

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

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

the Gulf of Guinea and the South Atlantic Ocean during the early rainy season. However, tree growth was influenced by ENSO in both regions. In the Mayombe, La Niña years were associated with stronger tree growth whereas in Ivory Coast, El Niño years corresponded with stronger tree growth. The presented relation between ENSO, precipitation and tree growth is original for equatorial African forests, suggesting an influence of global climate variability on tree growth.

Keywords Africa · Dendroclimatology · ENSO · Sea surface temperature · Tree rings · Tropical forest

Introduction

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

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site conditions. The link between light-demanding trees and significant climate correlations was already presumed in the 1920s (Douglass 1920).

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

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

for human welfare and socio-economic development (Boninsegna et al. 2009).

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

Moreover, the abovementioned anomalies of SSTs of the equatorial Pacific Ocean are generally used to calculate ENSO indices (Trenberth 1997). ENSO is the result of the coupling between oceans and the atmosphere (Nicholson and Entekhabi 1987), but most ENSO indices, including the Niño3.4 index, are based on anomalies of SSTs in the region between 5°N–5°S and 120°–170°W (Trenberth 1997). Camberlin et al. (2001) studied the gridded response of African precipitation on Niño3 indices and found no consistent large-scale relation in West Africa. Surprisingly, they observed a clear negative relation in March–June and August–November in western equatorial Africa [Cameroon, Gabon, Republic of Congo and the coastal region of the Democratic Republic of Congo (DRC)], a region which had never before been shown to exhibit significant correlations with ENSO.

The studied species is *T. superba*, a long-living pioneer tree species, characterized by large buttresses and typically found in secondary forests and fallows (Groulez and Wood 1985; Hawthorne 1995; Humblet 1946; Swaine and Whitmore 1988). This tree species has a large range of distribution on both hemispheres (from Sierra Leone to Angola) (Groulez and Wood 1985). The climate within this region [dry season with <60 mm monthly precipitation in at least 3 months (Worbes 1995)] is believed to provoke the formation of yearly growth rings. Moreover, *T. superba* was also planted over vast areas, including DRC, and the known planting dates allowed for exact dating and confirmation of the annual character of tree rings in this species (De Ridder et al. 2010). The formation of tree rings was already studied by Mariaux (1969), who used periodic wounding and dendrometers to monitor tree growth, but his study was limited to <20 trees younger than 20 years.

Therefore, proper cross-dating and comparison with climate was not possible. Worbes et al. (2003) also used *T. superba* discs and wood cores from Cameroon yet without climate matching. In our study, tree rings of *T. superba* from old plantations (ca. 50- to 55-year old) and natural forests in the Mayombe Forest (southern hemisphere) and western Ivory Coast (northern hemisphere) were analyzed in combination with climate data to analyze the following hypotheses:

1. Planted and natural *T. superba* trees reveal different growth patterns due to different site conditions and/or different responses to climate.
2. Trees of *T. superba* show cambial growth in one hemisphere, but not in the other hemisphere and vice versa due to the shift of 6 months in the precipitation seasonality.
3. This means that trees react sensitively to climate at one site, but do not incorporate these climate conditions at the other site and vice versa. Climate conditions can include regional climate variability, and can be influenced by SST anomalies in the surrounding tropical ocean sectors as well as by ENSO events.

Materials and methods

Study sites

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

The three Congolese study sites (Fig. 1) are located at the southern border of the Mayombe Forest that covers the western parts of Gabon, the Republic of Congo, DRC and Cabinda (Angola). Two study sites were chosen within the UNESCO Man and Biosphere Reserve of Luki (05°30' to 05°45'S and 13°07' to 13°15'E). The first study site was a natural forest stand close to the climate station of the reserve, and the second study site was located at a distance of 15 km in a plantation of *T. superba*, established between 1955 and 1957 in the village of Monzi. Plantations were installed on clear-felled areas, at planting distances of 8 × 12 m. After the installation, no structured management was carried out. Natural regeneration of *T. superba* and other species took place after a few years (De Ridder et al. 2010). A third study site was selected in a natural forest stand near Tshela, about 70 km to the north. All study sites were situated at altitudes <300 m above sea level. The region is characterized by a dry season of approximately 5 months (May to September/October) and

a short period with less precipitation during the rainy season (January–February). The proximity of the ocean, manifested by a strong nebulosity, buffers the intensity of both dry periods. Relative humidity remains more or less constant throughout the year (84 % in the rainy season, 82 % in the dry season). The average annual precipitation based on precipitation data from 1959 to 1996 is 1,168 mm, but some years are particularly dry (Fig. 1). For instance, the annual precipitation in 1972 and 2002 was <800 mm and the lowest values were registered in 1954, 1978 and 1997 with annual precipitation values of respectively 657, 692 and 626 mm. Temperatures oscillate around 26 °C in the rainy season and drop to a minimum of 20 °C in the dry season. The soils of the Luki Reserve are classified as orthic Ferralsols, but Tshela is characterized by ferric Acrisols (FAO 2008). Most soils are argillaceous with a pH between 4 and 6 and a C/N between 4 and 9.

In western Ivory Coast (06°07' to 07°15'N, 07°30' to 08°15'W), the four study sites (Fig. 1) are located in natural forests. The forest of Scio can be considered as primary forest whereas the forests of Goya, Bin Houye and Danane are secondary forests, often with cacao plantations in the understory. Unlike in DRC, study sites were widespread and sometimes more than 100 km apart. Moreover, no central climate station was available and data (including monthly precipitation and temperature) from six surrounding climate stations (Table 1; Fig. 1) were therefore averaged. Ivorian climate data were extracted from the KNMI explorer (van Oldenborgh and Burgers 2005). In this region, the dry season generally lasts for 3 months (December–February). In July and August, a period of less precipitation is observed. Relative humidity drops from approximately 88 % during the rainy season to approximately 70 % during the dry season. The average annual precipitation, based on precipitation data from 1959 to 1996, is 1,650 mm. Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March (van Oldenborgh and Burgers 2005). Study sites were situated between 200 and 370 m above sea level. Soils have a pH between 4 and 7, a C/N of 8–12 and are classified as Ferralsols and Acrisols, i.e. typical acid soils of tropical lowlands (FAO 1986).

Sampling strategy

A total of 41 stem discs were collected from natural forests in the Mayombe and western Ivory Coast (one stem disc per tree). In Monzi, two perpendicular wood cores were taken per tree, resulting in a total of 120 cores from 60 planted trees (Table 2). Cores were taken above the buttresses where possible. All samples were air-dried to prevent fungal infestation. Wood cores were frozen for 2 weeks to prevent insect infestation. Stem discs were too

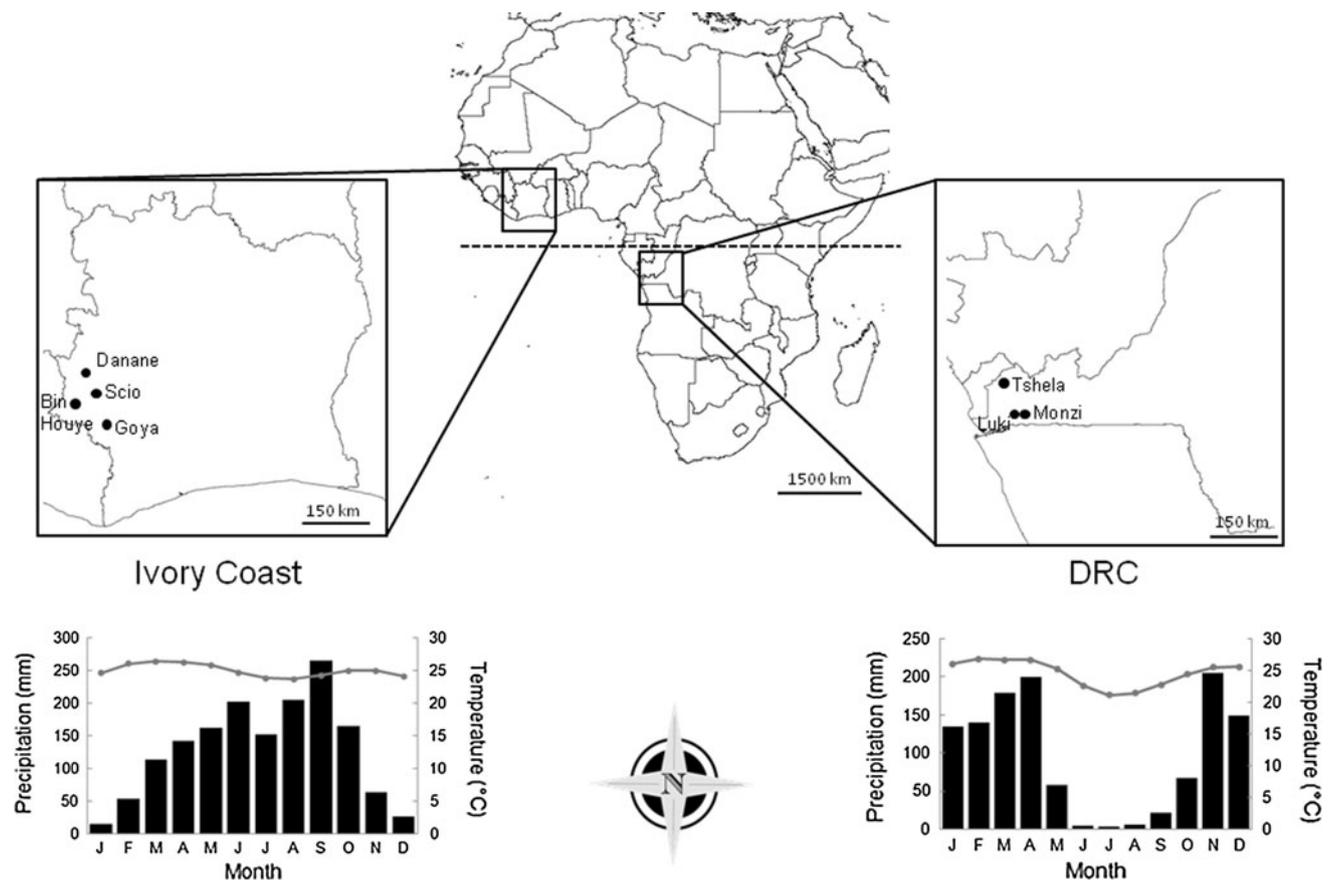


Fig. 1 Geographical location of all study sites in Ivory Coast and the Mayombe Forest in the Democratic Republic of Congo (DRC) with a climate diagram for the Mayombe Forest (climate station of Luki, 1959–1996) and Ivory Coast [regional climate average from 6 climate

stations, 1959–1996, extracted from the KNMI explorer (van Oldenborgh and Burgers 2005); for temperature data only two stations, Man and Gagnoa, provided data from 1959 to 1984]. The dashed line represents the equator

large for freezing and therefore only superficially disinfected before storage in the Tervuren Xylarium. All discs and cores were sanded with gradually increasing grid from 50 to 600 or 1,200.

Table 1 Characteristics of climate stations around Ivorian study sites and the Mayombe (station, precipitation, dry season (<60 mm), distance to the closest study site)

| Station | Region | Annual precipitation (mm) | Dry season | Distance to closest study site (km) |
|-----------|-------------|---------------------------|------------|-------------------------------------|
| Daloa | Ivory Coast | 1,256 | Nov–Feb | 140 (Goya) |
| Guiglo | | 1,644 | Nov–Feb | 52 (Scio) |
| Man | | 1,607 | Nov–Feb | 58 (Danane) |
| Soubre | | 1,401 | Dec–Jan | 110 (Goya) |
| Toulepleu | | 1,668 | Dec–Feb | 25 (Bin Houye) |
| Nzerekore | Guinea | 1,838 | Dec–Feb | 100 (Danane) |
| Luki | Mayombe | 1,168 | May–Sep | 5 (natural forest of Luki) |

The common time span in all stations is from 1959 to 1996

Tree ring analysis

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

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

Table 2 Summary of the details of the sampling campaigns in the Mayombe and Ivory Coast

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

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

Two statistical parameters are taken into account to evaluate the success of cross-dating: the Pearson's correlation (r) and the t value of Baillie–Pilcher (Baillie and Pilcher 1973). Another non-statistical parameter is *Gleichläufigkeit* (Eckstein and Bauch 1969) or percentage of parallel run (ppr), which reflects the percentage of oscillations in the same direction within the overlapping interval. Still, especially for tropical trees, visual control and expert knowledge of *Terminalia* wood anatomy and tree rings are indispensable. The work of Trouet et al. (2010) is referred to for a detailed explanation on the lower thresholds for ppr ($\geq 60\%$) and t values (≥ 2) in tropical trees compared to temperate regions. Autocorrelation (AC) was checked to filter possible age trends and standardize the tree ring series to enable dendroclimatological analysis (Fritts 1976). For site and regional chronologies, series were standardized using a one-sided moving average over 5 years (Baillie and Pilcher 1973). The mean sensitivity (MS) of these standardized chronologies reflects the sensitivity of tree growth to a common external factor (Fritts 1976). For each site chronology, the expressed population signal (EPS) was also calculated (Haneca et al. 2005; Wigley et al. 1984) to quantify uncertainty due to decreasing sample replication. As such, the EPS indicates

how well the finite-sample chronology matches the theoretical population chronology. A value of 0.85 was considered as a reasonable limit for a reliable chronology (Wigley et al. 1984).

Analysis of climate–growth relationships

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

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

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

months (El Niño years) or -0.4 °C for 6 or more consecutive months (La Niña years) (Trenberth 1997).

Phenological data

Historical phenological data were available for the Congolese Mayombe study site (Couralet 2010). From 1948 to 1957, phenological data on 3,750 woody plants were collected in Biosphere Reserve of Luki. Patterns of defoliation, flowering, fruiting and dissemination of fruits were studied, also for *T. superba* ($n = 184$ trees). These data were compared to precipitation and tree-ring chronologies within the overlapping time span. No phenological data were collected or available for western Ivory Coast.

Results

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

Tree rings were distinct and measurements were possible in the Mayombe as well as in western Ivory Coast. Tree rings in *T. superba* are also annual: this was confirmed by nine plantation trees that had the pith included in one of the wood cores and were located within the planting schemes. Those nine trees had ages comparable to the planting period, with differences between tree-ring dated and known planting age of up to 3 years. This discrepancy can be attributed to the sampling height and a more or less continuously active cambium during the first years, resulting in ill-defined or non-detectable tree-rings (Mariaux 1969). The structure of juvenile rings is somewhat different from other tree rings in Ivory Coast as well as the Mayombe: smaller vessels, less parenchyma and lighter fibre tissues. However, the anatomical structures of tree rings differed between the two regions. In general, with exclusion of the first juvenile rings, tree rings in the Mayombe (Fig. 2a) have mostly (sparse) aliform parenchyma. Banded parenchyma is sparse and when it is present, it is located in the middle and/or at the end of the tree ring. Confluent parenchyma is regularly present, but connects only a few vessels. Marginal parenchyma is distinct (Fig. 2a), but is often only present in most recent rings. The sharp transition between light and dark tissues (flattened fibres) in particular substantially simplifies tree-ring delineation. In Ivory Coast (Fig. 2b), tree rings were more undulating than in the Mayombe and transitions in colour were not as sharp. Ivorian *T. superba* wood contained a lot of parenchyma. In addition to a small amount of aliform parenchyma, the majority of tree rings contained confluent parenchyma, extending over several vessels. In the middle and at the end of tree rings, narrow parenchyma bands can occur.

Marginal parenchyma bands were generally discontinuous and often hard to distinguish from other bands of parenchyma. In some tree rings, the anatomical structure was even inverted: flattened fibres (dark tissue) and banded parenchyma were found in the earlywood of the tree ring. In summary, tree-ring delineations were more complex on Ivorian stem discs.

Marking tree-ring boundaries was rather straightforward in young trees (<30 years), from both regions. Occasionally, the first rings showed intra-annual density variations but they were not considered problematic on stem discs because they were not present on the whole circumference. After a period of fast growth with wide tree rings, ring width drops significantly in the most recent rings. This decrease usually occurs gradually and could be linked to the age trend. False rings and double rings were easy to detect but wedging rings formed the main problem in identifying annual tree rings in *T. superba*. Wood cores from the planted trees in the Mayombe offered the opportunity to quantify these ring anomalies. A tree-ring chronology of stem discs from the natural Mayombe forest was developed (see below) and subsequently used to test through cross-dating if tree-ring series from wood cores were accurate enough to construct a tree-ring chronology. More than 28 % of the measured wood cores showed no false or wedging tree rings upon comparison with the natural forest chronology. Those wood cores formed the foundation of a plantation chronology that spans from 1959 to 2007. On average, per tree, 1 false ring (3 %) occurred and 0.5 ring (1 %) was at least partially missing. In the

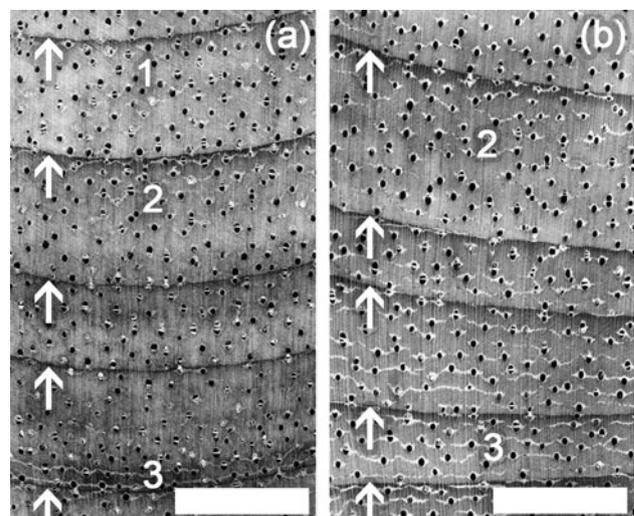


Fig. 2 Transversal view on **a** Congolese *T. superba* tree rings and **b** Ivorian tree rings, with aliform parenchyma (1), confluent parenchyma (2) and narrow bands of parenchyma (3). Tree-ring boundaries are marked. The white bar represents 5 mm. In both cases, the cambium side corresponds with the upside and the pith side with the underside of the pictures

latter case, the tree ring was visible on one wood core of a tree but not on the other one. Analysis of the exact location of tree-ring anomalies shows that 45 % of the anomalies were found between the age of 21 and 30 years (0.15 anomalies/ring). In sections over 30 years, the number of anomalies decreased to 21 % or 0.11 anomalies/ring (31–40 years), thus the most recent formed rings were not necessarily more sensitive to anomalous rings. However, plantation trees were not older than 55 years and wedging rings also caused many problems in 9 stem discs >100 years. Unfortunately, quantifying these wedging rings was less straightforward due to the low growth rates and therefore, low visibility.

Growth patterns in natural and planted African forests

Cross-dating was successful at all sites in the Mayombe and Ivory Coast and site chronologies with a minimum of four contributing trees were developed for every site (Table 4). The t value of the combination Luki–Tshela is not significant, but the ppr, inter series correlation and visual control confirm that a preliminary regional chronology covering the natural Mayombe forests can be constructed (Table 3; Fig. 3). The chronology of the plantation (Table 3; Fig. 3) was compared to this preliminary regional chronology, showing co-varying growth patterns ($r = 0.89$; t value = 4.0; $p < 0.001$). The regional chronology for the Mayombe thus includes all tree-ring series from the trees that were part of the site chronologies of Monzi, Luki and Tshela. In Ivory Coast, some sites show satisfactory results visually as well as for a minimum of two statistical parameters. Nevertheless, the relations are generally less strong and less significant than in the Mayombe (Table 4). Unlike in the Mayombe, not all trees from the Ivorian site chronologies were used to build the regional chronology (Tables 3, 4; Fig. 3). Instead, all individual Ivorian tree-ring chronologies were compared to each other, and 22 trees that showed the strongest common signal were extracted. Those 22 trees were used to construct the regional chronology for western Ivory Coast.

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

Comparing the two regional chronologies, we found a weak long-distance relationship for the period 1959–2008 (ppr = 55 %; $r = 0.39$; $t = 3.7$). The ppr is low, but the Pearson correlation and t value are significant ($p < 0.01$). A visual check confirms this correspondence and revealed a short discrepancy only during the 1990s (Fig. 4). In addition, there exists a significant positive correlation between the precipitation from November to April in both regions ($r = 0.42$; $p < 0.01$).

Response of *T. superba* growth to interannual climate variability

At a local scale, Mayombe tree growth was primarily positively correlated with precipitation. However, a significantly ($p < 0.05$) positive correlation was found only for November, at the start of the rainy season and also the month with the maximum precipitation of the year (Figs. 5, 6). Correlation values for Ivory Coast were much lower, and no significant correlations were found.

At a regional scale, November precipitation in the Mayombe was used for correlation maps with SSTs and was positively influenced by SSTs of the Gulf of Guinea and mostly the coastal South Atlantic Ocean during the months of October–December (Fig. 7a). SSTs during this time of year were also positively correlated with our Mayombe tree-ring chronology in a part of the Gulf of Guinea and the South Atlantic Ocean (Fig. 7b).

At a global scale, early rainy season precipitation in both regions was influenced by ENSO, with negative ENSO (La Niña) years resulting in wetter than normal early rainy season conditions in the Mayombe region (Fig. 7c). As a result, tree growth in the Mayombe was significantly higher in La Niña years than in ‘normal’ years (Table 5). In Ivory Coast, no significant correlations were found between ENSO and precipitation on the sample sites. However, positive ENSO years corresponded with higher precipitation in northern Ivory Coast (Fig. 7c), likely reflected by stronger tree growth during El Niño years (Table 5).

Discussion

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

Mariaux (1969) was the first to describe annual tree rings in *T. superba*. His description was based on young trees with a lot of juvenile wood. Mature tree rings appear to differ substantially. In trees older than 30 years, bands of parenchyma were less abundant and the marginal parenchyma (if present) was not always continuous. However, the large variations between years that Mariaux (1969)

Table 3 Site and regional chronology characteristics of natural forests in Ivory Coast (IC) and the Mayombe (*n* samples, diameter, number of tree rings, mean growth, MS (mean sensitivity), AC (auto-correlation), time span, Pearson correlation, EPS (expressed population signal))

| | Natural forest IC | Plantations Mayombe | Natural forest Mayombe |
|--------------------------------|-------------------|----------------------|------------------------|
| Total <i>n</i> sampled trees | 29 | 60 | 12 |
| No. of samples in chronology | 22 (81 %) | 28 (47 %) | 11 (92 %) |
| Mean diameter (cm) | 56 ± 11 | 41 ± 12 ^a | 57 ± 15 |
| Mean no. of tree rings | 46 ± 34 | 40 ± 6 | 47 ± 38 |
| Time span chronology | 113 (1895–2008) | 49 (1959–2007) | 36 (1973–2008) |
| Mean growth of chronology (mm) | 4.53 ± 1.64 | 5.45 ± 2.60 | 7.19 ± 2.67 |
| AC | 0.64 | 0.91 | 0.84 |
| MS after standardisation | 0.26 | 0.16 | 0.16 |
| Pearson <i>r</i> | 0.14 | 0.36 | 0.33 |
| EPS | 0.79 | 0.94 | 0.84 |

^a Based on the cumulative tree-ring measurements, not on standing tree measurements

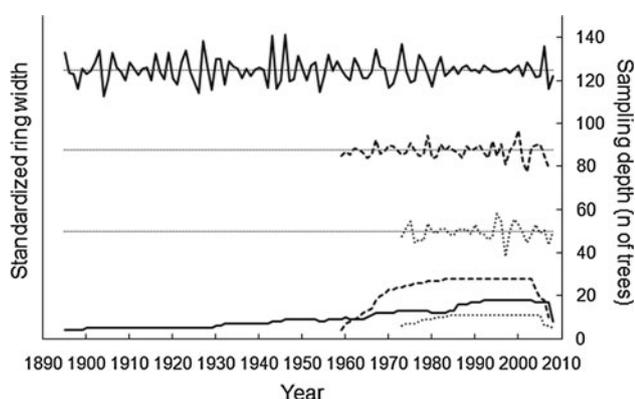


Fig. 3 Standardized chronologies for natural forest (dotted line) and plantations (dashed line) in the Mayombe and the natural forests of Ivory Coast (full line). The lower part of the graph indicates the number of trees included in the chronologies (sampling depth)

reported were also found in our study. In some years, there is a vessel-less area at the start of a growing season. Also, the normal anatomical structure within a ring can be

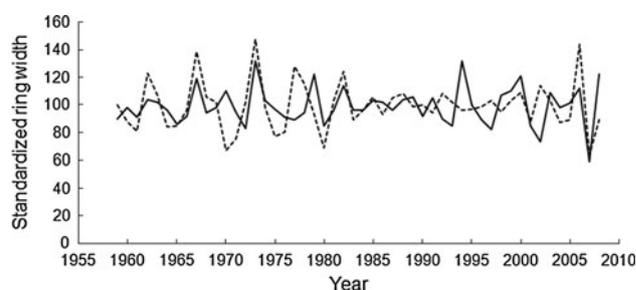


Fig. 4 Standardized regional chronologies of the Mayombe (full line) and Ivory Coast (dashed line). Comparing both chronologies results in a *t* value of 3.7 and a correlation of 0.39 (both $p < 0.01$)

inversed, as was the case in some Ivorian tree rings. Clearly, the anatomical tree-ring structure can differ in *T. superba* from different regions.

Tree rings were easier to detect in the Mayombe compared to Ivory Coast. This is potentially related to a difference in leaf shedding behaviour in the two regions and

Table 4 Ppr (percentage of parallel run), *t* value Baillie–Pilcher and Pearson's correlation coefficient for cross-dating of local chronologies in the Mayombe and Ivory Coast

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

Overlap refers to the time period the two site chronologies have in common and *n* refers to the number of trees included in the site chronologies

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

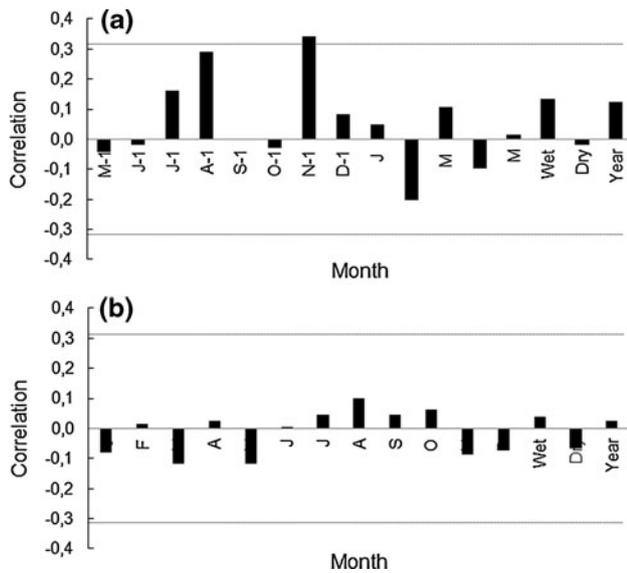


Fig. 5 Correlations between **a** the Mayombe chronology, **b** the Ivorian chronology, and the monthly, seasonally and annual precipitation. The dotted lines indicate the $p < 0.05$ level

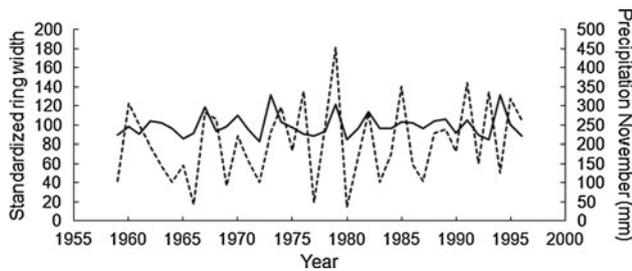


Fig. 6 Correlation between the chronology of the Mayombe and November precipitation. The precipitation curve is a dashed line and the regional chronology is a full line

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

Problems to define tree rings were caused by the first unclear juvenile tree rings, false rings, double rings and especially ring wedging (Mariaux 1969). Worbes (2002) also classified *Terminalia* as a taxon that tends to form wedging rings. Ring wedging has been noted in many tropical tree species (e.g., Trouet et al. 2010; Tarhule and Hughes 2002), but the exact cause for this phenomenon is

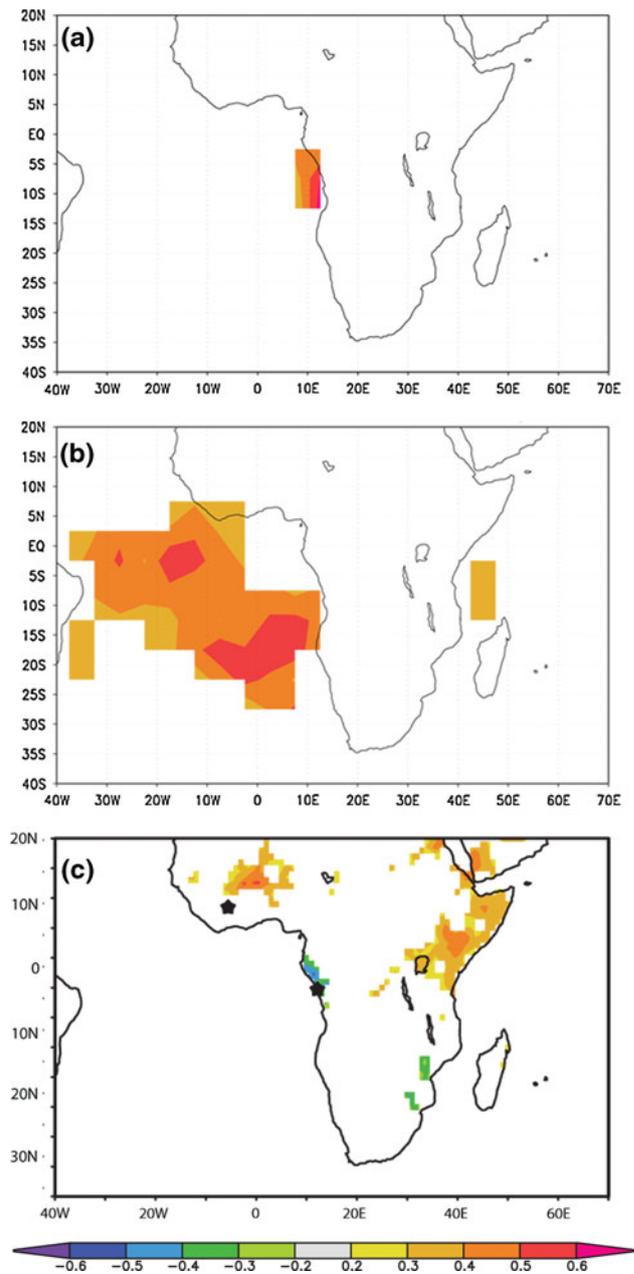


Fig. 7 Correlation maps between **a** November precipitation, **b** tree growth, and gridded average SSTs for the months October–December, all for the Mayombe over the period 1959–1996. The correlation map (1959–2008) between the annual Niño 3.4 time-series and gridded October–November precipitation is shown in (c). The two study sites are indicated as black stars in (c)

unknown. Our study confirms that wedging mostly occurs in the outer parts of the tree circumference, when the tree starts to grow slower due to its inherent growth trend and forms buttresses (Worbes 2002). Buttresses become larger when tree diameters increase (De Ridder et al. 2010), and could also cause wedging. Worbes (2002) related ring wedging to trees that grew under poor light conditions and under competition. *T. superba*, abundantly present in

Table 5 Visualization of two sample tests evaluating the influence of ENSO events on tree growth

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

Ring-width indices during the ENSO event and one year after the event were compared in the Mayombe region and western Ivory Coast (both from 1959 to 2008)

* $p < 0.05$

fallows and forest gaps, mostly receives full light during its juvenile phase. Afterwards, when canopy closure occurs or trees of the climax forest reach their full height, competition for light could cause wedging, especially in the most recent tree rings. To answer Worbes' hypothesis on competition, more ecological data on *T. superba* and the accompanying tree species need to be collected within the sampled forests.

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

Growth patterns in natural and planted African forests

In the Luki Reserve (DRC), Couralet et al. (2010) found between-trees correlations for understory trees that were similar in magnitude to our results. The correlation strength in our study was also in accordance with the findings of Bräuning et al. (2009) and Brienen and Zuidema (2005), lower than those of Stahle et al. (1999) and Therrell et al.

(2006), and higher than the correlations of Trouet et al. (2006, 2010). Auto-correlation is high compared to other tropical tree species (Bräuning et al. 2009; Couralet et al. 2010; Trouet et al. 2006, 2010) but not unusual because *T. superba* has a strong and known age trend, colonizing fallows with fast growth during the first years and strongly decreasing in growth after this juvenile phase.

Fifty-year-old plantations and 40- to 50-year-old natural forest of the same tree species in the Mayombe enable an original comparison of growth patterns in natural versus planted trees. Eshete and Stahl (1999) as well as Worbes (1999) used plantation trees but their time-series were too short for chronology development (<25 years). In our study, the overlap between planted and natural trees is 36 years, and planted and natural trees showed similar growth patterns. The studied plantation is a production forest that is not intensively managed, but nevertheless, the natural forests were more diverse with a more explicit competition for light and nutrients. The average growth as well as the initial growth (first 20 years) was lower in the plantation compared to the natural forest. Two extremely dry years (1956 and 1958) and the use of inferior planting material have been shown to explain the loss of plantation trees immediately after the installation (De Ridder et al. 2010) and have likely also influenced the growth of surviving trees.

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

Our regional chronologies for the Mayombe and Ivory Coast were located more than 2,600 km apart, overlapped in time for 50 years (1959–2008), and showed a weak synchronization. Fichtler et al. (2004) did not find a match between two sites in southern Africa that were 900 km apart and used spectral analysis to reveal similar long-term oscillation patterns. Trouet et al. (2010) cross-dated chronologies from five Miombo woodland sites in Zambia over a distance of more than 1,000 km and found long-distance growth correlations between some sites. To our knowledge, our study is the first to indicate long-distance growth correspondence in rainforests. One hypothesis for these synchronized growth variations could be the presence of a common growing season as Mariaux (1969) confirmed with dendrometer studies. On a limited number of trees, he found that tree growth in both the Mayombe and central Ivory Coast mainly occurred during October–December. Tree growth and November–April precipitation are not directly related in either of the regions, but both tree growth and November–April precipitation showed similar variability. Other relations between tree growth and climate are discussed in detail in the next paragraph.

Response of *T. superba* growth to interannual climate variability

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

Thus, no comparable relation appears to exist between tree growth and precipitation in the two regions, despite long-distance connections for growth on one hand and November–April precipitation on the other hand. Differences in response to climate could be related to climate sensitivity of the trees or the use of short precipitation time series. Regarding climate sensitivity, western Ivory Coast is located in a wetter region than the Mayombe. This could cause a stronger climate signal in the Mayombe following the principle of limiting factors (Fritts and Swetnam 1989). Also, trees near the margins of their climatic distribution have a higher climate-sensitivity (Cook and Kairiukstis 1990). The microclimate in the Congolese Mayombe still enables the growth of tropical trees while in fact, annual precipitation is too limited for their growth (optimal annual precipitation for *T. superba* is 1,500 mm; Groulez and

Wood 1985). In addition, our climate–growth relations were only tested over a rather short but common time span to enable comparison between the two regions (1959–1996). We correlated growth and precipitation from 1959 to 2006 with data from the Luki climate station (Mayombe) to illustrate the influence of longer climate series. In addition to a stronger relation with November precipitation ($r = 0.42$; $p < 0.01$), summed October–December precipitation also showed a strong positive relation with tree growth ($r = 0.37$; $p < 0.01$). So, more and stronger climate correlations in the Mayombe were found if the most recent precipitation data were included. This difference could not be tested in Ivory Coast (shorter precipitation time series, more stations with lacking data), but we hypothesize that stronger relations with precipitation in Ivory Coast could come out if longer precipitation time series, including the most recent years, were available. This is indirectly confirmed by the ENSO study (see below), which was run for the two regions from 1959 to 2008, resulting in a significant relation between tree growth and ENSO climate indices in both regions.

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

Finally, anomalous ENSO conditions were associated with growth effects in both Ivory Coast and the Mayombe, even though local precipitation patterns did not influence tree growth in both regions. So far, the effect of ENSO on African tree growth in two different hemispheres has not been encountered in literature. Because the influence of ENSO on precipitation occurred during the growing season, tree growth could be influenced by ENSO. Schöngart et al. (2006) only found an influence of ENSO on precipitation during the dry season and subsequently, no relationship with tree growth. In general, the Mayombe region appears to be more sensitive to climate variability than Ivory Coast, with higher October–November precipitation and higher growth clearly observed during La Niña years.

In Ivory Coast, higher precipitation during El Niño years slightly northward of the sample sites was found during the growing season, probably resulting in higher growth during El Niño years. In literature, most studies in West and Central Africa are focused on the relation between precipitation and ENSO. Camberlin et al. (2001) found a negative correlation between ENSO and precipitation in August–November for Cameroon, Gabon, the Republic of Congo and coastal DRC, confirming the higher precipitation during La Niña years in the Mayombe, as did Paeth and Friederichs (2004). For Ivory Coast, Paeth and Friederichs (2004) did not observe a consistent relationship for West Africa between ENSO and precipitation. However, we compared the actual zones of higher precipitation in October–November during El Niño years in Fig. 7c with the precipitation response map of Camberlin et al. (2001), Fig. 4, resulting in a response type with some dry months during El Niño years but with wet conditions in October–November. Still, this type of response in October–November is not as strong as the response in the Mayombe, both for precipitation as well as growth. Again, the principle of limiting factors (Fritts and Swetnam 1989) and the presence of *T. superba* trees near the margins of their climatic distribution (Cook and Kairiukstis 1990), could explain the higher climate-sensitivity in the Mayombe.

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

Conclusion and perspectives

Although planted and natural forests with *T. superba* have distinct differences in site conditions such as structure and light competition, both forest types showed significantly similar growth patterns and responses to climate. Cambial growth probably occurs at the same time in planted and natural forests and was influenced by the onset of the rainy season in the Mayombe. Unfortunately, precipitation did not correlate with the Ivorian regional chronology. This is possibly the result of limited precipitation data, rendering the hypothesis on cambial growth shifts with precipitation inconclusive. However, regional climate variability was influenced by SST anomalies in the Mayombe whereas ENSO indices controlled climate variability over both hemispheres in October–November with, on the one hand, higher growth at the northern hemisphere sites during El

Niño years and, on the other hand, higher growth at the southern hemisphere sites during La Niña years.

Importantly, if length or quality of precipitation data hampers proper correlation with tree ring data, comparison with large-scale climate factors as SSTs is valuable and can pinpoint at important influences on precipitation patterns and tree growth. Therefore, in tropical regions, where climate data are often scarce, comparison with these SSTs and derived ENSO indices offers interesting possibilities for future dendroclimatological studies in the tropics, even in equatorial Africa.

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References

- Baillie MGL, Pilcher JR (1973) A simple program for tree-ring research. *Tree Ring Bull* 33:7–14
- Balas N, Nicholson SE, Klotter D (2007) The relationship of rainfall variability in West Central Africa to sea-surface temperature fluctuations. *Int J Climatol* 27:1335–1349
- Boninsegna JA, Argollo J, Aravena JC, Barichivich J, Christie D, Ferrero ME, Lara A, Le Quesne C, Luckman BH, Masiokas M, Morales M, Oliveira JM, Roig F, Srur A, Villalba R (2009) Dendroclimatological reconstructions in South America: a review. *Paleogeogr Paleoclimatol Paleoecol* 281:210–228
- Bräuning A, Volland-Voigt F, Burchardt I, Ganzhi O, Nauss T, Peters T (2009) Climatic control of radial growth of *Cedrela montana* in a humid mountain rainforest in southern Ecuador. *Erdkunde* 63:337–345
- Brienen RJW, Zuidema PA (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146:1–12
- Camberlin P, Janicot S, Pocard I (2001) Seasonality and atmospheric dynamics of the teleconnection between African rainfall and tropical sea-surface temperature: Atlantic vs ENSO. *Int J Climatol* 21:973–1005
- Cook ER, Kairiukstis LA (1990) *Methods of dendrochronology. Applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht
- Coualet C (2010) *Community dynamics, phenology and growth of tropical trees in the rain forest Reserve of Luki, Democratic Republic of Congo*. PhD thesis, Ghent University
- Coualet C, Sass-Klaassen U, Sterck FJ, Bekele T, Zuidema PA (2005) Combining dendrochronology and matrix modelling in

- demographic studies: an evaluation for *Juniperus procera* in Ethiopia. For Ecol Manage 216:317–330
- Couzalet C, Sterck FJ, Sass-Klaassen U, Van Acker J, Beeckman H (2010) Species-specific growth responses to climate variations in understory trees of a Central African rain forest. Biotropica 42:503–511
- CTFT (1959) Monographie du limba (*Terminalia superba* Engler et Diels). CTFT, Paris
- CTFT (1983) Bois tropicaux (5^{ième} édition). CTFT, Nogent-sur-Marne
- De Ridder M, Hubau W, Van den Bulcke J, Van Acker J, Beeckman H (2010) The potential of plantations of *Terminalia superba* Engl. & Diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo). Ann For Sci 67:501. doi:10.1051/forest/2010003
- Détienne P, Mariaux A (1970) La périodicité de formation des cerne dans le bois d'okoumé. Bois For Trop 131:37–50
- Détienne P, Mariaux A (1975) Nature et périodicité des cerne dans le bois de Niangon. Bois For Trop 159:29–37
- Détienne P, Mariaux A (1976) Nature et périodicité des cerne dans le bois de samba. Bois For Trop 169:29–35
- Détienne P, Mariaux A (1977) Nature et périodicité des cerne dans les bois rouges de méliacées africaines. Bois For Trop 175:52–61
- Devall MS, Parresol BR, Wright JS (1995) Dendroecological analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in Central Panama. IAWA J 16:411–424
- Douglas AE (1920) Evidence of climatic effects in the annual rings of trees. Ecology 1:24–32
- Douglas AE (1941) Crossdating in dendrochronology. J For 39:825–831
- Dünisch O, Montoia VR, Bauch J (2003) Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. Trees 17:244–250
- Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwiss Centralb 88:230–250
- Eshete G, Stahl G (1999) Tree rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. For Ecol Manag 116:107–117
- FAO (1986) Atlas of African agriculture. FAO, Rome
- FAO (2008) Digital soil map of the world. FAO, Rome
- Fichtler E, Trouet V, Beeckman H, Coppin P, Worbes M (2004) Climatic signals in tree rings of *Burkea africana* and *Pterocarpus angolensis* from semiarid forests in Namibia. Trees 18:442–451
- Friedrich M, Remmele S, Kromer B, Hofmann J, Spurk M, Kaiser KF, Orsel C, Küppers M (2004) The 12,460-year Hohenheim oak and pine tree-ring chronology from Central Europe—a unique annual record for radiocarbon calibration and paleoenvironment reconstructions. Radiocarbon 46:1111–1122
- Fritts HC (1976) Tree rings and climate. Academic Press, London
- Fritts HC, Swetnam TW (1989) Dendroecology: a tool for evaluating variations in past and present forest environments. Adv Ecol Res 19:111–188
- Gebrekistos A, Mitlöhner R, Teketay D, Worbes M (2008) Climate-growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. Trees 22:631–641
- Gourlay ID (1995) The definition of seasonal growth zones in some African Acacia species—a review. IAWA J 16:353–359
- Groulez J, Wood PJ (1985) A monograph on *Terminalia superba*. Centre Technique Forestier Tropical & Commonwealth Forestry Institute, Nogent-sur-Marne
- Haneca K, Boeren I, Van Acker J, Beeckman H (2005) Dendrochronology in suboptimal conditions: tree rings from medieval oak from Flanders (Belgium) as dating tools and archives of past forest management. Veg Hist Archaeobot 15:137–144
- Haneca K, Cufar K, Beeckman H (2009) Oaks, tree-rings and wooden cultural heritage: a review of the main characteristics and applications of oak dendrochronology in Europe. J Archaeol Sci 36:1–11
- Hawthorne WD (1995) Ecological profiles of Ghanaian forest trees. Tropical forestry papers 29, University of Oxford
- Humbert P (1946) Aménagement des forêts climatiques tropicales au Mayumbe. Bull Agric Congo Belge 37:15–87
- Hummel FC (1946) The formation of growth rings in *Entandrophragma macrophyllum* A. Chev. and *Khaya grandifolia* C. DC. Int For Rev 25:103–107
- Joly M, Voldoire A, Douville H, Terray P, Royer J-F (2007) African monsoon teleconnections with tropical SSTs: validation and evolution in a set of IPCC4 simulations. Clim Dyn 29:1–20
- Kennedy JJ, Rayner NA, Smith RO, Saunby M, Parker DE (2011a) Reassessing biases and other uncertainties in sea-surface temperature observations since 1850 part 1: measurement and sampling errors. J Geophys Res 116:D14103. doi:10.1029/2010JD01521
- Kennedy JJ, Rayner NA, Smith RO, Saunby M, Parker DE (2011b) Reassessing biases and other uncertainties in sea-surface temperature observations since 1850 part 2: biases and homogenisation. J Geophys Res 116:D14104. doi:10.1029/2010JD015220
- Köppen WP, Geiger R (1930) Handbuch der Klimatologie. Verlag von Gebrüder Borntraeger, Berlin
- Mariaux A (1969) La périodicité des cerne d'accroissement dans le bois de *Terminalia superba*. Bois For Trop 128:39–54
- McKnight TL, Hess D (2000) Climate zones and types: the Köppen system. Physical geography: a landscape appreciation. Prentice Hall, Upper Saddle River
- Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int J Climatol 25:693–712
- Nicholson SE, Entekhabi D (1987) Rainfall variability in equatorial and southern Africa: relationships with sea surface temperatures along the southwestern coast of Africa. J Clim Appl Meteorol 26:561–578
- Paeth H, Friederichs P (2004) Seasonality and time scales in the relationship between global SST and African rainfall. Clim Dyn 23:815–837
- Pumijumnong N, Eckstein D, Sass U (1995) Tree-ring research on *Tectona grandis* in northern Thailand. IAWA J 16:385–392
- Rinn F (2003) TSAP-WinTM user reference. Rinntech, Heidelberg
- Sass-Klaassen U, Couzalet C, Sahle Y, Sterck FJ (2008) Juniper from Ethiopia contains a large-scale precipitation signal. Int J Plant Sci 169:1057–1065
- Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Hüttermann A, Worbes M (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. Glob Change Biol 10:683–692
- Schöngart J, Orthmann B, Hennenberg KJ, Porembski S, Worbes M (2006) Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Glob Change Biol 12:1139–1150
- Stahle DW (1999) Useful strategies for the development of tropical tree-ring chronologies. IAWA J 20:249–253
- Stahle DW, Mushove PT, Cleaveland MK, Roig F, Haynes GA (1999) Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. For Ecol Manag 124:217–229
- Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86
- Tarhule A, Hughes MK (2002) Tree-ring research in semi-arid West Africa: need and potential. Tree Ring Res 58:31–46
- Therrell MD, Stahle DW, Ries LP, Shugart HH (2006) Tree-ring reconstructed rainfall variability in Zimbabwe. Clim Dyn 26:677–685

- Trenberth KE (1997) The definition of El Niño. *Bull Am Meteorol Soc* 78:2771–2777
- Trenberth KE, Stepaniak DP (2001) Indices of El Niño evolution. *J Clim* 14:1697–1701
- Trouet V, Haneca K, Coppin P, Beeckman H (2001) Tree ring analysis of *Brachystegia spiciformis* and *Isobertinia tomentosa*: evaluation of the ENSO-signal in the miombo-woodland of eastern Africa. *IAWA J* 22:385–399
- Trouet V, Coppin P, Beeckman H (2006) Annual growth ring patterns in *Brachystegia spiciformis* reveal influence of precipitation on tree growth. *Biotropica* 38:375–382
- Trouet V, Esper J, Beeckman H (2010) Climate/growth relationships of *Brachystegia spiciformis* from the miombo woodland in south central Africa. *Dendrochronologia* 28:161–171
- van Oldenborgh GJ, Burgers G (2005) Searching for decadal variations in ENSO precipitation teleconnections. *Geophys Res Lett* 32:L15701
- White F (1983) The vegetation of Africa. UNESCO, Switzerland
- Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with application in dendroclimatology and hydrometeorology. *J Clim Appl Meteorol* 23:201–213
- Wils THG, Sass-Klaassen U, Eshetu Z, Brauning A, Gebrekirstos A, Couralet C, Robertson I, Touchan R, Koprowski M, Conway D, Briffa K, Beeckman H (2011) Dendrochronology in the dry tropics: the Ethiopian case. *Trees* 25:345–354
- Worbes M (1995) How to measure growth dynamics in tropical trees. A review. *IAWA J* 16:337–351
- Worbes M (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. *J Ecol* 87:391–403
- Worbes M (2002) One hundred years of tree-ring research in the tropics - A brief history and an outlook on future challenges. *Dendrochronologia* 20:217–231
- Worbes M, Staschel R, Roloff A, Junk WJ (2003) Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *For Ecol Manage* 173:105–123
- Trouet V, Van Oldenborgh GJ (2013) KNMI Climate Explorer: a web-based research tool for high-resolution paleoclimatology. *Tree Ring Res* 69:3–13