Solórzano *et al*., 2012; Fofana *et al*., 2014). This influence of tree juvenility may give rise to the following interrogation: Do the younger trees growth dynamics reflect tree juvenility or the influence of site conditions? This interrogation paves a way for further investigations aiming to dissociate the role of tree juvenility from the influence of environmental factors such as climate when examining growth responses.

6.2.3. Assessing the positive role of sylviculture on growth rate and sensitivity to climate

Growth synchronizing effect

Tree-ring analysis (Chapter 4) confirmed the role of the sylvicultural treatments, namely the thinnings, in accelerating wood productivity: the wider growth rings were observed in the thinned stand (Séguié). During this study, the juvenile phase demarcation was only possible in trees collected from the thinned plantation, while those from the non-thinned stand showed no segmented ring widths profile. This difference in growth performance and ring widths profiles segmentation can probably be ascribed to the sylvicultural treatments. Thinnings thus offer other advantages such as contributing in the observation of trees juvenile growth period.

The crossdating and standardisation procedures were successful in both study sites. The Séguié teak plantation, however, showed higher values compared to that of Gagnoa. Thinnings applied in Séguié had a growth synchronizing effect on trees reflected, particularly, in the high value of the total tree population expressed signal (EPS = 0.90; see Chapter 4, table 4.1 in section 4.2.2).

The low growth synchronicity observed in Gagnoa, resulting in low crossdating values, can be related to the eccentricity in ring formation around the pith. Growth eccentricity can originate from buttresses formation in these stem discs collected from the stumps of the felled trees. However, the sampling height may not be the plausible reason of low crossdating in Gagnoa because all discs including those from Séguié were collected at the same height above the ground level. We observe that the lack of thinnings in Gagnoa increased competition for growth resources between tree individuals, leading to uneven growth distribution around the pith (eccentricity). This analysis is in line with previous results obtained from non-thinned East Timor and Indian teak (Ram *et al*. 2010; Sousa *et al*., 2012). The lack of external growth enhancing interventions has probably facilitated the continuous decrease in ring widths in line with the biological growth process. Reducing the stand density, through periodic thinnings, could have reversed this decreasing growth trend. The present result should, however, be taken with caution because of the small sample size.

Climate-growth sensitivity

In the tree-ring analysis, we aimed to examine the climate-growth responses of teak in a thinned stand in Séguié. To that effect, we intended to collect tree stem discs from two plantations (one thinned and a non-thinned one) growing in the same microenvironment. This intention could not be satisfied because all the teak stands of Séguié are under periodic thinnings. The Gagnoa site, where the plantation received no sylvicultural treatments, was therefore selected. The text box 4.1 (Chapter 4) gives the reasons motivating the selection of both Séguié and Gagnoa sites.

In both sites (Gagnoa and Séguié), trees responded significantly to intra-annual precipitation (major wet season and monthly). Séguié thinned plantation gave additional significant but moderately low correlation with annual precipitation contrary to Gagnoa where the non-thinned stand showed no correlation with that climate variable. This difference in the climate-growth responses may reflect the fact that, despite disturbances in precipitation noticed at both sites, thinnings applied at Séguié were more responsive. A plausible explanation of this positive effect of thinnings is that the reduction of the stand density, which contributes also in reducing crown rainfall interception, leads to more rainfall infiltration in the forest soil (Bréda *et al*., 1995; Gea-Izquierdo *et al.* 2009; Martin-Benito *et al.* 2010; Moreno-Gutierrez *et al.* 2012; Zhang *et al*., 2013). Soil water reserve is thereby substantial due to important water availability resulted from previous year rainfall. This substantial soil water availability makes trees to respond to the annual precipitation when they do not suffer water deficit during the major part of the vegetative period.

The reverse case was observed in Gagnoa where the growth of trees crown volume increases leaf rainfall interception in this unthinned stand with almost close density (high number of trees/ha). This can result in low water infiltration and lower soil water availability for each tree; leading to increased competition for water and others growth resources between individuals. In these unfavourable soil moisture conditions, trees are expected to be highly water demanding soon after the onset of cell divisions; which explains the strong correlation with the intra-seasonal rainfall (see Chapter 4, section 4.2.3).

Microdensitometry profiling as new proxy to study climate-growth sensitivity in teak

This experimental setup performed in Chapter 5 is the first establishing a direct correlation between climate and wood density in teak, based on the statistical analysis of field data. Furthermore, we recorded significant values of crossdating and standardization applied to the total ring density profiles of all the six studied trees ($Tv_{BP} = 3$; ppr = 69; ms = 0.43; ac = -0.021) but a low EPS value (EPS = 0.43). The non significant common signal expressed by all the six trees (EPS) can probably be attributed to the small sample size. The overall result of crossdating and standardization indicates a strong effect of climate on wood density, since the standardisation extracted the age effect from the density values. Furthermore, the responses of the non standardized absolute density profiles of the total ring (TotrD), earlywood (EwD) and latewood (LwD) to climate provide further information on the intra-annual precipitation variations which could not be extracted from the tree-ring analysis.

The precipitation related cambium dynamics combined with the significant correlation newly recorded between precipitation and wood density represents a new methodological approach for climate-growth responses analysis at the intra-annual scale in tropical trees. Future studies should (i) increase the sample size, (ii) consider the different ring components (TotrD, EwD, LwD, Ewp and Lwp) and (iii) test and integrate the responses of the standardized density profiles to climate. Considering the relation between standardized density dynamics can help to distinguish between the age effect and the climate influence when analyzing wood density variability.

All ring components responded to intra-seasonal precipitation and not to the total annual rainfall. This most probably explains the lack of significant correlation observed between wood density and total annual rainfall in teak by Nocetti and co-authors (2011). The significant role of the intra-annual climate fluctuations in inducing density variations strongly sustains the correspondence established between the growth year precipitation and wood features in figure 5.5 (Chapter 5). The formation of the xylem growth zones (XGZs) observed in the examined rings results from a growth recovery following a growth interruption caused by unfavorable water conditions during the vegetative period. This phenomenon is associated with xylem anatomy fluctuations within the current growth ring: a latewood like zone of thick-walled and narrow lumen cells is followed by an earlywood like zone characterized by thin wall and wide lumen cells.

Despite their negative role, in inducing wood density changes in trees and making the ring delineation more difficult, the XGZs formation represents an anatomical adjustment of trees to maintain efficient growth in changing ecological conditions. Trees form new xylem conduits – with appropriate vessels diameter – to ensure water ascent to sustain growth activities during the current vegetative period. For example, some species are said to form small vessels in response to extreme site moisture conditions (Hacke *et al.*, 2001). While the work of Moya and co-authors (2009) indicated that in dry climate, teak forms wide diameter more solitary vessels. In our study, the diameter of some vessels formed in the Ewlike zone within the true Lw could compare to vessel diameter of the true Ew (Appendix 5.4, supplementary figure S1). This indicates that during the Lw formation, a period characterized by decreasing rainfall, trees produced wider vessels for efficient water uptake. This cambial functioning shows that the mitigation of the impact of the varying environmental factors necessitates the development of adaptative strategies in trees.

Teak forestry provides multiple services (wood and non-wood products, see Chapter 2, section 2.1.5) to the local population (both rural and urban) as well as to the international market. *Tectona grandis* still delivers these ecosystem services since the current climatic disturbances represent no threat to the survival of the species in plantation.

The present work gave evidence of teak growth sensitivity to climate change, particularly to rainfall disturbances, by integrating the different applied methodologies. Under the predicted climate change resulting in persistent rainfall disturbances (shortening of the wet seasons, decrease in rainfall intensity), the species growth dynamics can be negatively affected: low photosynthetic activities and wood biomass productivity. As a result, the wood and non-wood services delivered by teak would be reduced: decreased crown volume, decrease in wood products for carpentry but also decrease in energy wood (charcoal fabrication) for rural and urban households.

6.3. Strengths and weaknesses of the applied methodologies

Thirty-four trees were used for tree-ring research (16 trees from Séguié and 18 from Gagnoa) and 2 to 3 trees were monthly sampled for the cambial activity. Probably a better procedure would have been to use a larger number of trees, in order to increase the number of replicates when investigating growth responses in young planted forests where the extent of trees juvenile phase was still unknown. While this juvenility is likely to account for more in tree growth and wood variability. The number of trees used in the present work is that allocated by the Forest Authorities who granted the authorization to sample in the respective sites.

Larger size samples are logically recommended to obtain strong statistics and extrapolate the results at the stand or forest level. Nevertheless, the results obtained from the examination of our small size samples allowed to provide insights which could be confirmed when using a larger number of trees.

The implementation of tree-ring analysis in a thinned and non-thinned stands preferably sharing identical microsite conditions is recommended for future investigations of teak climate-growth responses under thinnings. We suggest to combine this sampling strategy with the monitoring of crown volume changes, variations in leaf area index, potential evapotranspiration and soil available water content (SWC). This will lead to (i) a more representative sample and (ii) better understand thinnings contribution in trees responses to precipitation. This methodology can be applied to local and neighboring tree species which receive the same sylvicultural treatments.

The time consuming water displacement method (WDD) applied to determine wood density can be substituted by the high-resolution CT-Scan for density calculation, since both methods showed good correspondence. In addition, ring boundaries determined on the reconstructed CT-images of the wood strips corresponded to those obtained on the same strips under the stereomicroscope during tree-ring analysis. This shows the potential of the CT-Scan use for dendroclimatological studies in the tropics. Second, our study on microdensity profiling also confirms that Ewp remains a more or less constant parameter of teak growth ring, in regard to the Ewp within both the narrow and wide rings (Chapter 5, table 5.1). Furthermore, table 5-1B shows that wider rings, formed under favourable growth conditions, contain higher proportion of Lw; which will confer a higher wood density to the total growth ring given the TotrD-LwD correlation ($r = 0.94$; $p < 0.05$). This indicates that an accelerated growth rate (fast-growth) may not be detrimental to the wood density.

In spite of all its multiple advantages in improving wood and tree growth research, the CT-Scan device however remains an expensive option.

Ten and six tree samples were used for fibre length measurements and microdensity profiling respectively; giving accurate evaluation of the wood studied properties at the inter- and intra-tree levels, but also at the intra-ring scale. It also contributed for accurate demarcation of the juvenile wood based on the use of wood density and fibre length. Logically, 6 or 10 trees may not be representative of large forest stands owing to the influence of the micro environment conditions. Considering wood variability in an individual tree is, however, essential when breeding for high quality wood production rather than taking into account the mean variation of all the trees.

Given the importance of earlywood (Ew) and latewood (Lw) features (anatomy, width and wood density) in the intra-annual climate analysis (Kern *et al*., 2012; Matisons *et al*., 2015), it is essential to apply a reliable methodological approach for accurate demarcation of these ring zones.

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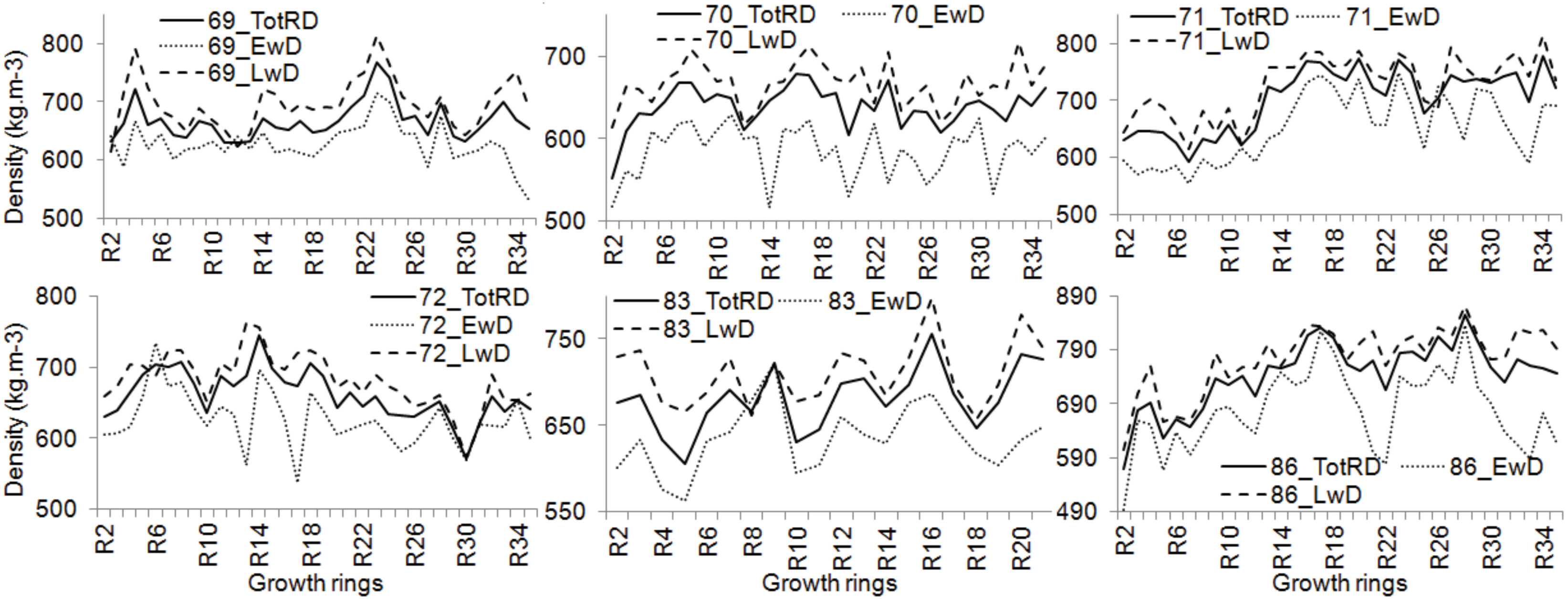
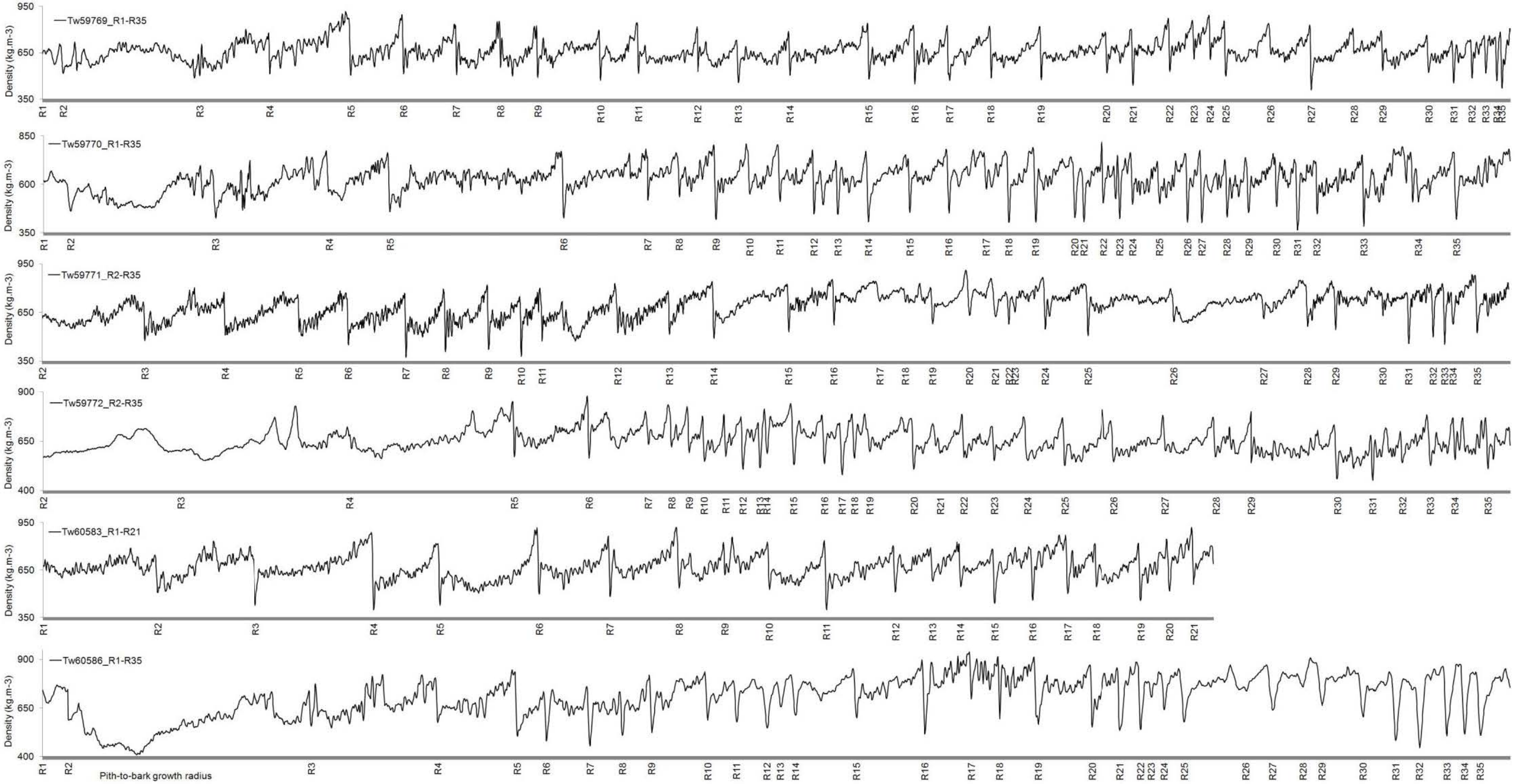
Appendix 5.1: Pith-to-bark mean density of the total ring (TotRD), earlywood (EwD) and latewood (LwD)



Appendix 5.2: Total pith-to-bark intra-ring density profiles for all samples

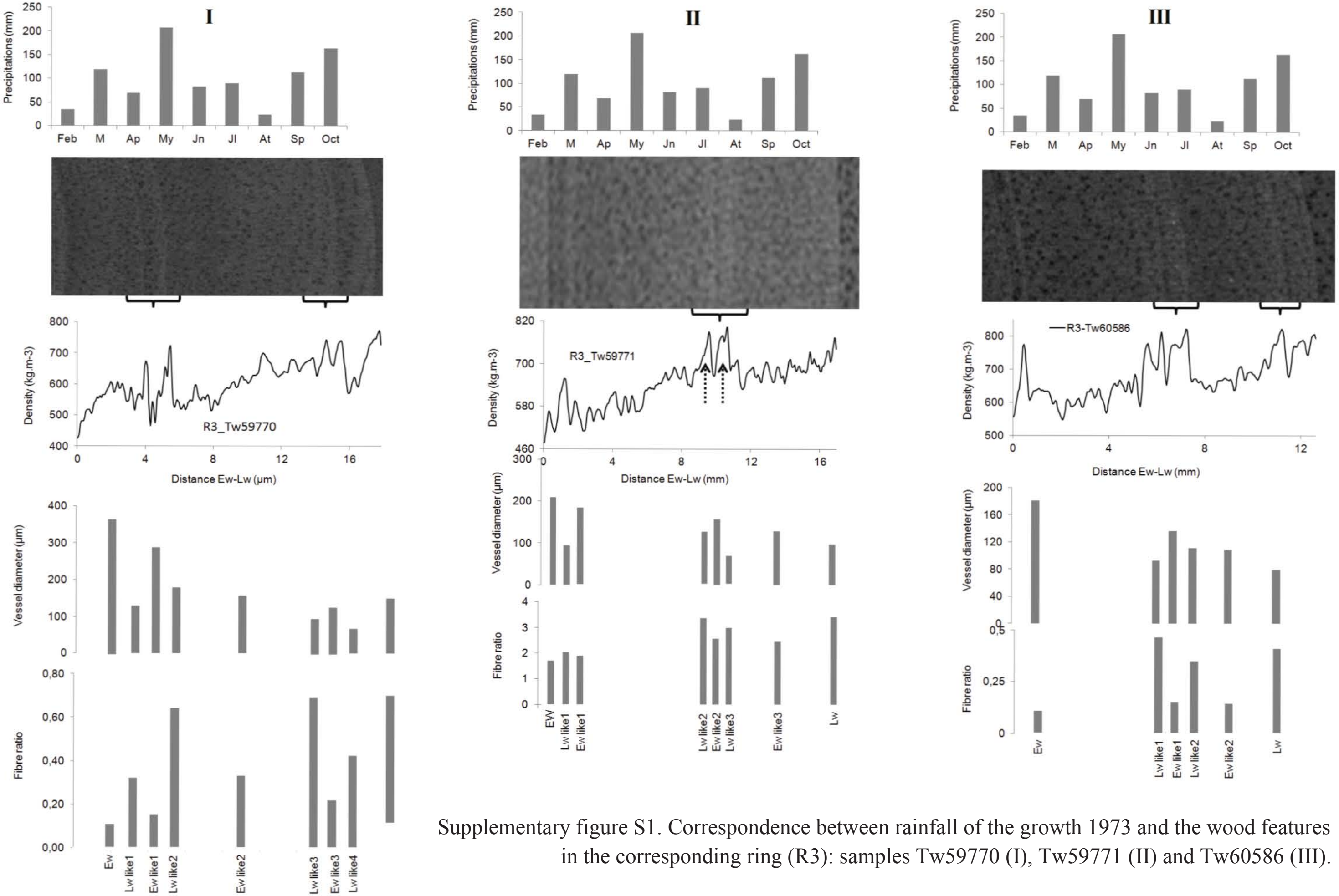


Appendix 5.3: Basic statistics per ring

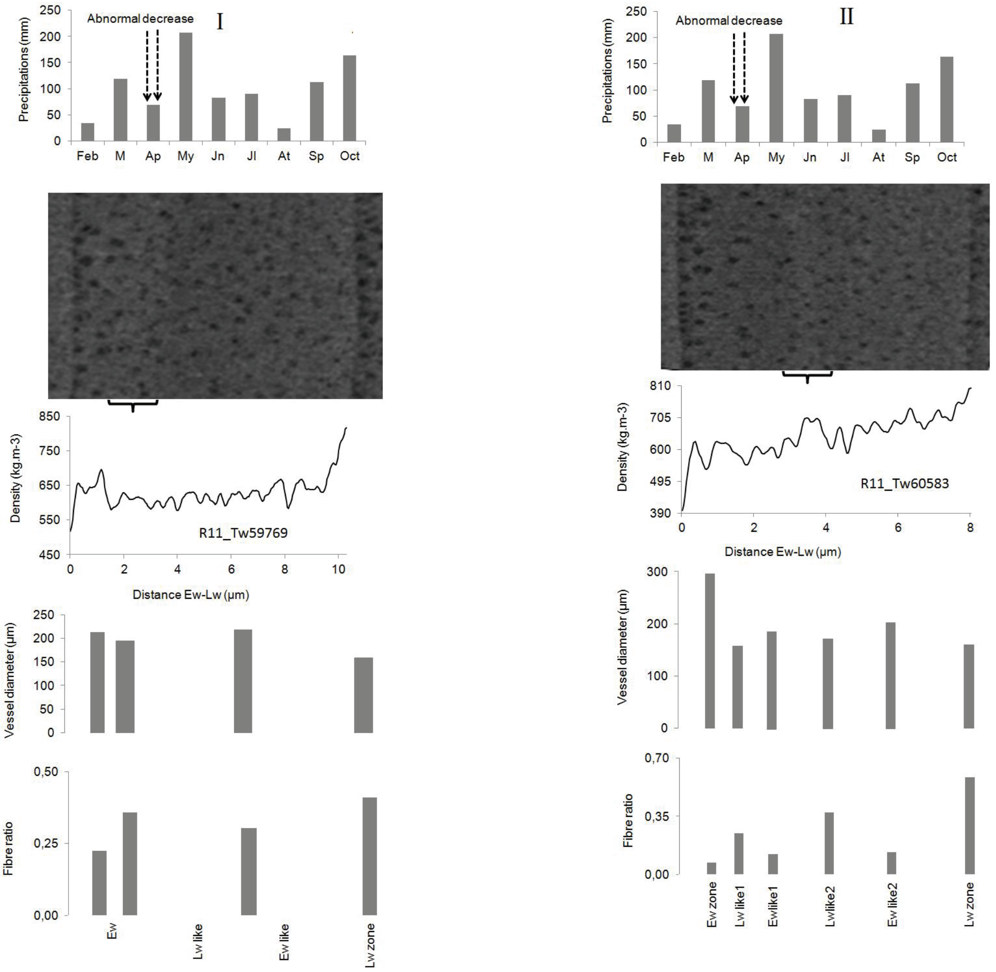
	Mean density per ring						**Stdev**						**CV**					
	Tw69	Tw70	Tw71	Tw72	Tw83	Tw86	Tw69	Tw70	Tw71	Tw72	Tw83	Tw86	Tw69	Tw70	Tw71	Tw72	Tw83	Tw86
R2	633	553	629	630	676	568	50	58	51	42	75	84	8	10	8	7	11	15
R3	663	609	646	640	685	679	73	68	67	53	75	68	11	11	10	8	11	10
R4	722	630	646	664	633	692	85	62	69	62	75	61	12	10	11	9	12	9
R5	661	630	644	689	606	627	78	47	70	52	85	56	12	7	11	8	14	9
R6	671	645	625	704	665	661	58	53	58	49	61	51	9	8	9	7	9	8
R7	642	668	592	699	692	647	71	48	72	50	75	52	11	7	12	7	11	8
R8	639	668	632	707	666	681	68	63	72	50	54	65	11	9	11	7	8	9
R9	666	644	627	677	722	738	48	73	61	42	53	65	7	11	10	6	7	9
R10	660	654	657	636	630	726	70	66	78	51	59	44	11	10	12	8	9	6
R11	631	650	621	687	645	742	43	47	75	51	64	49	7	7	12	7	10	7
R12	629	611	649	674	699	704	46	59	60	52	53	77	7	10	9	8	8	11
R13	631	627	723	688	704	761	50	58	70	110	60	56	8	9	10	16	8	7
R14	672	647	715	745	672	757	53	64	64	48	44	44	8	10	9	7	7	6
R15	657	659	733	698	696	765	68	56	55	51	67	52	10	9	8	7	10	7
R16	652	679	769	678	756	817	65	66	49	48	82	81	10	10	6	7	11	10
R17	667	676	766	674	686	832	66	57	23	95	65	48	10	8	3	14	10	6
R18	647	651	748	705	647	812	59	84	31	52	57	58	9	13	4	7	9	7
R19	653	655	736	687	676	763	47	64	66	46	75	51	7	10	9	7	11	7
R20	667	605	774	642	755	752	59	87	47	47	83	73	9	14	6	7	11	10
R21	692	647	723	664	726	769	72	77	44	51	52	109	10	12	6	8	7	14
R22	711	634	708	645		716	70	59	52	37		89	10	9	7	6		13
R23	769	671	772	659		784	63	83	41	47		40	8	12	5	7		5
R24	741	612	748	633		787	51	50	54	52		55	7	8	7	8		7
R25	669	634	678	632		770	69	66	57	61		48	10	10	8	10		6
R26	676	632	705	630		816	51	85	46	42		38	8	14	6	7		5
R27	644	607	745	642		789	69	62	61	44		54	11	10	8	7		7
R28	698	621	733	651		855	34	66	67	48		44	5	11	9	7		5
R29	642	642	738	616		805	47	57	37	37		38	7	9	5	6		5

R30	633	646	731	571	758	39	53	26	35	48	6	8	3	6	6
R31	652	635	743	619	730	62	84	70	52	89	10	13	9	8	12
R32	674	621	748	659	772	65	54	81	53	117	10	9	11	8	15
R33	699	653	698	637	760	64	90	85	56	120	9	14	12	9	16
R34	669	640	779	654	756	112	57	71	58	105	17	9	9	9	14
R35	653	662	723	641	746	98	67	55	42	92	15	10	8	7	12

Appendix 5.4: Other samples of tree ring features showing correspondence to sudden stepwise changes in monthly precipitation



Supplementary figure S1. Correspondence between rainfall of the growth 1973 and the wood features in the corresponding ring (R3): samples Tw59770 (I), Tw59771 (II) and Tw60586 (III).



Supplementary figure S2. Correspondence between rainfall of the growth 1981 and the wood features in the corresponding ring (R11): samples Tw59769 (I) and Tw60583 (II).

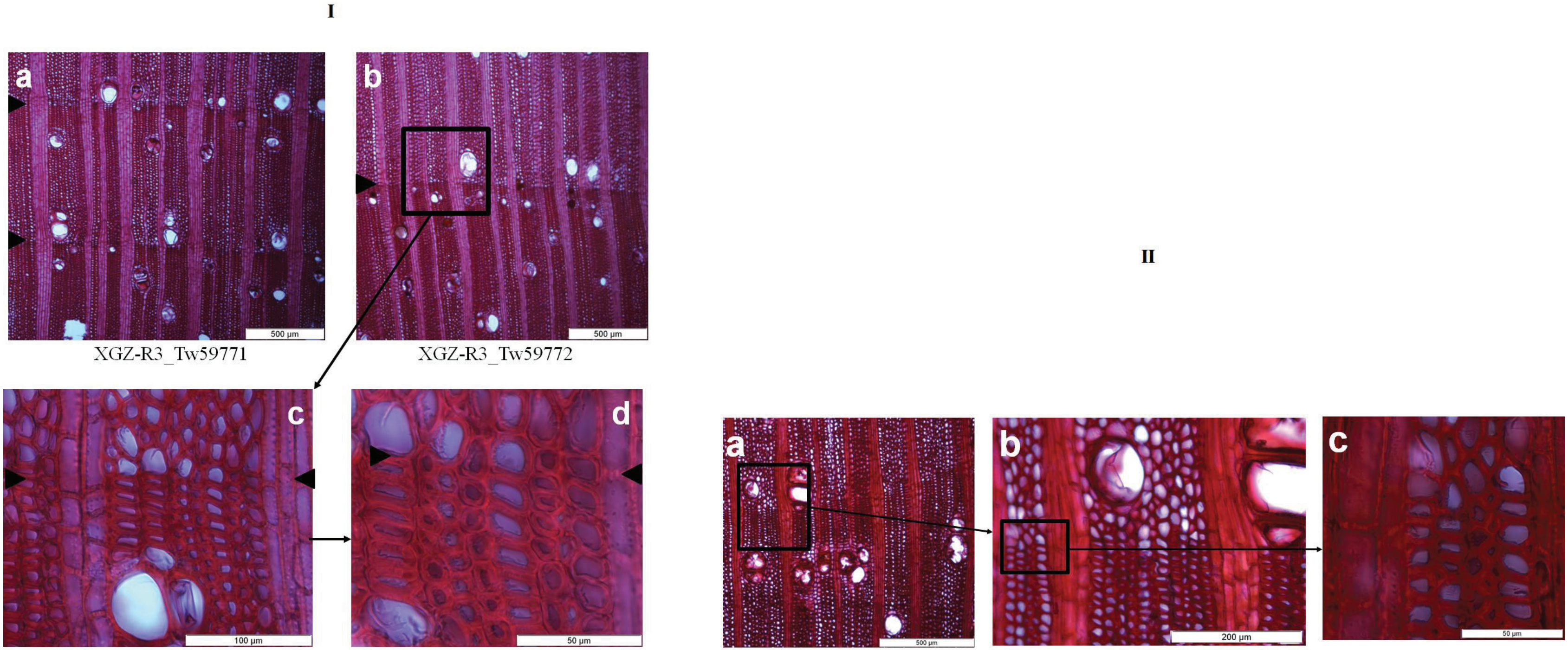


Figure S3. Photographs showing clearly distinct boundary (figure I) of the XGZ formed in ring 3 of tree samples Tw59771 (a) and different magnifications of XGZ boundary in Tw59772 (b, c, d). the black arrow heads indicate the boundary of the XGZ. Figure II shows the boundary of XGZ formed in the same ring 3 but in tree sample Tw59769 with different magnifications. Note that the boundary appears diffuse compared to those found in Tw59771 and Tw59772.

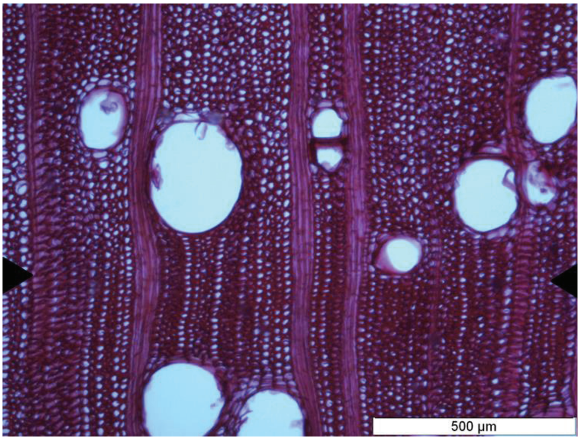


Figure S3. Photograph of a diffuse boundary of XGZ formed in ring 11 of tree samples Tw59769.

Curriculum Vitae

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Programme aiming to the Biological Prevention and Eradication of Schistosomiasis in Taabo and Tiassalé (Centre Suisse, /Ivory Coast): Quantitative and qualitative analysis of Plants and Algae in the wet zones in relation with Schistosomiasis. 31st August- September 30th 1998

Scientific output and publications

Dié A., M. De Ridder, P. Cherubini, F.N. Kouamé, A. Verheyden, P. Kitin, B.B. Toirambe, J. Van den Bulcke, J. Van Acker, H. Beeckman, 2015. A. Dié, J. Van den Buclke, P. kitin, H. Beeckman and J. Van Acker. Microdensitometrical profiling of *Tectona grandis* L. reveals latewood sensitivity to climate. Under revision by Dendrochronologia.

Dié A., M. De Ridder, P. Cherubini, F.N. Kouamé, A. Verheyden, P. Kitin, B.B. Toirambe, J. Van den Bulcke, J. Van Acker, H. Beeckman, 2015. Tree rings show a different climatic response in a managed and a non-managed plantation of 1 teak (*Tectona grandis* L.f.) in West Africa. IAWA J. 36(4): 409-427, DOI: 10.1163/22941932-20150111.

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Dié, A.; H. Beeckman; F.N. Kouame; A. Verheyden, D. Traore 2004. Conditions écologiques et Croissance du teck: *Tectona grandis* L. de la Région de Gagnoa (Centre-Ouest de la Cote d’Ivoire). Poster Symposium Ecosyn (Université de Wageningen/Pays-Bas - Université de Cocody/Côte d’Ivoire); 6-10 Septembre 2004, Abidjan (Côte d’Ivoire).

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Dié, A.; H. Beeckman; F.N. Kouame; A. Verheyden, D. Traore 2003. Radial growth pattern of plantation teak: *Tectona grandis* L. f. (Verbenaceae), in Gagnoa (Central-West of Ivory Coast). Poster; Conference of the European Working Group for Dendrochronology; Obergurgl, Tyrol, Austria September 10th - 14 th, 2003 (Abstract online).