

Species-Specific Growth Responses to Climate Variations in Understory Trees of a Central African Rain Forest

Camille Couralet^{1,2,4}, Frank J. Sterck³, Ute Sass-Klaassen³, Joris Van Acker², and Hans Beeckman¹

¹ Laboratory for Wood Biology and Xylarium, Royal Museum for Central Africa, Leuvensesteenweg 13, 3080 Tervuren, Belgium

² Laboratory for Wood Technology, Gent University, Coupure Links 653, 9000 Gent, Belgium

³ Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

ABSTRACT

Basic knowledge of the relationships between tree growth and environmental variables is crucial for understanding forest dynamics and predicting vegetation responses to climate variations. Trees growing in tropical areas with a clear seasonality in rainfall often form annual growth rings. In the understory, however, tree growth is supposed to be mainly affected by interference for access to light and other resources. In the semi-deciduous Mayombe forest of the Democratic Republic of Congo, the evergreen species *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* dominate the understory. We studied their wood to determine whether they form annual growth rings in response to changing climate conditions. Distinct growth rings were proved to be annual and triggered by a common external factor for the three species. Species-specific site chronologies were thus constructed from the cross-dated individual growth-ring series. Correlation analysis with climatic variables revealed that annual radial stem growth is positively related to precipitation during the rainy season but at different months. The growth was found to associate with precipitation during the early rainy season for *Aidia* but at the end of the rainy season for *Corynanthe* and *Xylopia*. Our results suggest that a dendrochronological approach allows the understanding of climate–growth relationships in tropical forests, not only for canopy trees but also for evergreen understory species and thus arguably for the whole tree community. Global climate change influences climatic seasonality in tropical forest areas, which is likely to result in differential responses across species with a possible effect on forest composition over time.

Abstract in French is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: *Aidia ochroleuca*; climate–growth relationships; *Corynanthe paniculata*; Democratic Republic of Congo; tropical dendrochronology; *Xylopia wilwerthii*.

TROPICAL FORESTS ARE UNDER COMBINED PRESSURE of global macroclimate changes and deforestation that rapidly modify local climatic conditions (Bonan 2008). In Africa, the average temperature is expected to rise by 3–4°C during the 21st century, which is 1.5 times more rapid than the foreseen global temperature change (Boko *et al.* 2007). Future climate scenarios also predict a 5–15 percent decrease in precipitation during the rainy season and a decline of 3–4 percent in annual rainfall per decade in the African tropics (Malhi & Wright 2004, Boisvenue & Running 2006). In addition, direct human pressure is likely to increase the vulnerability of forests to these warmer and drier conditions (Koenig 2008). Recent modeling studies showed that deforestation enforces the effects of warming and drought events (Malhi *et al.* 2008). It is, however, unknown how different forest types will develop under these constraints, since long-term records on responses of tropical tree species to changes in environmental factors are lacking (Clark 2004, Phillips *et al.* 2009). Depending on climate region, forest type or canopy position, tree species can differ in their tolerance to drought and shade (Condit *et al.* 1995, Sterck *et al.* 2006, Engelbrecht *et al.* 2007). The high diversity of species and their variable ecological preferences potentially allow a high diversity of reactions within the tree communities. Yet, testing this hypothesis has so far proved difficult, due to the limited research on species-specific responses to environmental factors in different tropical forest types. Field studies using perma-

nent plots in the tropics provide growth data of at most a few decades and rarely with an annual resolution (Clark *et al.* 2003).

Dendrochronology can provide long-term records of tree growth with annual resolution, but is most successful where climate shows strong and regular seasonality triggering annual ring formation (Jacoby 1989, Schweingruber 1996). Rain forest trees have long been thought not to form annual rings because of weak seasonality and low variability in temperature and day length in the tropics (Whitmore 1998). This persistent assumption caused many dendrochronologists to focus their efforts on temperate trees rather than tropical trees. Such preference is also explained by the extensively complex wood anatomy in tropical trees (Détienne 1989). Nevertheless, across the various tropical biomes and for most trees, alternating environmental conditions induce periods of reduced or suspended cambial activity leading to the formation of identifiable growth layers (Détienne 1989, Mariaux 1995, Worbes 2002). In lowland tropical rain forests, regular growth periodicity allowed the construction of species-specific tree-ring chronologies for several species (Devall *et al.* 1995, Mariaux 1995, Détienne *et al.* 1998, Schöngart *et al.* 2002, Worbes *et al.* 2003, Brien & Zuidema 2005, Brookhouse 2006, Pumijumong & Wanyaphet 2006, Schöngart *et al.* 2006, Buckley *et al.* 2007, Lisi 2008, Brien *et al.* 2009). Such long-term growth series can be cross-compared with climate records to unravel the species-specific sensitivity to past climatic conditions. This is a prerequisite to evaluate the response of vegetation formations to future environmental changes (Condit *et al.* 1995, Pumijumong & Park 1999, Chidumayo 2005, Trouet *et al.* 2006).

Received 25 June 2009; revision accepted 13 October 2009.

⁴Corresponding author; e-mail: couraletc@gmail.com

© 2010 The Author(s)

Journal compilation © 2010 by The Association for Tropical Biology and Conservation

From this perspective, the floristic and structural complexity of tropical rain forests encourages consideration of the large range of species they harbor. Much knowledge has been generated on upper-canopy trees that are, at the adult stage, not light-limited and strongly exposed to water stress. On the other hand, the growth of lower-canopy or understory species spending their lifetime under other trees is assumed to be more limited by local site factors, such as light, than by water (Phipps 1982). Moreover, small-stature trees with ambiguous seasonal variability in leaf fall preferentially use deeper sources of soil water than larger or deciduous trees (Meinzer *et al.* 1999). Ring-width series of understory trees are thus supposed to show a much more variable ontogenetic growth trend, less directly related to external environmental factors and to water stress in particular. Studies of radial growth responses to climate in understory trees of temperate forests support this hypothesis (Liu 1993, Orwig 1997, Rasmussen 2007, Martín-Benito *et al.* 2008). Nevertheless, growth response to climate is hardly documented for evergreen tree species. While in deciduous trees leaf shedding is an obvious sign of cambial dormancy and suggests a clear link between environmental factors and phenology, for evergreen trees this relation is thought to be erratic (Jacoby 1989, Worbes 1999).

We conducted a study on three common, evergreen understory tree species from the Mayombe forest, a tropical semi-evergreen rain forest west of the Democratic Republic of Congo (DRC). Climate changes are expected to affect the region significantly in the 21st century but studies of the influence of climate variations on tree growth in African forests are scarce (Détienne *et al.* 1998, Worbes *et al.* 2003, Couralet *et al.* 2005, Verheyden *et al.* 2004, Schöngart *et al.* 2006, Trouet *et al.* 2006, Sass-Klaassen *et al.* 2008) and to our knowledge still lacking for lower-canopy tree species. We aimed to assess whether dendrochronology is applicable to these understory tree species and, if so, whether and how their radial growth dynamics is related to inter- and intra-annual changes in climate (temperature, precipitation and solar radiation).

In this study, after demonstrating the annual nature of tree rings in three understory species, we address the following questions: (1) Do trees within and across species synchronize stem growth in response to the same environmental factors? (2) How do trees of different species respond in radial stem growth to year-to-year and within-year variations in climate? We expect to reveal diversity ingrowth patterns across different understory tree species and given the seasonality in rainfall, we predict positive growth responses to precipitation.

METHODS

STUDY SITE.—The Luki forest reserve is located in the southwestern Democratic Republic of Congo (DRC) ($5^{\circ}28'–42'$ N, $13^{\circ}4'–18'$ E), 30 km north from the port city of Boma (Fig. 1A). It is the southernmost remnant of the Mayombe forest, stretching along the Atlantic Ocean from the central coast of Gabon and renowned for its high floristic diversity and the presence of large timber trees (Monteiro 1962). The protected forest area covers 32,700 ha of hilly landscape (150–500 m asl) on heterogeneous soils, generally ferrallitic and with poor chemical content (Monimeau 1990).

Climate records (1959–2006) were available from the Luki meteorological station for precipitation, air temperature, relative humidity and solar irradiance (Fig. 1B). The climate is characterized by a mean annual temperature of 24.6°C with limited yearly variation and a mean annual rainfall of 1180 mm/yr. A distinct dry period lasts from June to September. Such low annual rainfall and 3–4 mo with < 50 mm monthly precipitation generally do not favor the presence of a dense humid forest; however, the strong oceanic influence, the landscape of the region and the self-regulating effect of the vegetation create favorable conditions for the establishment of dense humid forest (Sénéchal *et al.* 1989, Pendje & Baya ki 1992, Lubini 1997). Mists are present all yearlong and during the driest months a thick, low-level but non-precipitating cloud layer blocks solar irradiance and causes temperature to drop. The rainfall

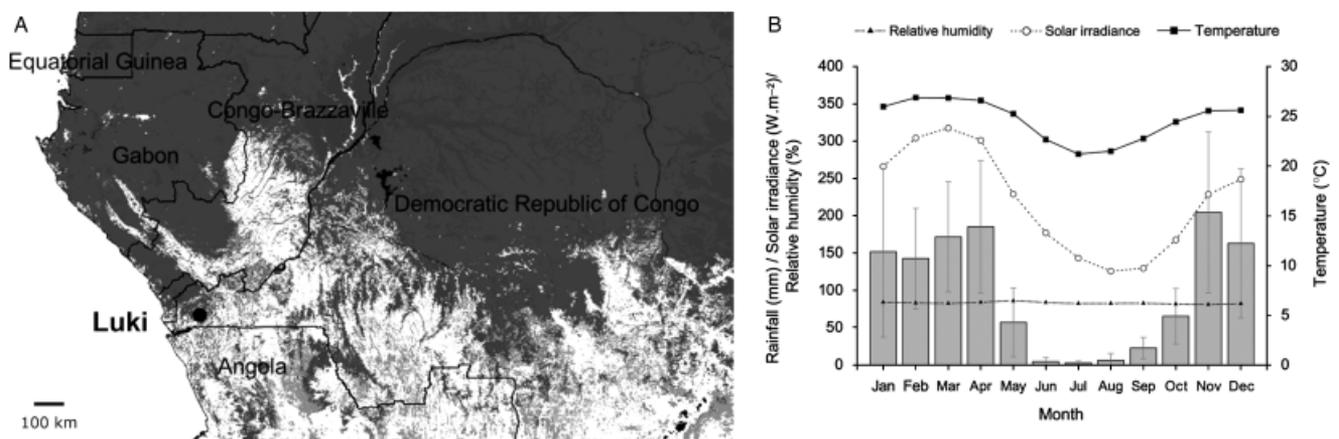


FIGURE 1. (A) Location of the study site with simplified vegetation cover of the area from Global Land Cover 2000 (Mayaux *et al.* 2004): darker zones are a mosaic of evergreen, deciduous and mixed forests with a minimum of 15 percent tree cover. (B) Climate diagram of the Luki meteorological station, Democratic Republic of Congo: monthly means of rainfall (\pm SD), temperature, air humidity (1959–2006) and solar irradiance (1959–1994).

shortage is thus partially compensated and the relative air humidity remains constantly high, always > 80 percent. Consequently, despite a clear seasonal rainfall pattern plants may not suffer extreme water stress during the dry season.

The forest of Luki can be generally classified as a tropical semi-evergreen rain forest of the Guineo-Congolean forest domain (Lebrun & Gilbert 1954, Lubini 1997, Whitmore 1998) but occurs in a mosaic landscape with patches of agricultural fields and settlements. It consists of a mixture of deciduous and evergreen tree species in the upper-stratum and mostly evergreen species in the understory.

STUDY SPECIES.—*Aidia ochroleuca* (K. Schum.) Bullock ex E.M.A. Petit, *Corynanthe paniculata* Welw. (both Rubiaceae) and *Xylopia wilwerthii* Wild. & T. Durand var. *cuneata* De Wild. (Annonaceae) are abundant and commonly co-occurring species in the Guineo-Congolean rain forests, from Gabon to the eastern DRC (Petit 1962, Schmitz 1988, Sénéchal *et al.* 1989, Lubini 1997). In the secondary forest of Luki they can contribute to > 60 percent of the total basal area (Donis & Maudoux 1951; C. Couralet, unpubl. data). These evergreen, medium-sized trees of up to 20 m in height and 60 cm diameter at breast height (dbh) are confined to the lower-canopy level and understory (Aubréville 1961, Petit 1961, Lubini 1997, Lebrun & Stork 2003). *Corynanthe paniculata* and *X. wilwerthii* have a straight trunk whereas *A. ochroleuca* is often ramified from the base. All three species are characterized by a very hard and fine-textured wood used by local communities to produce solid tools and high-quality charcoal (Fouarge & Gérard 1964).

SAMPLING AND SAMPLE PREPARATION.—Stem discs of five trees per species were collected in 2005. We selected representative trees of each species, with crowns under the closed upper canopy layer and diameters within the predominantly observed range (15–40 cm). Trees were cut at 0.5–1 m aboveground level such that a maximum number of growth rings were visible. The 4–6-cm-thick sections were deep-frozen for 2 wk to prevent insect or fungal attacks and subsequently air-dried. Their cross-sectional surface was planed and sanded up to a grid size of 1200.

DETECTION OF CONCENTRIC GROWTH LAYERS IN THE WOOD.—Growth-ring structure was analyzed macroscopically and microscopically following the International Association of Wood Anatomists hardwood feature list (Wheeler *et al.* 1989). Ring boundaries of tropical tree species are characterized by a variety of features such as marginal parenchyma bands, alternation of fiber and parenchyma tissues, variation in the vessel size and distribution, variation in the fiber wall thickness, or a combination of all these features (Détienne 1989, Worbes 1995). The wood of the three species is diffuse-porous with different rhythmic variations in wood structure visible to the naked eye (Fig. 2); however, microscopic observations were required to reliably detect anatomical features that mark growth–ring boundaries and distinguish them from, *e.g.*, intra-annual density variations. The main difficulties for the three study species were their low growth

levels (average ring width of 1.13–1.65 mm) leading to frequently wedging or absent rings.

Ring widths were measured to the nearest 0.01 mm under a stereo-microscope coupled with a Lintab measuring device and TsapWin software (Rinn 2003), on two or three (for irregularly shaped samples) radii for each stem disc. Because the supposed growth season spans two calendar years (rainy season typically from October_{*n*-1} to May_{*n*}), the year in which annual cambial activity is expected to stop (year *n*) was nominated to define the growth year and the corresponding ring-width value.

DENDROCHRONOLOGICAL ANALYSES.—Tree-ring analyses were applied to all samples to show whether stem growth rate was synchronized over time for all trees. Cross-dating, *i.e.*, the matching of ring-width series, allows for the detection of missing rings (if one tree in the sample set did not form a ring in a particular year) or false rings (variations in the wood anatomy mistaken with ring boundaries; Wils *et al.* 2009). Successful cross-dating of ring-width series denotes consistent and synchronous patterns of variation (Cook & Kairiukstis 1992) and indicates that a common external factor controls ring formation in different trees (Pilcher & Gray 1982, Worbes 1995, Cherubini *et al.* 1998). Cross-dating was performed visually in combination with a correlation analysis using Cofecha software (Tree-Ring Laboratory, Columbia University, New York, U.S.A.; Holmes 1983). Starting with radii from the same tree, alignment of the ring-width series allowed the identification of anomalies that were then corrected after investigation on the stem discs. The series were then averaged per tree and the cross-dating process was repeated between tree averages. The detection of pointer years, *i.e.*, extreme years common within a site, served as an extra-check during the cross-dating process (Schweingruber 1996).

Tree growth is affected by climatic fluctuations and by a wide array of non-climatic factors (Brookhouse 2008), *e.g.*, canopy dynamics or individual size-related trends (Pilcher & Gray 1982). Tree-ring width series thus reflect a complex set of variations. To amplify the climate-induced signal, the series were standardized using Arstan software (Tree-Ring Laboratory; Cook 1985) to remove low-frequency, most likely non-climatic trends. A smoothing spline (wavelength of 32 yr) was first fitted to each raw series (Cook & Kairiukstis 1992), then each measure was divided by the corresponding value of the function to transform the original curves into stationary time-series (mean = 1 and homogenous variance). A ring-width index series was created for each radius then tree. Autocorrelation (AC, year-to-year dependence of ring-width values due to the influence of a growth season on the next) was removed by applying an autoregressive model of the adequate order for each series. Eventually, the indexed curves were averaged to produce the final species chronologies.

Statistical information on the tree-ring measurements is summarized in Table 1. The mean sensitivity (MS) indicates the level of between-ring variability in the measured series and reflects the sensitivity of radial tree growth to a common external signal (Fritts 1976, Schweingruber 1996). Inter-series Pearson's correlations ($P < 0.05$) were calculated between radii of each tree, between trees and between species to express the level of affinity of the measured curves and evaluate the quality of the computed mean series. Student's *t*-values and coefficients

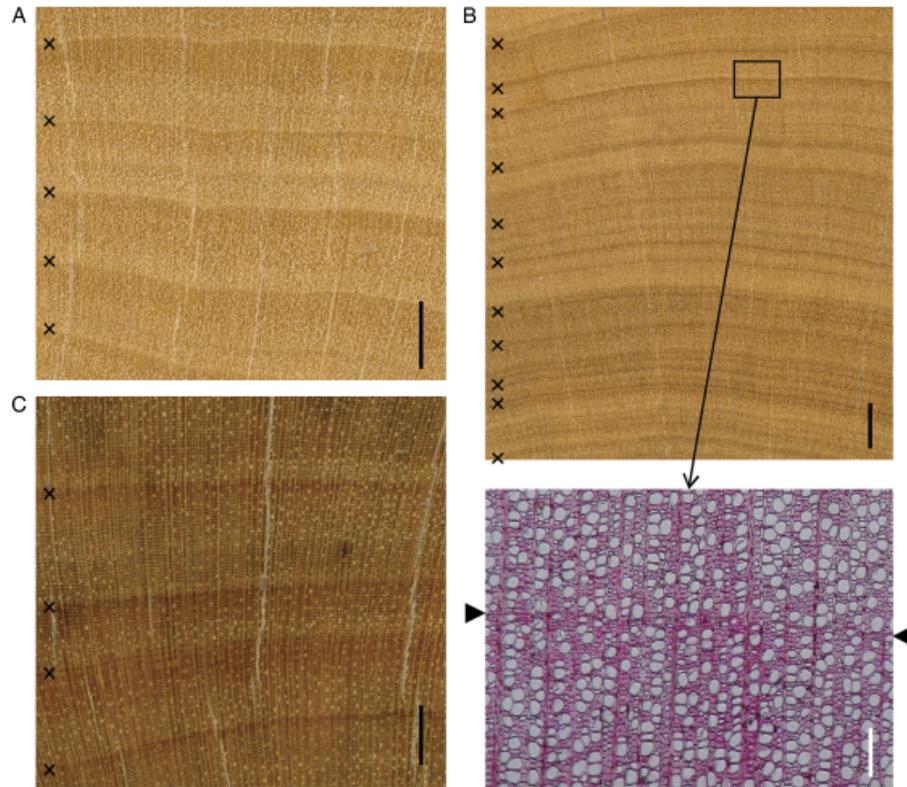


FIGURE 2. Tree-ring structure and growth-ring boundaries of three understory species of the Luki forest reserve, Democratic Republic of Congo. (A) *Aidia ochroleuca*: vessel frequency steadily decreases toward the ring boundary, marked by a vessel-free fiber band. (B) *Corynanthe paniculata*: ring boundary is marked by one or two lines of radially flattened fibers, but can be confused with the numerous fiber-wall density variations visible on the wood. Black arrows point at these lines on a thin section that allows seeing the microscopic wood anatomical structure. (C) *Xylopi wilwerthii*: ring boundary is marked by two to three lines of very thick-walled latewood fibers, making the wood appear darker. Notice the ladder-like pattern of axial parenchyma cells (scalariform parenchyma), typical for Annonaceae. Black crosses indicate ring boundaries. Radial growth direction is from bottom to top. Black scale bars = 1 cm, white scale bar = 1 mm.

TABLE 1. Descriptive statistics and quality control of the ring-width series contributing to the chronologies for three understory species of the Luki forest reserve, Democratic Republic of Congo: *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopi wilwerthii*. *SD*, standard deviation, *AC*, autocorrelation (1-year lag); *MS*, mean sensitivity; *Glk*, Gleichaufgkeitskoeffizient. Average of Pearson's correlations, *t*-value ($P < 0.05$) and *Glk* or coefficient of parallel variation.

Species	<i>Aidia ochroleuca</i>	<i>Corynanthe paniculata</i>	<i>Xylopi wilwerthii</i>
Number of samples	5	5	5
Mean diameter (cm) (range)	21 (18–25)	24 (17–40)	16 (14–17)
Mean age (yr) (range)	55 (39–85)	97 (69–112)	39 (26–49)
Time span (yr)	1922–2006	1895–2006	1958–2006
Ring width (mean \pm SD, mm) ^a	1.65 \pm 1.14	1.13 \pm 0.70	1.62 \pm 0.98
AC ^a	0.61	0.54	0.19
MS ^a	0.42	0.42	0.50
Within-tree correlation ^b	0.70	0.60	0.72
Between-tree			
Correlation ^b	0.36	0.24	0.27
<i>t</i> -value (\pm SD) ^b	5.6 \pm 0.7	5.9 \pm 2.0	4.4 \pm 1.7
<i>Glk</i> (\pm SD, %) ^b	72.3 \pm 7.2	67.0 \pm 4.9	73.2 \pm 17.3

Values based on:

^aRaw series.

^bDetrended data.

of parallel variation (*Gleichaufigkeitskoeffizient* [Glk]) were calculated between trees of each species to assess the quality of the final chronologies developed for climate–growth analysis (Baillie & Pilcher 1973).

ANALYSIS OF CLIMATIC EFFECTS.—To investigate the link between the radial stem growth of understory trees and climate, we compared each species chronology with annual records of total rainfall, average temperature and average solar radiation from the Luki meteorological station. Moreover, to test whether the within-year timing of climate variation plays an important and differential role for the three species studied, Pearson's correlations ($P < 0.05$) were computed between the species chronologies and contemporary time-series of climate variables on a monthly basis and for groups of months (Fritts 1976). According to results from earlier studies on tree growth in a seasonal tropical climate (Couralet *et al.* 2005, Trouet *et al.* 2006) and high-resolution measurements of radial growth the growing period was assumed to coincide approximately with the rainy season lasting from October to May. We calculated correlations for a 12-mo period from September_{year $n-1$} to August_{year n} thus amply covering the rainy season.

In addition, the dbh of 10 trees per species was measured every month with graduated tape during 15 mo (April 2006–June 2007) to study seasonal growth dynamics of *Aidia*, *Corynanthe* and *Xylopia* in response to contemporary weather conditions. Because correlations with growth were found only with precipitation, the measurements were visually compared with contemporary monthly precipitation records to explore intra-annual climate–growth relationships and refine the results obtained from the ring-width chronologies.

RESULTS

STATISTICAL CHARACTERISTICS OF SINGLE RING-WIDTH SERIES AND CHRONOLOGIES.—Mean ring width ranged from 1.13 mm for *C. paniculata* to 1.62 and 1.65 mm for *X. wilwerthii* and *A. ochroleuca*, respectively. The large standard deviations for this trait indicated a high variation in average ring width between trees of a same species (Table 1).

Within-tree correlations were high and allowed to merge the growth series into mean curves for each individual tree. Trees of the same species were also characterized by high values for mean series inter-correlations, t -values and Glk, thus providing robust chronologies per species. The rather high values of MS indicated that ring width varied widely between years. The higher AC values in stem growth between successive years for *Aidia* and *Corynanthe* probably resulted in slightly lower values for MS of these species. Overall, these results exhibit that trees of the same species synchronized their radial stem growth to the same external environmental factor. On the other hand, the correlations between species chronologies were low or very low (*Aidia*–*Xylopia*: 0.20, *Corynanthe*–*Xylopia*: 0.15, *Aidia*–*Corynanthe*: 0.03), suggesting that the three species differ in response to climatic factors. This is visible when looking at the three chronologies that show almost no common variation (Fig. 3).

CLIMATE–GROWTH RELATIONSHIPS.—There was no significant correlation between the three species chronologies and annual total rainfall, average temperature or average solar radiation, indicating that radial growth of the study species was not controlled by long-term

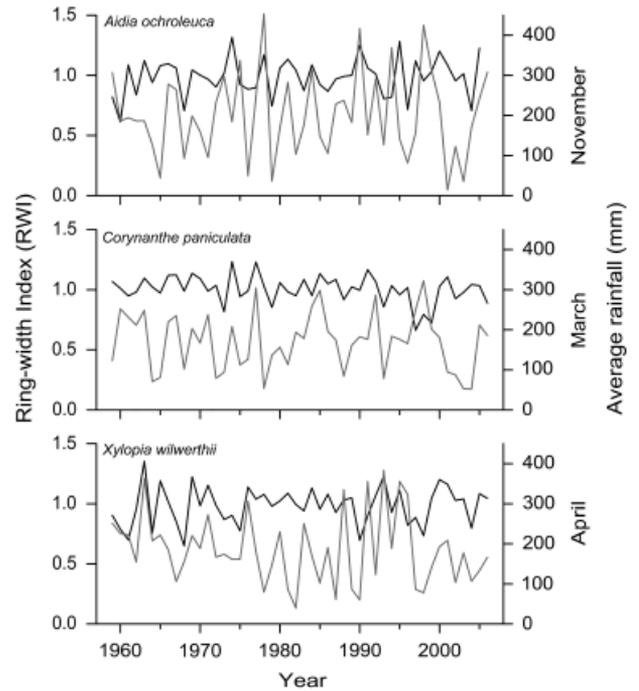


FIGURE 3. Illustration of the correlation ($P < 0.05$) between the ring-width index (RWI) of three understory tree species and single-month climatic records in the Luki forest reserve, Democratic Republic of Congo (1959–2006): *Aidia ochroleuca* and November rainfall ($r = 0.27$), *Corynanthe paniculata* and March rainfall ($r = 0.29$), *Xylopia wilwerthii* and April rainfall ($r = 0.34$).

annual variation of these climate factors. Single-month temperature and solar radiation were also not associated with the annual variation in radial growth of the studied species; however, significant positive correlations appeared between ring width and single-month precipitation values for the three species. Remarkably, the months for which significant values were found differed between species (Fig. 3). For *Aidia* the correlation between radial growth and rainfall was significant at the onset of the rainy season, in November, whereas for *Corynanthe* and *Xylopia* the correlation was significant at the end of the rainy season, in March and April, respectively (Figs. 3 and 4).

These trends were supported by correlations between radial growth and monthly values of precipitation over the studied period, most clearly during the rainy season (Fig. 4). *Aidia* showed an overall positive growth response to rainfall in the early rainy season (September–February), culminating in November, and no specific trend in the late rainy season. Inversely, the radial growth of *Corynanthe* was negatively correlated to rainfall in the early rainy season (September–January) and positively correlated to rainfall in the late rainy season with a peak in March. For *Xylopia* there was no such clear pattern but the correlation between radial growth and rainfall was mostly positive over the whole rainy season and was strongest in the end, in April. Both types of analysis (Figs. 3 and 4) thus suggest that the amount of precipitation was critical for radial stem growth during the transition months from dry to wet season for *Aidia*, and from wet to dry season for *Corynanthe* and *Xylopia*.

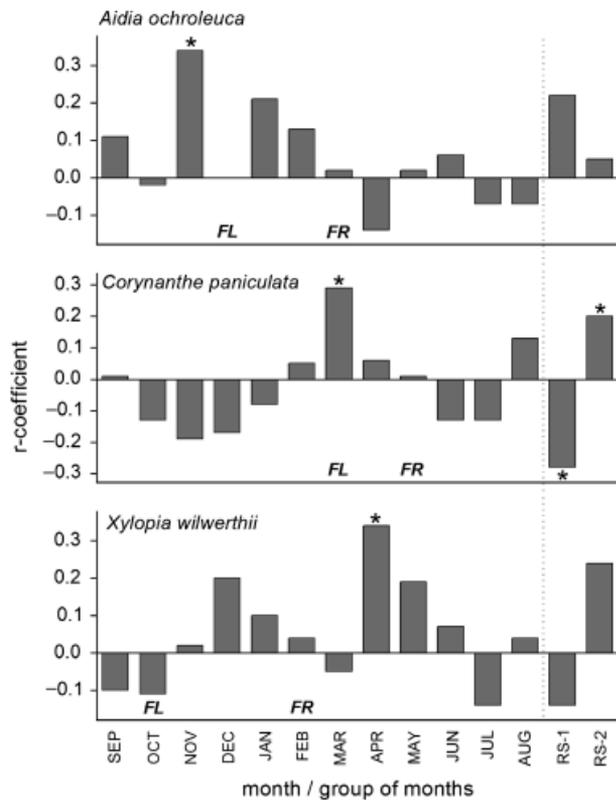


FIGURE 4. Correlations between the tree-ring chronologies of *Aidia ochroleuca*, *Corynanthe paniculata*, *Xylopia wilwerthii* and rainfall (1959–2006) in the Luki forest reserve, Democratic Republic of Congo. Correlations are shown with monthly average rainfall from August to September. In addition, we used rainfall averages over the first four (RS-1: October–January) and last four months (RS-2: February–May) of the rainy season, respectively. *Significant correlation values ($P < 0.05$). Rainy season months appear in capital letters and dry season months in lower case. Flowering (FL) and fruiting (FR) are reported when most trees entered these stages (C. Couralet, pers. obs.).

INTRA-ANNUAL RADIAL STEM GROWTH.—The 15-mo-long time series of monthly dbh measurements showed the nonlinear dynamics of radial growth and its association to seasonality in rainfall (Fig. 5). Stems exhibited shrinkage due to dehydration during the dry season (May–September). Subsequently, all trees returned to pre-dry season dbh values then showed substantial radial growth, although with variation in timing across species. *Aidia* trees regained previous stem diameter values rapidly after the onset of rains in October/November, while for *Corynanthe* and *Xylopia* this recovery occurred only 3 mo later, in January/February. Moderate standard deviations (error bars) indicate high homogeneity of radial growth between trees of the same species.

DISCUSSION

In the present study we investigated the relationships between radial tree growth and external environmental factors in the understory of a tropical rain forest, using three model species: *A. ochroleuca*,

C. paniculata and *X. wilwerthii*. While increasing empirical support has been found for the existence of annual rings in tropical trees in response to seasonal changes, primarily in rainfall (Worbes 2002), such evidence is restricted to deciduous canopy species growing in the upper canopy layer and fully exposed to external environmental factors (Pumijumnong & Park 1999, Worbes 1999, Brienen & Zuidema 2005). Moreover, the specific seasonal climate of the Mayombe region with a relatively low transpiration demand during the dry season, due to high air humidity as a consequence of cloud cover, does not seem prone to inducing a clear growth periodicity. Accordingly, missing rings, wedging rings and intra-annual zones of reduced growth ('false rings') complicated the detection of growth rings in the investigated evergreen, understory species, as commonly seen for other tropical tree species (Ogden *et al.* 1981, D tienne 1989, Dunisch *et al.* 2003). Nevertheless, species-specific anatomical markers and cross-dating techniques allowed for demonstrating the existence and annual nature of growth rings for the three study species. The presence of annual growth rings is thus proved for evergreen understory species, adding to successful tree-ring studies of deciduous canopy trees. As seen in Worbes *et al.* (2003) or Brienen *et al.* (2009), our results further substantiate the possibility to study the productivity, vitality and dynamics of whole communities of trees in tropical forests based on tree-ring analysis.

The successful cross-dating between tree-ring series of the same species denotes the shared influence of external environmental factors on seasonal wood formation. The chronologies of the three species, however, did not show common fluctuations over the past 50 yr. This indicates that radial growth is determined by either differing external factors or by a differing timing of the factor(s). More specifically, the synchronized growth per species did not correlate significantly with annual variation in rainfall, temperature or radiation as observed in other studies on rain forest trees (Sch ngart *et al.* 2006). However, the three species exhibited significant and distinct responses to rainfall during specific periods of the year. Increased growth of *Xylopia* occurred in response to high rainfall over the whole rainy season. In contrast, increased growth of *Aidia* and *Corynanthe* occurred mainly early and late in the rainy season, respectively.

The monthly diameter measurements supported these results. Cambium reactivation occurred at the onset of the rainy season for *Aidia*, while radial stem growth of *Xylopia* and *Corynanthe* resumed and peaked only later in the wet season. Toward the end of the rainy season the radial growth of all three species levels-off before showing an abrupt decline indicating stem shrinkage in July. Radial stem shrinkage due to loss of water from storage pools is a well-known phenomenon in seasonal tropics (Kozlowski & Winget 1964, Borchert 1994, Sheil 1995, Zweifel *et al.* 2007).

The features of *Aidia* growth are in line with several studies on stem growth of rain forest trees under seasonal climates. The role of rainfall has been stressed in the transition months between dry and wet season as a trigger for the initiation of cambial activity (Pumijumnong 1995, Dunisch *et al.* 2003, Brienen & Zuidema 2005, Pumijumnong & Wanyaphet 2006, Buckley *et al.* 2007) and in the early wet season as the determinant of ring width

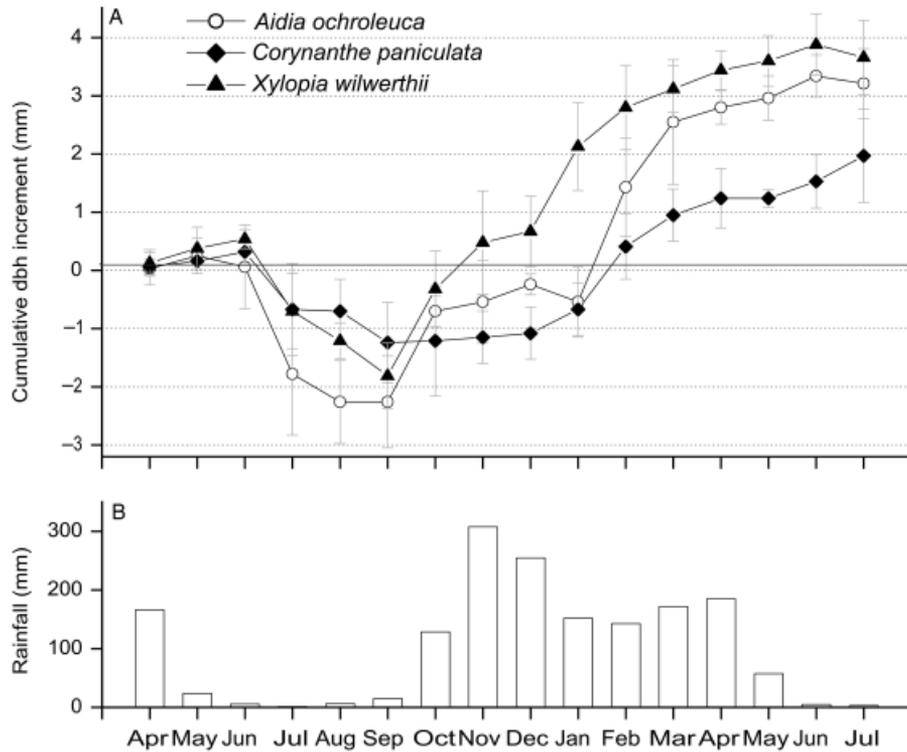


FIGURE 5. (A) Cumulative diameter increments from monthly measurements at breast height on 10 trees of *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* for 15 consecutive months (April 2006–May 2007). Error bars represent ± 1 SD. (B) Monthly precipitation for the corresponding period in the tropical rainforest of Luki, Democratic Republic of Congo.

(Pumijumngong 1995, Dunisch *et al.* 2003, Fichtler *et al.* 2004, Brienen & Zuidema 2005). Late-season responses have been reported but to a lesser extent (Devall *et al.* 1995). The major known difference following this segregation is the aboveground morphology of the trees: *Aidia* has a ramified trunk from the base whereas stems of adult *Corynanthe* and *Xylopia* are mostly straight, with high branching. Roots depth and morphology may be linked to these features, with *Aidia* forming more shallow roots than the other two species. The phenology of trees is closely linked to seasonal changes in soil water status and depends on their water uptake and storage capacity (Borchert 1994). In the Luki forest reserve, there is no proper aquifer layer in the subsoil (Donis 1948). Moreover, the superficial soil horizons are very permeable, with great surface runoff and leaching leading to rapid desiccation after the end of the rainy season (Donis 1948, Meulenbergh 1949). Superficial roots of *Aidia* would allow the prompt reaction to the first rains that directly penetrate the upper soil layers after the dry months. Stem growth would mostly occur at the beginning of the wet season and slow down as the topsoil gradually dries out. On the contrary, *Xylopia* and *Corynanthe* having a deeper, pivot-like root system would explain their delayed growth response, as long as the water did not reach deeper soil layers (Cao 2000). This would, however, enable growth toward the end of the rainy season and provide an explanation for the effect of late-season rains on ring width.

Our results showed that understory species could strongly differ in the periodicity of their wood production. The link between

radial stem growth and tree phenology is fundamental yet poorly understood for tropical rain forest species (Borchert *et al.* 2002, O'Brien 2008). Based on personal observations, the phenology of wood production was compared with the reproductive phenology of the study species. *Xylopia* trees produce flowers mostly in October at the onset of the rainy season, while radial stem growth is still minimal. For *Aidia* and *Corynanthe*, however, blossoming and production of new wood seem to be synchronized. Matching radial stem increment, flowering occurs predominantly at the beginning of the rainy season for *Aidia* (December) and later in the rainy season for *Corynanthe* (March). The relation and potential tradeoffs between flower or fruit production and stem growth need to be further explored to evaluate the consequence of increased seasonality on species growth patterns and performances.

CONCLUSIONS.—Our study proves that dendrochronology can be successfully applied for reconstructing radial growth patterns of tropical understory species in relation to climate. Hence it can be extended to the whole tropical tree community. Moreover, we uncovered significant interspecific differences in stem growth response to climate variations. This differential timing across the species studied is remarkable and implies that species at the same site and with seemingly similar life histories can vary widely in growth dynamics. Global climate change and deforestation influence the seasonality of climate in tropical forest areas. This may result in differential responses across species varying in phenology of radial

stem growth and in the long term contribute to shifts in the species composition of tropical forests.

ACKNOWLEDGMENTS

This study would not have been possible without the kind assistance of staff in the Luki forest reserve, from INERA (Institut National pour l'Etude et la Recherche Agronomiques), MAB (Man And Biosphere program) and World Wide Fund-DRC. Their help is warmly acknowledged. Authors are grateful to L. Nsenga and M. Ngoma, in particular. U. Sass-Klaassen is supported by 'Meervoud' grant 83605030 from the Netherlands Organisation of Scientific Research (NWO). We wish to thank L. Poorter and A. Nemri for providing valuable corrections and comments on the manuscript, as well as the anonymous reviewers.

LITERATURE CITED

- AUBRÉVILLE, A. 1961. Flore du Gabon. Museum National d'Histoire Naturelle, Paris, France.
- BAILLIE, M. G. L., AND J. R. PILCHER. 1973. A simple cross-dating program for tree-ring research. *Tree-Ring Bull.* 33: 7–14.
- BOISVENUE, C., AND S. W. RUNNING. 2006. Impacts of climate change on natural forest productivity; evidence since the middle of the 20th century. *Global Change Biol* 12: 862–882.
- BOKO, M., I. NIANG, A. NYONG, C. VOGEL, A. GITHEKO, M. MEDANY, B. OSMAN-ELASHA, R. TABO, AND P. YANDA. 2007. Africa. Climate change 2007: Impacts, adaptation and vulnerability. In O. F. C. M. L. Parry, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson (Eds.). Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change, pp. 433–467. Cambridge University Press, Cambridge, UK.
- BONAN, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecol. – Ecol. Soc. Am.* 75: 1437–1449.
- BORCHERT, R., G. RIVERA, AND W. HAGNAUER. 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34: 27–39.
- BRIENEN, R., AND P. ZUIDEMA. 2005. Relating tree growth to rainfall in Bolivian rain forests: A test for six species using tree ring analysis. *Oecologia* 146: 1–12.
- BRIENEN, R. J. W., L.-T. EDWIN, B. MICHIEL VAN, A. P.-G. EDUARDO, B. FRANS, A. M. JORGE, AND M.-R. MIGUEL. 2009. The potential of tree rings for the study of forest succession in Southern Mexico. *Biotropica* 41: 186–195.
- BROOKHOUSE, M. 2006. Eucalypt dendrochronology: Past, present and potential. *Aust. J. Bot.* 54: 435–449.
- BROOKHOUSE, M., J. LINDESEY, C. BRACK. 2008. The potential of tree rings in *Eucalyptus pauciflora* for climatological and hydrological reconstruction. *Geogr. Res.* 46: 421–434.
- BUCKLEY, B. M., K. DUANGSATHAPORN, K. PALAKIT, S. BUTLER, V. SYHAPANYA, AND N. XAYBOUANGEUN. 2007. Analyses of growth rings of *Pinus merkusii* from Lao P.D.R. *For. Ecol. Manage.* 253: 120–127.
- CAO, K. 2000. Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *J. Trop. Ecol.* 16: 101–116.
- CHERUBINI, P., M. DOBBERTIN, AND J. L. INNES. 1998. Potential sampling bias in long-term forest growth trends reconstructed from tree rings: A case study from the Italian Alps. *For. Ecol. Manage.* 109: 103–118.
- CHIDUMAYO, E. N. 2005. Effects of climate on the growth of exotic and indigenous trees in central Zambia. *J. Biogeogr.* 32: 111–120.
- CLARK, D. A. 2004. Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Phil. Trans. R. Soc., Ser. B., Biol. Sci.* 359: 477–491.
- CLARK, D. A., S. C. PIPER, C. D. KEELING, AND D. B. CLARK. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Natl. Acad. Sci. USA* 100: 5852–5857.
- CONDIT, R., S. P. HUBBELL, AND R. B. FOSTER. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* 65: 419–439.
- COOK, E. R. 1985. A time series approach to tree-ring standardization. PhD dissertation, University of Arizona, Tucson, Arizona, USA.
- COOK, E. R., AND L. A. KAIRIUKSTIS. 1992. Methods of dendrochronology—applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- COURALET, C., U. SASS-KLAASSEN, F. STERCK, T. BEKELE, AND P. A. ZUIDEMA. 2005. Combining dendrochronology and matrix modelling in demographic studies: An evaluation for *Juniperus procera* in Ethiopia. *For. Ecol. Manage.* 216: 317–330.
- DÉTIENNE, P. 1989. Appearance and periodicity of growth rings in some tropical woods. *IAWA Bull.* 10: 123–132.
- DÉTIENNE, P., F. OYONO, L. DURRIEU DE MADRON, B. DEMARQUEZ, AND R. NASI (Eds.). 1998. L'analyse de cernes, applications aux études de croissance de quelques essences en peuplements naturels de forêt dense africaine. CIRAD-Forêt, Montpellier, France.
- DEVAL, M., B. PARRÉSOL, AND S. J. WRIGHT. 1995. Dendroecological analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in central Panama. *IAWA J.* 16: 411–424.
- DONIS, C. 1948. Essai d'économie forestière au Mayumbe. Institut National pour l'Etude Agronomique du Congo belge (INEAC), Brussels, Belgium.
- DONIS, C., AND E. MAUDOUX. 1951. Sur l'uniformisation par le haut - Une méthode de conversion des forêts sauvages. Institut National pour l'Etude Agronomique du Congo belge (INEAC), Brussels, Belgium.
- DUNISCH, O., M. SCHULTE, AND K. KRUSE. 2003. Cambial growth of *Suietenia macrophylla* king studied under controlled conditions by high resolution laser measurements. *Holzforschung* 57: 196–206.
- ENGELBRECHT, B. M. J., L. S. COMITA, R. CONDIT, T. A. KURSAR, M. T. TYREE, B. L. TURNER, AND S. P. HUBBELL. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447: 80–82.
- FICHTLER, E., V. TROUET, H. BEECKMAN, P. COPPIN, AND M. WORRES. 2004. Climatic signals in tree rings of *Burkea africana* and *Pterocarpus angolensis* from semiarid forests in Namibia. *Trees – Struct. Funct.* 18: 442–451.
- FOUARGE, J., AND G. GÉRARD. 1964. Bois du Mayumbe. Institut National pour l'Etude Agronomique du Congo belge (INEAC), Brussels, Belgium.
- FRITTS, H. C. 1976. Tree rings and climate. Academic Press, London, UK.
- HOLMES, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43: 69–78.
- INEAC. 1948–1960. Flore du Congo belge et du Ruanda-Urundi. Institut National pour l'Etude Agronomique du Congo belge (INEAC), Brussels, Belgium.
- JACOBY, G. C. 1989. Overview of tree-ring analysis in tropical regions. *IAWA Bull.* 10: 99–108.
- KOENIG, R. 2008. Critical time for African rainforests. *Science* 320: 1439–1441.
- KOZLOWSKI, T. T., AND C. H. WINGET. 1964. Diurnal and seasonal variation in radii of tree stems. *Ecology* 45: 149–155.
- LEBRUN, J., AND G. GILBERT. 1954. Une classification écologique des forêts du Congo. Institut National pour l'Etude Agronomique du Congo belge (INEAC), Brussels, Belgium.
- LEBRUN, J.-P., AND A. L. STORK. 2003. Tropical African flowering plants: ecology and distribution, volume 1. Annonaceae-Balanitaceae. Conservatoire Botanique de Genève, Switzerland.
- LISI, C. S. 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in Southeast Brazil. *IAWA J.* 29: 189–207.
- LIU, Y. 1993. Effect of drought and frost on radial growth of overstory and understorey stems in a deciduous forest. *Am. Midland Nat.* 129: 19–25.

- LUBINI, C. A. 1997. La végétation de la Réserve de Biosphère de Luki au Mayombe (Zaïre). Jardin Botanique National de Belgique, Meise, Belgium.
- MALHI, Y., J. T. ROBERTS, R. A. BETTS, T. J. KILLEEN, W. LI, AND C. A. NOBRE. 2008. Climate change, deforestation, and the fate of the Amazon. *Science* 319: 169–172.
- MALHI, Y., AND J. WRIGHT. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Phil. Trans. R. Soc. Lond., Ser. B., Biol. Sci.* 359: 311–329.
- MARIAUX, A. 1995. Periodicity of growth in tropical trees. *IAWA J.* 16: 329–335.
- MARTÍN-BENITO, D., P. CHERUBINI, M. DEL RÍO, AND I. CAÑELLAS. 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees – Struct. Funct.* 22: 363–373.
- MAYAUX, P., E. BARTHOLOMÉ, S. FRITZ, AND A. BELWARD. 2004. A new land-cover map of Africa for the year 2000. *J. Biogeogr.* 31: 861–877.
- MEINZER, F. C., J. L. ANDRADE, G. GOLDSTEIN, N. M. HOLBROOK, J. CAVELIER, AND S. J. WRIGHT. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121: 293–301.
- MEULENBERG, J. 1949. Etude pédologique des sols du territoire du Bas Fleuve (Congo Belge). Mém. Institut Royal Colonial Belge, Brussels, Belgium.
- MONIMEAU, A. 1990. Etude des solutions du sol sous forêt dense équatoriale. Bilan d'un an de collecte à Dimonika (Mayombe, Congo). Mars 1989–Mars 1990. ORSTOM (Institut français de recherche scientifique pour le développement en coopération), Pointe-Noire, République Populaire du Congo.
- MONTEIRO, R. F. R. 1962. Le massif forestier du Mayombe angolais. *Bois et Forêts des Tropiques* 82: 3–17.
- O'BRIEN, J. 2008. Phenology and stem diameter increment seasonality in a Costa Rican wet tropical forest. *Biotropica* 40: 151–159.
- OGDEN, J., G. C. JACOBY, J. ASH, D. ECKSTEIN, F. H. BORMANN, AND G. BERLYN. 1981. Dendrochronology—Age and growth rate determination in tropical trees: The application of dendrochronological methods. Age and growth rate of tropical trees: New directions for research. *Proceedings of the workshop on age and growth rate determination for tropical trees*, held at the Harvard Forest, Petersham, Massachusetts, April 1–3, 1980, pp. 83–106. Yale University, New Haven, Connecticut.
- ORWIG, D. A. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees – Struct. Funct.* 11: 474–484.
- PENDJE, G., AND M. BAYA KI. 1992. La réserve de biosphère de Luki (Mayombe, Zaïre). Patrimoine floristique et faunistique en péril. PNUD – UNESCO–MAB, Paris, France.
- PETT, E. 1961. Quelques espèces nouvelles ou mal connues du groupe *Randia-Gardenia* (Rubiaceae) au Congo. *Bulletin du Jardin botanique de l'État a Bruxelles* 31: 1–13.
- PETT, E. 1962. Rubiaceae africanæ IX: Notes sur les genres *Aidia*, *Atractogyne*, *Aulacocalyx*, *Batopedina*, *Gaertnera*, *Morinda*, *Mussaenda*, *Nauclea*, *Sabicea*, *Schizocolea* et *Tricalysia*. *Bulletin du Jardin botanique de l'État a Bruxelles* 31: 173–198.
- PHILLIPS, O. L., L. E. O. C. ARAGAO, S. L. LEWIS, J. B. FISHER, J. LLOYD, G. LOPEZ-GONZALEZ, Y. MALHI, A. MONTEAGUDO, J. PEACOCK, C. A. QUESADA, G. VAN DER HEIJDEN, S. ALMEIDA, I. AMARAL, L. ARROYO, G. AYMARD, T. R. BAKER, O. BANKI, L. BLANG, D. BONAL, P. BRANDO, J. CHAVE, A. C. A. DE OLIVEIRA, N. D. CARDOZO, C. I. CZIMCZIK, T. R. FELDPAUSCH, M. A. FREITAS, E. GLOOR, N. HIGUCHI, E. JIMENEZ, G. LLOYD, P. MEIR, C. MENDOZA, A. MOREL, D. A. NEILL, D. NÉPSTAD, S. PATINO, M. C. PENUELA, A. PRIETO, F. RAMIREZ, M. SCHWARZ, J. SILVA, M. SILVEIRA, A. S. THOMAS, H. T. STEEGE, J. STROPP, R. VASQUEZ, P. ZELAZOWSKI, E. A. DAVILA, S. ANDELMAN, A. ANDRADE, K.-J. CHAO, T. ERWIN, A. DI FIORE, E. H. C. H. KEELING, T. J. KILLEEN, W. F. LAURANCE, A. P. CRUZ, N. C. A. PITMAN, P. N. VARGAS, H. RAMIREZ-ANGULO, A. RUDAS, R. SALAMAO, N. SILVA, J. TERBORGH, AND A. TORRES-LEZAMA. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323: 1344–1347.
- PHIPPS, R. L. 1982. Comments on interpretation of climatic information from tree rings, Eastern North America. *Tree-Ring Bull.* 42: 11–22.
- PILCHER, J. R., AND B. GRAY. 1982. The relationships between oak tree growth and climate in Britain. *J. Ecol.* 70: 297–304.
- PUMIJUMNONG, N. 1995. Tree-ring research on *Tectona grandis* in northern Thailand. *IAWA J.* 16: 385–392.
- PUMIJUMNONG, N., AND W. K. PARK. 1999. Vessel chronologies from teak in northern Thailand and their climatic signal. *IAWA J.* 20: 285–294.
- PUMIJUMNONG, N., AND T. WANYAPHET. 2006. Seasonal cambial activity and tree-ring formation of *Pinus merkusii* and *Pinus kesiya* in Northern Thailand in dependence on climate. *For. Ecol. Manage.* 226: 279–289.
- RASMUSSEN, K. K. 2007. Dendroecological analysis of a rare sub-canopy tree: Effects of climate, latitude, habitat conditions and forest history. *Dendrochronologia* 25: 3–17.
- RINN, F. 2003. TSAP-Win, Software for tree-ring measurement, analysis and presentation. Rinntech, Heidelberg, Germany.
- SASS-KLAASSEN, U., C. COURALET, Y. SAHLE, AND F. J. STERCK. 2008. Juniper from Ethiopia contains a large-scale precipitation signal. *Int. J. Plant Sci.* 169: 1057–1065.
- SCHMITZ, A. 1988. Révision des groupements végétaux décrits du Zaïre du Rwanda et du Burundi. Royal Museum for Central Africa, Tervuren, Belgium.
- SCHÖNGART, J., B. ORTHMANN, K. J. HENNENBERG, S. POREMBSKI, AND M. WORBES. 2006. Climate–growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. *Global Change Biol.* 12: 1139–1150.
- SCHÖNGART, J., M. T. F. PIEDADE, S. LUDWIGSHAUSEN, V. HORNA, AND M. WORBES. 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *J. Trop. Ecol.* 18: 581–597.
- SCHWEINGRUBER, F. H. 1996. Tree rings and environment dendroecology. Paul Haupt Verlag, Bern, Switzerland.
- SÉNÉCHAL, J., M. KABALA, AND F. FOURNIER. 1989. Revue des connaissances sur le Mayombe. UNESCO/PNUD/République Populaire du Congo, Paris, France.
- SHEIL, D. 1995. A critique of permanent plot methods and analysis with examples from Budongo-Forest, Uganda. *For. Ecol. Manage.* 77: 11–34.
- STERCK, F. J., L. POORTER, AND F. SCHIEVING. 2006. Leaf traits determine the growth-survival trade-off across rain forest tree species. *Am. Nat.* 167: 758–765.
- TROUET, V., P. COPPIN, AND H. BEECKMAN. 2006. Annual growth ring patterns in *Brachystegia spiciformis* reveal influence of precipitation on tree growth. *Biotropica* 38: 375–382.
- VERHEYDEN, A., G. HELLE, G. H. SCHLESER, F. DEHAIRS, H. BEECKMAN, AND N. KOEDAM. 2004. Annual cyclicity in high-resolution stable carbon and oxygen isotope ratios in the wood of the mangrove tree *Rhizophora mucronata*. *Plant, Cell Environ.* 27: 1525–1536.
- WHEELER, E. A., P. BAAS, AND P. E. E. GASSON. 1989. IAWA list of microscopic features for hardwood identification. *IAWA Bull.* 10: 219–332.
- WHITMORE, T. C. 1998. An introduction to tropical rain forests. Oxford University Press, Oxford, UK.
- WILS, T. H. G., I. ROBERTSON, Z. ESHETU, U. G. W. SASS-KLAASSEN, AND M. KOPROWSKI. 2009. Periodicity of growth rings in *Juniperus procera* from Ethiopia inferred from crossdating and radiocarbon dating. *Dendrochronologia* 27: 45–58.
- 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 to future challenges. *Dendrochronologia* 20: 217–231.
- WORBES, M., R. STASCHEL, A. ROLOFF, AND W. J. JUNK. 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *For. Ecol. Manage.* 173: 105–123.
- ZWEIFEL, R., K. STEPPE, AND F. J. STERCK. 2007. Stomatal regulation by microclimate and tree water relations: Interpreting ecophysiological field data with a hydraulic plant model. *J. Exp. Bot.* 58: 2113–2131.