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TREE RINGS SHOW A DIFFERENT CLIMATIC RESPONSE IN A MANAGED AND A NON-MANAGED PLANTATION OF TEAK (*TECTONA GRANDIS*) IN WEST AFRICA

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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).

Keywords: Sylviculture, thinnings, climate variability, sea-surface temperature anomalies, ENSO.

[In the online version of this paper Figures 2–5 are reproduced in colour.]

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), semi-deciduous to evergreen forest (Mopri, Séguié), and in zones with different 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 Niño-Southern Oscillation (ENSO) (Kouadio *et al*. 2003; Balas *et al*. 2007; Joly *et al*. 2007). As a light-demanding species (Dupuy *et al*. 1999) teak can be expected to be sensitive to this complex climate variability.

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 (Worbes 1995; Dupuy *et al*. 1999). These plantations are becoming important since they represent a major timber source which satisfies the increasing need 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 focusing 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?

MATERIALS AND METHODS

Sampling sites and sample procedure

All study sites belong to the Guineo-Congolian regional center 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. 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} and it has never been managed.

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} (at the harvest time). Illegal loggings or other wood products harvesting activities were not allowed in the two study plantations which are under the protection of the forest Security Agents "Gardes forestiers".

At both sites, trees were randomly sampled. Stem discs were taken at 50–70 cm above ground level from the stumps of trees felled in August 2002 (Gagnoa) and in 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).

Ring-width measurements and crossdating

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
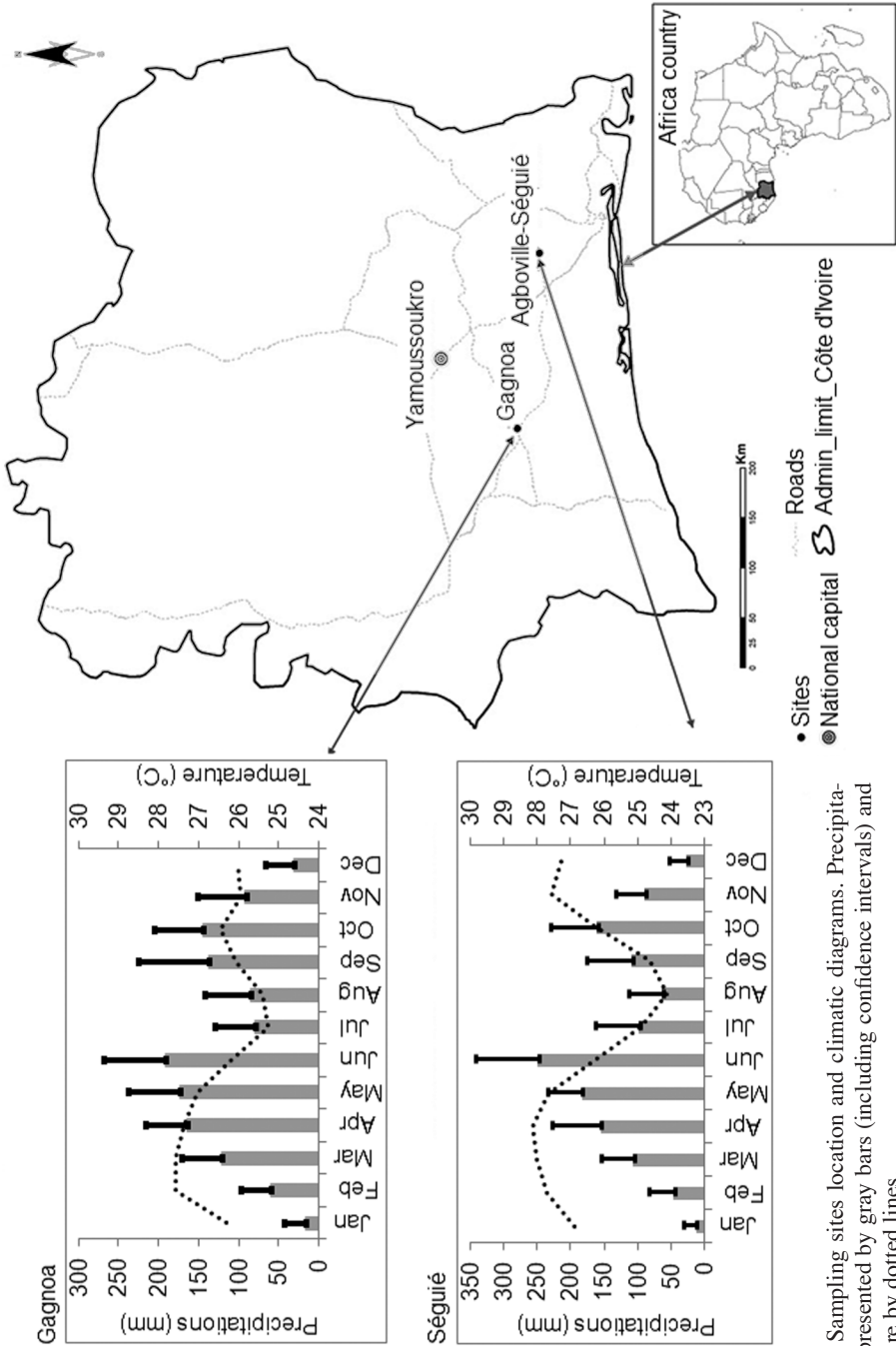
Figure 1. Sampling sites location and climatic diagrams. Precipitation is represented by gray bars (including confidence intervals) and temperature by dotted lines.

same site. Successful crossdating of several trees indicates the presence of a common external growth controlling factor (Cook *et al*. 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.*, p.p.r. ≥ 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 (Wigley *et al*. 1984; Haneca *et al*. 2005). 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).

Climate description

Rainfall data covering the periods of 1966–2002 for Gagnoa (National Oceanic and Atmospheric Administration: NOAA) and of 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.

Gagnoa, located in the center of the country, shows a more stable annual rainfall pattern with a long-term average of 1296 ± 204 mm (CV = 14 %). While Séguié, exhibits a similar average of 1298 ± 249 mm but with a moderately higher variability (CV = 19 %). 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 (MinPrec. = 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.

Climate-growth relationship

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° × 5° 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° × 1° 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 Niño 3.4 region (51N-51S, 1201-1701W) exceeding +0.4 °C for 6 or more consecutive months (El Niño years) (Trenberth 1997). The correlations were studied, using DendroClim2002+ (Biondi & Waiku 2004).

RESULTS

Tree-ring characteristics and growth anomalies

At both sites, teak formed distinct annual growth rings and shows (semi-)ring porosity (Fig. 2 & 3). 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.

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).
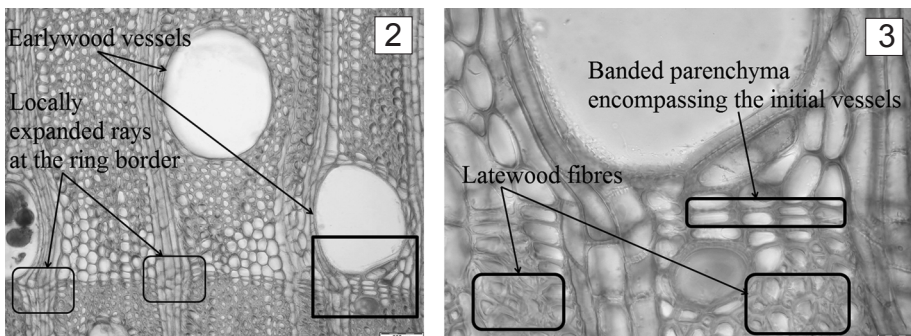

Figure 2 & 3. Anatomical structure of a tree-ring boundary in plantation teak from Ivory Coast. – 2: Low magnification of the growth boundary showing expanded xylem rays (rounded rectangles) and wide diameter earlywood vessels (rectangle). – 3: High magnification of the growth boundary showing thick-walled latewood fibres of the previous growth ring and banded parenchyma encompassing the initial vessels. — Scale bar in 2 = 200 μm, in 3 = 50 μm.
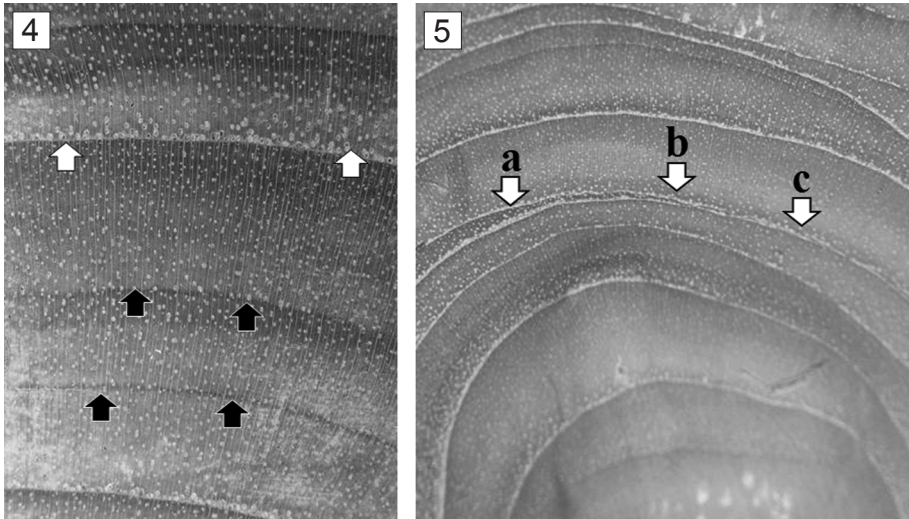
Figure 4 & 5. True tree-ring characteristics and ring anomalies under the stereomicroscope. – 4: The black arrows point to the borders of the intra-annual xylem growth zones (XGZ) and the white arrows indicate the true growth boundary. – 5: Arrows show the merging of two true ring limits resulting in the phenomenon of a wedging/missing ring indicated by arrow c.

Gagnoa samples displayed more frequently wedging or locally missing rings in comparison to Séguié where trees mostly exhibited intra-annual xylem growth zones (XGZ) morphologically different from the true annual ring (Fig. 4 & 5). 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.

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. 6), variations with higher magnitudes were detected in the year-to-year tree-ring index chronology of Séguié compared to Gagnoa (Fig. 7). 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.

A strong tree age effect, reflecting the natural biological declining growth trend, was observed in the raw ring-width at both sites (Fig. 6) and confirmed by the high values of autocorrelation (AC) before standardization (Table 1). In addition to the
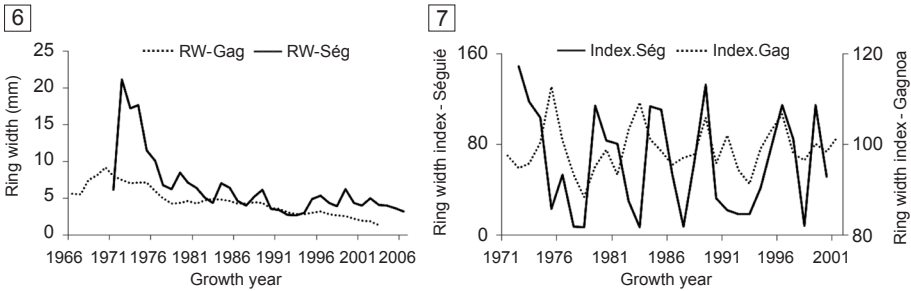
Figure 6 & 7. – 6: Mean raw ring-width series. – 7: Site chronologies. The dotted line represents growth parameters in Gagnoa and the solid line indicates those of Séguié in both 6 and 7. The most juvenile rings (first 5 and first 2 rings for Gagnoa and Séguié, respectively), included when estimating the wood production (Fig. 6), were excluded from the chronologies (Fig. 7) for climate analysis purposes.

age effect, a periodicity in growth recovery is detectable, every 4–5 years, in the Séguié site chronology from the 5th growth year. The values of $T_{v\text{-}BP}$, p.p.r., EPS and MS were lower in the non-managed trees (Gagnoa site) compared to the managed trees at Séguié (Table 1). The crossdating and standardization 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 $T_{v\text{-}BP}$ and p.p.r. were below the thresholds for acceptable crossdating.

Table 1. Results of cross-dating and standardization (mean values from each parameter). The p.p.r. and $T_{v\text{-}BP}$ are the averaged values obtained from all pairs of comparisons.

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

p.p.r.: percentage of parallel run; $T_{v\text{-}BP}$: value of t-test of Baillie-Pilcher; ac: autocorrelation; EPS: expressed population signal; ms: mean sensitivity.

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's 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 = 0.38 and r = 0.50; p < 0.05).
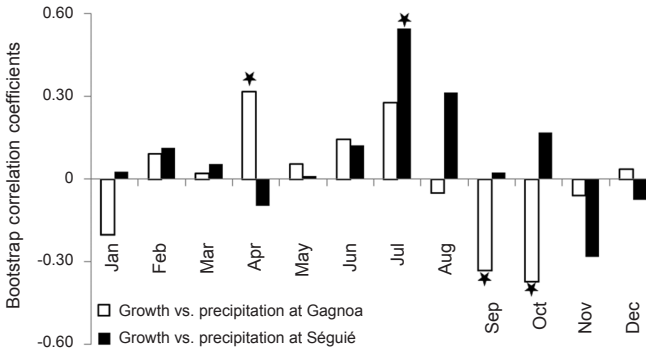
Figure 8. Relationship between monthly precipitation and site chronologies from Gagnoa (white bars) and Séguié (black bars). Analysis was performed with Dendroclim2002+ over the period 1971–2001 for Gagnoa and 1972–2000 for Séguié. The black stars indicate significant correlations (p < 0.05).

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. 8).

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. 9 & 10). 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. 9 & 10). On average, the influence of SSTs anomalies on tree growth was observed with a lag of one month in Gagnoa compared to Séguié.

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 both sites.

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 the 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).
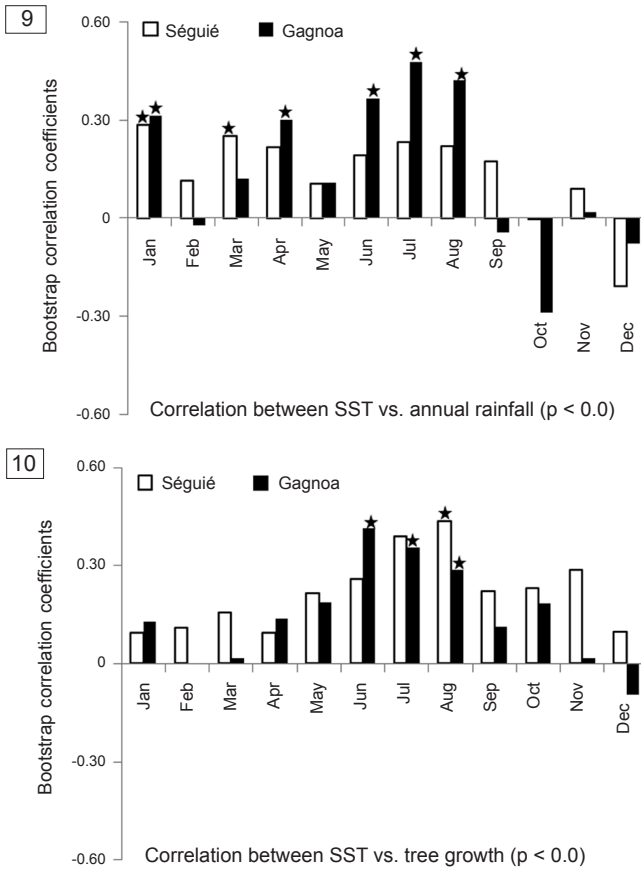
Figure 9 & 10. Influence of anomalies in monthly sea surface temperatures on growth and precipitation in Ivory Coast. – 9: Relation between monthly sea surface temperatures of the Gulf of Guinea and annual precipitation. – 10: Relation between monthly sea surface temperatures of the Gulf of Guinea and tree growth (site chronologies). The correlation was performed using Dendroclim2002+ (p < 0.05). White bars represent data for Gagnoa and black bars data for Séguié. Stars indicate significant correlation values (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 2).

DISCUSSION

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

Table 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	AD	ENSO events
	Gagnoa	Séguié	Gagnoa	Séguié				
1970–1980			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	1972–73 1976–77 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 607 narrow rings at the site level; CRR: rainfall reduction at the country level; WRR/WAD: West-608 African drought episodes; AD: African drought episodes; ENSO: El Niño Southern Oscillation 609 events.

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; Apr: 121 mm; May:

137 mm; Jun: 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 importance of wedging rings and XGZ for tree-ring delineation and their relevance for the analysis of intra-annual climate-growth responses (Battipaglia *et al*. 2014), their accurate characterization appears essential.

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 (Bréda *et al*. 1995; 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 the trees' lifespan (Fig. 7).

Thinnings start from the 4th year after the plantation is installed and they are repeated every 3–6 years depending on the 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* too (Gea-Izquierdo *et al*. 2009; Moreno-Gutiérrez *et al*. 2012).

Growth synchronicity in managed and non-managed stands

The crossdating 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 cambial 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.

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 it 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 tree 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 *et al.* (2005) who observed that the annual precipitation exceeded the evapotranspiration over the study period (precipitation - evapotranspiration > 0); indicative of a 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 & Mahalakshmi 2014), 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, 2014). We, therefore, 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. 8). 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, making the thinned trees to be less sensitive to a decrease in precipitation. Similar results were, recently, obtained in other species (Gea-Izquierdo *et al.* 2009; Martin-Benito *et al.* 2010; Moreno-Gutierrez *et al.* 2012; Zhang *et al.* 2013).

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.

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 the 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 in-fluence 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 relation-ship 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 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 rings 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.

Overall, it is noteworthy that the climate-growth relationship was moderately stronger at Gagnoa than at Séguié. Sylvicultural treatments, by reducing competition for growth factors, probably, obscured effects of precipitation variability on tree growth at Séguié.

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