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ORIGINAL ARTICLE

Climate/growth relationships of *Brachystegia spiciformis* from the miombo woodland in south central Africa

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Abstract

We present five *Brachystegia spiciformis* Benth. (BrSp) tree-ring chronologies from the seasonally dry miombo woodland in south central Africa. Between 9 and 34 stem discs were collected from three dry and two wet miombo sites. All samples showed distinct growth rings, which were marked by terminal parenchyma bands. Site chronologies varied in length between 43 and 149 years. An increase in the number of growth ring anomalies in older trees, however, resulted in an increase in dating error and a decrease in between-tree correlations with increase in the chronology length. Annual precipitation variability accounted for some 28% of the common variance in the BrSp chronologies and we found no difference in climate sensitivity between wet and dry miombo sites. The influence of climate, and of precipitation in particular, on tree growth was strongest at the core of the rainy season (December–February). This is also the time of the year when ENSO peaks in amplitude and ENSO effects on precipitation variability in southern Africa are the strongest. We found a negative response of tree growth to ENSO throughout most of the growth year, suggesting that the development of longer chronologies from the miombo region would allow for the investigation of temporal ENSO variability. A spatial extension of the miombo tree-ring network should therefore focus on regions where ENSO effects are the strongest (e.g., southeastern Africa).

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Introduction

In many tropical regions, long time series of climatic instrumental records are scarce. In sub-Saharan Africa in particular, regional precipitation data sets do not extend over more than 100 years and only represent high-frequency climate variability (Tyson, 1986). More-

over, for most parts of Africa, the network of climate stations is not dense enough to provide a coherent spatial picture of climate variability (Anyamba and Eastman, 1996). At the same time, the region is vulnerable to climate anomalies and extreme weather events due to poor infrastructure and low socio-economic development. This vulnerability, as well as the importance of the tropical climatic zone in regulating global climate dynamics, induces the need for long-term research of climate variability and for reliable high-resolution proxy data (Esper et al., 2007).

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Precipitation patterns in southern Africa are teleconnected to the El Niño Southern Oscillation (ENSO; Nicholson and Entekhabi, 1986; Ropelewski and Halpert, 1988; Nicholson and Kim, 1997): negative precipitation anomalies occur during warm ENSO phases, whereas positive anomalies are associated with cold phases. The ENSO effect on rainfall variability is strongest during the core of the rainy season, from January to March (Lindesay and Vogel, 1990; Camberlin et al., 2001). Long-term research on ENSO patterns and their influence on precipitation is necessary to understand this spatiotemporal variability and to predict the regional effect. Tree-ring data are particularly useful in this context, because of their annual resolution and the absolute time series they produce (Cook, 1992).

A dense network of tree-ring data exists for boreal and temperate latitudes (Esper et al., 2002, D'Arrigo et al., 2006), but the occurrence of climate-sensitive annual growth rings in tropical trees has long been and still is controversially discussed (Worbes 2002). Temperature and photoperiod are relatively constant throughout the year in tropical regions, but other seasonally occurring stress factors can induce cambial dormancy in tropical trees and, consequently, growth zones in the wood. This is not only true for regions with a distinct dry season (Worbes, 1995; Stahle et al., 1999) but also for periodically flooded areas (Schöngart et al., 2004, 2005). Many tropical regions are characterized by a distinct seasonality in precipitation, and annually resolved tree rings have been described for a large number of tropical species ranging from dry (Gourlay, 1995) to more humid zones (Fichtler et al., 2003) and mangroves (Verheyden et al., 2005, Chowdhury et al., 2008), for example. For tropical African species, the appearance and nature of tree rings has been described by Walter (1940), Hummel (1946), Mariaux (1967, 1969, 1970), Amobi (1973), Détienne (1989), Eshete and Stahl (1999), and Tarhule and Hughes (2002) amongst others. These studies suggest a strong potential for tree-ring analysis in the tropics, but the development of long chronologies has been hampered by a number of problems, including the occurrence of indistinct growth rings (Détienne, 1989; Sass et al., 1995) and growth ring anomalies (Priya and Bhat, 1998; Tarhule and Hughes, 2002), cross-dating problems (Belingard et al., 1996), and lack of correlation with climatic data (February and Stock, 1998).

Despite these limitations, an increasing number of reliable, climate-sensitive tree-ring chronologies has been developed in recent decades based on tropical trees from Asia (D'Arrigo et al., 1997, 2006), the Amazon region (Schöngart et al., 2004; Brienen and Zuidema, 2005), western Africa (Worbes et al., 2003, Schöngart et al., 2006), and Ethiopia (Couralet et al., 2005; Gebrekirstos et al., 2008; Sass-Klaassen et al.,

2008). In sub-Saharan Africa, the ring-porous species *Pterocarpus angolensis* has proven to be a reliable source for drought-sensitive chronologies (Stahle et al., 1999; Fichtler et al., 2004; Therrell et al., 2006). *Brachystegia spiciformis* Benth. (BrSp) is another dominant tree species in the miombo woodland of south central and eastern Africa that forms annual rings (Grundy, 1995; Trouet et al., 2001), is drought-sensitive (Trouet et al., 2006), and has an estimated life-span of over 150 years (Trouet, 2004). The longest BrSp chronology developed so far, however, does not extend further than 1940 (Trouet et al., 2006). In this study, we present five new BrSp chronologies that extend back to 1853 and we investigate the sensitivity of BrSp growth to precipitation and ENSO variability.

Material and methods

Study area and sampling strategy

Miombo woodland is the principle vegetation type of the region characterized by a tropical wet and dry climate in sub-Saharan Africa (White, 1983). It covers over 2.7 million square kilometer of generally nutrient-poor soils on the Central African plateau and its escarpments (Millington et al., 1994), and is dominated by three closely related genera from the *Leguminosae* family (*Brachystegia*, *Isoberlinia*, and *Julbernardia*). Mean annual rainfall in the miombo region ranges from 650 to 1400 mm, the majority of which falls in the summer season (October–March), with a dry season (<60 mm per month) lasting 5–7 months. Miombo woodland can be divided into dry miombo (<1000 mm mean annual rainfall) and wet miombo (>1000 mm) subtypes (White, 1983), the drier of which is characterized by floristically impoverished vegetation and lower canopy height (<15 m) compared to wet miombo woodland (Frost, 1996).

Most miombo species, including the dominant species, are deciduous and shed all of their leaves during the dry season, with leaf fall peaking from July to September (Malaisse et al., 1975). Leaf flush, particularly in the wet subtype, occurs before the onset of the wet season. The explanation for this pre-greening behaviour is unknown, but its onset appears to be related to high temperatures in the late dry season and is presumably restricted to areas with adequate ground water reserves (Chidumayo, 1993).

We collected samples, consisting of full stem discs, from BrSp trees at three dry miombo sites (Livingstone, Choma, and Mumbwa) and one wet miombo site (Mpika) in Zambia (Fig. 1). Samples were collected during two field campaigns in August 2000 (Choma) and in September–October 2002 (Livingstone, Mumbwa,

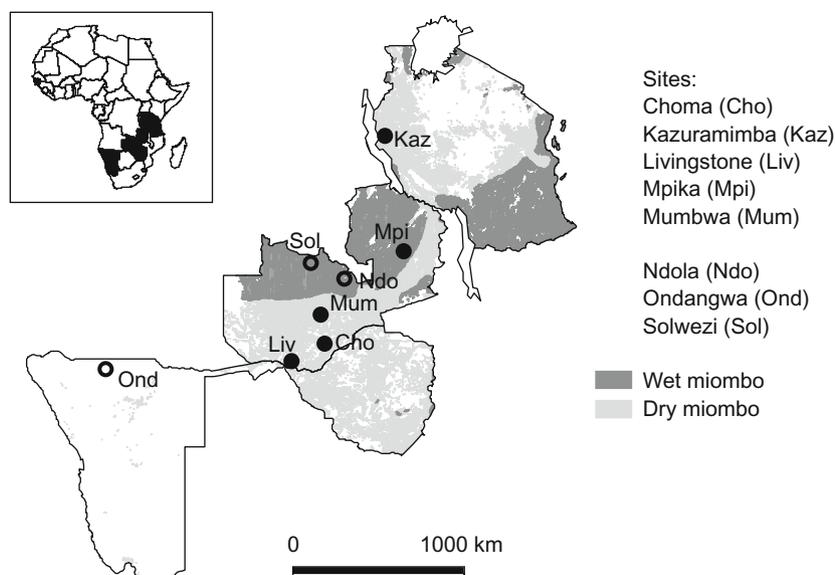


Fig. 1. Tree-ring sites in the miombo region in south central Africa. Cho, Kaz, Liv, Mpi, and Mum indicate the sites where BrSp was sampled (filled circles on the map).

and Mpika). All sites consisted of natural, closed woodland. We collected stem discs rather than increment cores, as they are more suitable at sites where growth ring anomalies occur frequently (Eshete and Stahl, 1999; February, 2000). To minimize damage to living trees, we took disc samples from stumps of trees that were cut for other purposes. Samples were taken from as near to breast height as the height of the existing stumps allowed (0.5–1.3 m). Between 9 (Choma) and 34 (Mpika) samples were collected per site. These data were completed with a set of BrSp samples from the wet miombo woodland in Tanzania (Kazuramimba). Cross-dating of this last set of samples has previously been reported (Trouet et al., 2001) and we here present an updated analysis, combining the existing data with the new collection from dry and wet miombo sites. All samples are lodged in the Xylarium of the Royal Museum for Central Africa in Tervuren, Belgium.

Tree-ring analysis

Stem discs were dried and transverse surfaces sanded progressively (grit 100–1200) and polished. Tree-ring structures were analysed under a stereo-microscope with low magnification, and ring boundaries were marked and measured from bark to pith. Special attention was given to the determination and registration of wedging (partially absent) rings. Ring widths were measured to the nearest 0.01 mm using LINTAB equipment and TSAP software (Rinn and Jäkel, 1997) along four radii per sample disc.

The ring width series of four radii of a tree were cross-dated and combined to form average series for each tree. These ring width series were then cross-dated for each site. We cross-dated ring width series by visually comparing them, and by calculating the Student's t - (Baillie and Pilcher, 1973) and *Gleichläufigkeit* values (GLK; Eckstein and Bauch, 1969). The cross-dating threshold applied in this study was set at a t -value of 2 ($P < 0.05$) and a GLK of 60%. This threshold is remarkably lower than the thresholds generally applied in dendrochronology in temperate and boreal regions ($t > 3.5$ and $GLK > 70%$), but lowering these thresholds for tropical regions can be justified for various reasons. Firstly, no reference chronologies are available for most tropical regions (including our study area) and individual tree-ring series are compared to other individual tree-ring series rather than to a chronology in the cross-dating process. As individual series contain more noise than mean chronologies, correlation coefficients are generally lower. Secondly, our samples were taken from trees with known cutting date, and an approximate date for the outermost ring was known. Due to the possible presence of false or missing rings, this date is an approximation, but the range of possible values is relatively narrow. Therefore, the thresholds applied to allow exact dating of floating time series can be lowered when a narrow range of possible dates is likely (Schöngart et al., 2004).

Age trends were removed by dividing mean tree series by a one-sided moving average over five years (Baillie and Pilcher, 1973). The resulting index time series were subsequently normalized over their full length (average = 0, standard deviation = 1 for all series), which allowed for comparison between trees and sites (Fritts,

Table 1. Precipitation stations and corresponding Nicholson regions.

Station	Annual precip (mm)	Dry season (< 60 mm/month)	Period	Nicholson region
Livingstone	740	April–October	1905–2000	60
Choma	810	April–October	1917–2000	57
Mumbwa	850	April–October	1905–2000	48
Mpika	1110	May–October	1922–2000	43
Kigoma	995	May–October	1923–1984	39

1976) and for correlation with climate data (Cook and Briffa, 1990). After cross-dating, average series from individual trees were combined into site chronologies, the length of which was limited to a replication of four trees minimum (Table 2).

We applied a principal component analysis (PCA) to investigate the common signal in the chronologies. PCA is limited to the common time period covered by all chronologies, and, to extend this period prior to 1930, we excluded the Kazuramimba site (1955–1998) from this analysis. The PCA was eventually based on 9 chronologies (Fig. 1), including four chronologies presented here, two chronologies (*P. angolensis* DC and *Burkea Africana* Hook) from Ondangwa, Namibia (Fichtler et al., 2004), and three chronologies (*Brachystegia boehmii* Taub. and *Erythrophleum africanum* (Welw. ex Benth) Harms) from northern Zambia (Trouet, 2004).

Climate data

Each tree-ring chronology was compared to monthly and seasonal precipitation data from a nearby meteorological station (Table 1) and to the average precipitation data of the three closest neighbouring stations. No data from neighbouring stations were available for Kazuramimba. Additionally, monthly and seasonal precipitation data were averaged for the corresponding Nicholson region (Nicholson, 2001; Table 1). These regions of the African continent have been shown to be climatically homogeneous with respect to intra-annual rainfall variability.

Data for the Nicholson regions were obtained from the US National Center for Atmospheric Research (http://ncardata.ucar.edu/data_sets). Mean monthly relative humidity and temperature data were derived from the US National Center for Environmental Protection (NCEP) reanalysis data set provided by the NOAA–CIRES Climate Diagnostics Center, Boulder, Colorado, USA (<http://www.cdc.noaa.gov/>). These data are interpolated over a global $2.5^\circ \times 2.5^\circ$ grid and are available for the 1948–2000 period. Climate data were completed by monthly values of the sea surface temperature index for the Niño3.4 region (Trenberth and Stepaniak, 2001; 1856–2000; <http://ingrid.ldgo.columbia.edu/SOURCES/KAPLAN/Indices/>), and for a two-year period straddling the growth year.

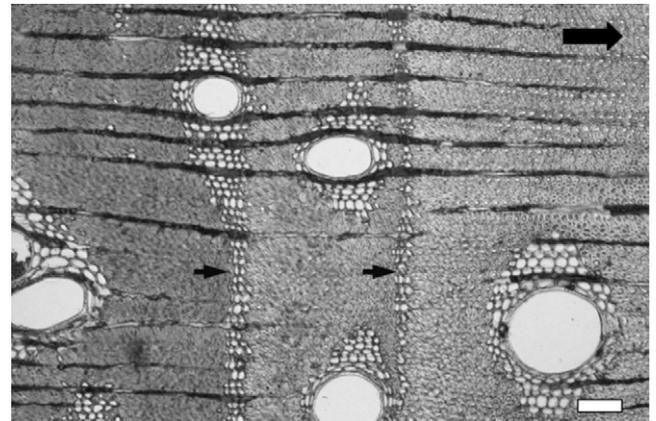


Fig. 2. Growth rings in BrSp. Ring boundaries consisting of marginal parenchyma cells are indicated with arrows. Black arrow indicates the growth direction. Scale bar is 0.1 mm.

<http://ingrid.ldgo.columbia.edu/SOURCES/KAPLAN/Indices/>), and for a two-year period straddling the growth year.

Results

Tree-ring chronologies

All specimens showed distinct growth rings (Fig. 2). A few specimens (one to three per site) showed distinct rings, but were excluded due to large wound formation (possibly caused by fires) or excessive ring wedging. Ring wedging tended to occur more frequently in older trees with slower growth and towards the outer parts of stem discs, where annual diameter expansion was lower.

Cross-dating between radii of a tree was successful for all trees at all sites. Cross-dating of average tree curves per site then allowed for the development of five site-specific chronologies (Fig. 3). Between 82% (Kazuramimba) and 93% (Mumbwa) of the sampled trees contributed to the site chronologies. Chronology lengths varied between 43 and 149 years (Table 2). Average ring widths (1.05–1.88 mm) and standard deviations (0.72–1.05 mm) were similar at all sites. The correlations between average tree series, a measure of

tree growth homogeneity, were lowest for Mumbwa and Mpika (0.13) and highest for Kazuramimba (0.19). Cross-dating between chronologies from different sites was successful ($t \geq 2.0$ or $GLK \geq 60\%$) in 40% of the cases: the Livingstone chronology corresponded to

the Kazuramimba, the Choma, and the Mpika chronologies, and the latter also corresponded to the Mumbwa chronology. The limited success of cross-dating between sites hints towards a fairly strong influence of local, site-specific variables (soil, disturbances, and competition).

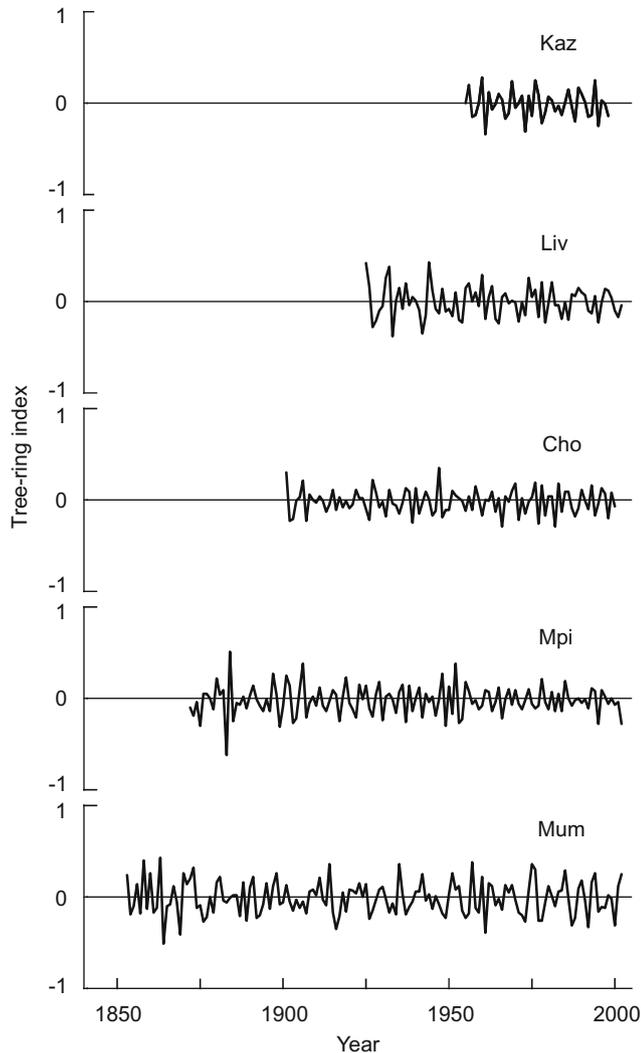


Fig. 3. High-pass filter detrended and normalized BrSp tree-ring chronologies from the miombo woodland.

Climate correlations

We found positive correlations between tree growth and annual rainfall from the corresponding meteorological station for all sites except Mumbwa (Fig. 4). Correlations with rainfall at the core of the growing season (December–February) were significantly positive for Livingstone, Choma, and Mpika. Positive correlations with regional averages (four stations and Nicholson region), however, were only found for Livingstone and Mpika. Noteworthy are the overall positive correlations revealed with precipitation of individual months. Negative correlations were only found at the beginning of the growing season (October and November).

The results of the correlation analysis with temperature and relative humidity are in line with the positive association found for precipitation. Overall, tree growth was positively correlated with relative humidity and negatively with temperature. Correlations were only significant, however, at the Livingstone site, where the strongest correlations were found at the core of the rainy season (December–February), when correlation coefficients varied between 0.29 and 0.34 (relative humidity) and -0.3 and -0.35 (temperature).

All chronologies showed negative correlations with Niño3.4 throughout the growth year (August–June) and positive correlations for the year following the growth year (Fig. 5). Negative correlations were significant at Mumbwa (1856–2002), Mpika (1871–2002), and Kazuramimba (1946–1998). Average winter (November–March) Niño3.4 values were also negatively correlated ($r = -0.17$ – $r = -0.32$; $P < 0.05$) at these three sites.

Table 2. BrSp site chronology characteristics. Lag1-autocorrelation is calculated for the raw ring width data. Inter-series correlation is calculated between trees (not radii) using high-pass filter detrended data.

	Liv	Cho	Mum	Mpi	Kaz
Number of trees (radii)	11(44)	8(32)	14(56)	29(116)	9(36)
Age range (years)	64–85	67–104	101–155	36–146	32–52
Chronology length (min. 4 trees) (years)	77	100	149	131	43
Period A.D.	1925–2002	1901–2000	1853–2002	1871–2002	1955–1998
Mean ring width (mm)	1.50	1.66	1.42	1.05	1.88
Lag1 autocorrelation	0.35	0.36	0.26	0.38	0.19
Inter-series correlation	0.17	0.16	0.13	0.13	0.19
Variance explained by first eigen vector(%)	22	27	22	17	26

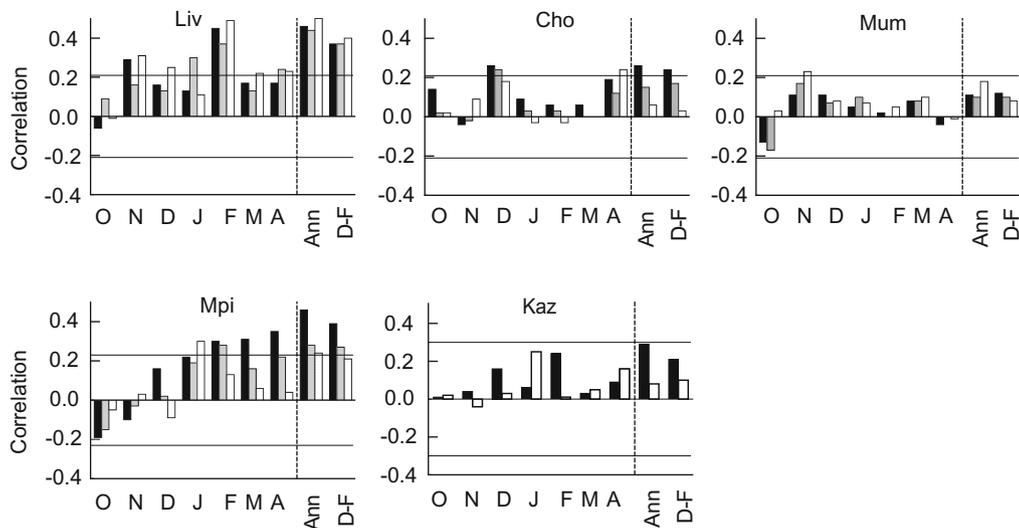


Fig. 4. Correlation of BrSp site chronologies with regional precipitation data. Sites Liv, Cho, and Mum are located in dry miombo, Mpi and Kaz in wet miombo. Results for the closest station next to a site (black bar), the mean of the four closest stations (grey), and the respective Nicholson region (white) are shown. O, N, D, J, F, M, and A represent the months October–April, Ann the total annual rainfall, and D–F the December–February seasonal sum. Horizontal lines indicate $P < 0.05$ significance levels.

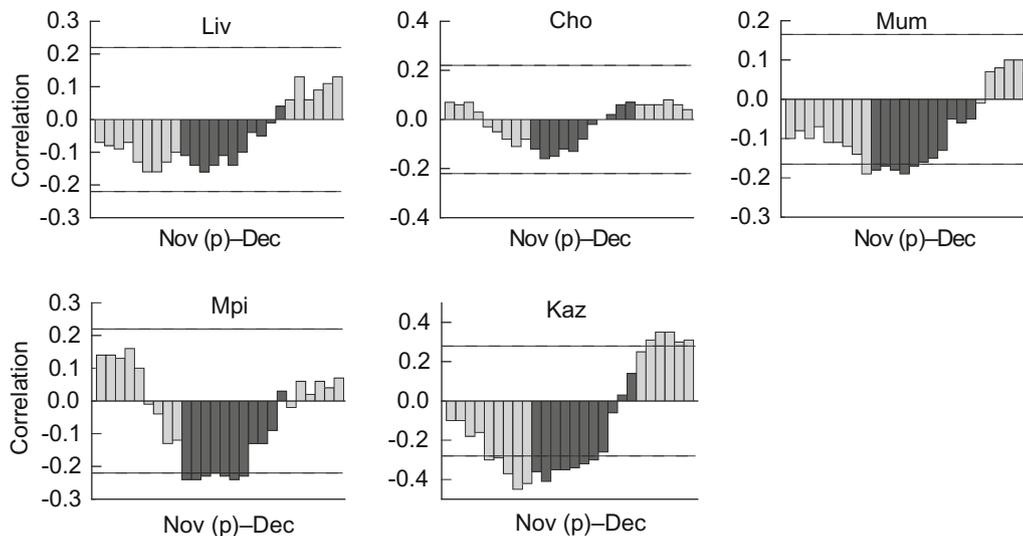


Fig. 5. Correlations between BrSp site chronologies and Niño3.4 index data. Sites Liv, Cho, and Mum are located in dry miombo; Mpi and Kaz in wet miombo. Results for monthly Niño3.4 data are shown for the year previous to the growth year (November (Nov(p)) to July), for the growth year (August–July; in dark grey), and for the year following the growth year (August to December (Dec)). Horizontal lines indicate $P < 0.05$ significance levels.

Principal components analysis

A first principal component explained 34% of the common variance in our BrSp chronologies (eigenvalue = 1.35) and 20% of the common variance in nine chronologies (eigenvalue = 1.78), including chronologies from other miombo species. All chronologies had

positive scores along the first PCA axis, ranging from 0.02 (Solwezi) to 0.72 (Mpika).

To extract a regional precipitation signal, we subjected the annual precipitation sums from the meteorological stations closest to the seven sites from where the tree-ring data originated to a PCA. The first principal component explained 38% of the variance in annual

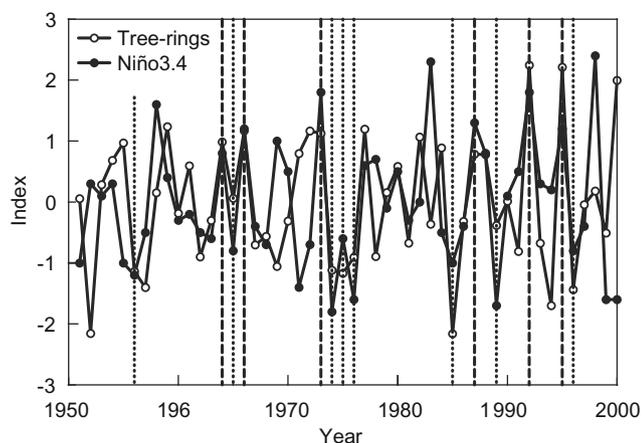


Fig. 6. Coherence between the first eigenvector scores of the PCA-transformed tree-ring chronology derived from all miombo tree-ring sites and the winter (December–February) Niño3.4 index over 1950–2000. Dashed lines indicate strong El Niño years, dotted lines La Niña years. PCA-transformed tree-ring time series has been inverted.

precipitation and all meteorological stations showed positive scores along the first PCA axis. The time series of the PCA-transformed tree-ring chronologies were positively correlated with this regional precipitation time series ($r=0.53$ for BrSp and $r=0.44$ for all chronologies; $P<0.01$).

Correlations of the PCA-transformed tree-ring time series with monthly Niño3.4 data were calculated for the period 1950–2000, over which the impact of ENSO on precipitation variability over southern Africa is strong and stable (Richard et al., 2001). We found negative correlations for the year prior to the growth year and for the growth year ($r=-0.22$ for May to $r=-0.31$ for December; $P<0.05$). In addition to this, significantly negative correlations were found with the average winter (December–February) Niño3.4 values of the growth year (Fig. 6).

Discussion

Many tree species from tropical forests with a distinct and predictable dry season form annual rings (Berlage, 1931; Détienne, 1989; Worbes, 1989, 1995). A dry season of more than three months with less than 60 mm of monthly rainfall (Worbes, 1995) is sufficient to invoke a period of cambial dormancy, one consequence of which is the formation of boundaries in the wood (Worbes, 1999). Here, we study the annual character and climate sensitivity of tree rings in BrSp trees from dry and wet miombo woodland sites. At all sites, the dry season lasts for six or seven months from April (May)–October and is thus sufficiently long for cambial dormancy and ring formation.

Growth ring boundaries in BrSp are marked by axial parenchyma bands that are produced at the end of the growing season and are typical for *Leguminosae* family and *Caesalpinioideae* subfamily in particular (Gourlay, 1995; Tarhule and Hughes, 2002). The primary function of marginal parenchyma is starch storage for bridging the dry season (Carlquist, 1988). Parenchyma bands can promote conduction when growth is renewed and the provision of starch can support rapid flushes of growth, flowering, and fruiting. This support appears to be of importance for tree species from the miombo woodland that produce new leaves, shoots, and flowers during the warm, dry, and pre-rains season (Campbell, 1996). Production in this season depends on carbohydrates and nutrient reserves stored from previous growing seasons (Rutherford, 1984). Dependence on nutrient storage can explain the large amount of parenchyma tissue generally found in the wood of *Caesalpinioideae* species. Apart from marginal parenchyma bands, a large amount of paratracheal parenchyma (associated with the vessels) can be found, especially in the earlywood (Fig. 2).

Despite the distinct character of growth ring boundaries, the development of long BrSp tree-ring chronologies is hampered by the frequent occurrence of growth ring anomalies. These anomalies, ring wedging in particular, occur primarily when growth rates are low (Stokes and Smiley, 1968), i.e., at extreme sites and in the outer rings of old trees. Other factors influencing the occurrence of anomalies can be local supply of carbohydrates, water, mineral elements, and phytohormones (Dünisch et al., 1999). In our chronologies, an increase in the number of growth ring anomalies in older trees resulted in an increase in dating error and a decrease in between-tree and between-site correlations (Table 2). Sampling a mixture of trees of various age groups may facilitate cross-dating, assuming that younger trees with more vigorous growth are less susceptible to growth ring anomalies (Tarhule and Hughes, 2002). We found no remarkable difference in the number of growth ring anomalies or their influence on cross-dating results between wet and dry miombo sites. At a much drier site in the Hwange National park in Zimbabwe (mean annual precipitation of 560 mm), however, the dendrochronological potential of BrSp was estimated to be very low (Stahle et al., 1996). This difference in potential can be related to the humidity level of bioclimatic regions and the associated differences in the growth rate. Similar differences were found for *Isobertinia tomentosa* trees, which showed clear growth rings in the wet miombo woodland of western Tanzania (mean annual precipitation >1000 mm; Trouet et al., 2001), but had very low dendrochronological potential when sampled in the Sudan savanna (mean annual precipitation 600 mm; Tarhule and Hughes, 2002).

Four out of five BrSp chronologies were positively influenced by annual precipitation (Fig. 4), suggesting water availability as the limiting factor for radial growth. We found no difference in sensitivity to water availability between wet and dry miombo sites. The strong influence of annual precipitation on tree growth was reflected in the correlation between the first eigenvector scores of PCA-transformed annual rainfall (a measure for regional precipitation variability) and the PCA-transformed tree-ring chronologies. Annual precipitation variability accounted for some 34% of the common variance in BrSp chronologies and 20% in all chronologies. These numbers correspond to correlations reported by Stahle et al. (1999) for wet season rainfall and *P. angolensis* chronologies from Zimbabwe. Our results show that the drying trend over southern Africa that is predicted for the 21st Century (IPCC, 2007) could result in a considerable reduction in tree growth in both wet and dry miombo woodland and in an associated decrease in net primary productivity. A shift towards a new, drier ecosystem, however, is unlikely (Hély et al., 2006).

A strong influence of local, stand-level conditions, as well as pre-greening behaviour can contribute to the overall low percentage of variance in tree growth explained by rainfall. Leaf flush in BrSp is not synchronized with the start of the rainy season and a part of the annual tree growth takes place outside the rainy season. Tree growth therefore appears to be not only dependent on water availability but also on carbohydrates and nutrient reserves stored from previous growing seasons (Rutherford, 1984). In addition to this, water availability involves more factors than precipitation only (Alexandre, 1977) and is dependent on vegetation characteristics and soil type. Therefore, more complex variables as precipitation surplus – the amount of precipitation that is not used for evapotranspiration by plants – or soil water availability might explain more variance in tree growth than precipitation *per se*.

Within the growth year, the influence of climate, and of precipitation in particular, on tree growth was strongest at the core of the rainy season (December–February), when precipitation rates are the highest. This is also the time of the year when ENSO peaks in amplitude and its effect on precipitation variability in southern Africa is the strongest (Camberlin et al., 2001; Anyamba et al., 2002). During warm El Niño phases (reflected by positive Niño3.4 values), precipitation is generally lower than normal in southern Africa, resulting in reduced tree growth. In subsequent La Niña phases, positive rainfall and tree growth anomalies have been recorded. The oscillating pattern of ENSO activity and the corresponding tendency for opposing interannual precipitation conditions (D'Arrigo and Jacoby, 1992) are reflected in the pattern of correlations with

tree-ring data. At three sites, as well as for the PCA-transformed tree-ring data, we found a negative response of tree growth to ENSO during most of the growth year (August–April) and positive responses for the year following the growth year (Fig. 5). This shift in correlation has previously been reported for tree-ring chronologies from Namibia (Fichtler et al., 2004) and corresponds to the ENSO phase shift that often occurs at the same time of the year (Camberlin et al., 2001).

The Niño3.4 sea surface temperature anomaly averaged over the Northern Hemisphere winter months is often used as a direct indicator for ENSO (Trenberth, 1997). The negative correlation between this index and our tree-ring chronologies was not very high but comparable (and significant) to correlations with other tree ring based proxies from ENSO-teleconnected regions (Jacoby and D'Arrigo, 1990, Schöngart et al., 2004). The strong El Niño events in the early nineties, for instance were clearly detectable in the PCA-transformed tree-ring time series as well as the prolonged La Niña period from 1974 to 1976 (Fig. 6).

BrSp is widely distributed throughout sub-Saharan Africa and can therefore contribute to the development of a tree-ring network for this region. Such a network could complement existing instrumental climatic data both in spatial and temporal coverage. On a spatial scale, the current network could be extended towards regions where the influence of climate is the strongest. Extension into drier areas might be hampered by slow growth, causing abundance of growth ring anomalies, and scarcity of trees. We therefore recommend focusing future research on areas that have a distinct dry season, but with sufficient annual rainfall (750–1000 mm) to secure adequate radial growth rates and stand densities. Large parts of southeastern Africa (southern Tanzania and northern Mozambique), a region where ENSO has a strong influence due to the proximity of the Indian Ocean (Matarira, 1990), are covered by wet miombo woodland, allowing for an expansion of the network in this area.

Both the ENSO and its influence in southern Africa have experienced changes in amplitude over the last century (Allan et al., 1996) and longer tree-ring chronologies would allow for the investigation of these temporal variations. Miombo trees have a natural lifespan of over 150 years (Trouet, 2004), which offers the opportunity to construct long chronologies. The availability of old wooden buildings and archaeological wood is limited in the miombo region and extending the chronologies further back in time will be a challenge. The recent discovery of subfossil wood in African lakes (D. Verschuren, personal communication) perhaps offers a possibility on this behalf as well as a multi-proxy approach that combines tree ring with other proxy data (e.g., Trouet et al., 2009).

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References

- Alexandre, D.Y., 1977. Le bilan de l'eau dans le miombo (forêt claire tropicale). *Bulletin de la Société Géographique de Liège* 13, 107–116.
- Allan, R., Lindsay, J., Parker, D.E., 1996. In: *El Niño-Southern Oscillation and Climate Variability*. CSIRO Publishing, Melbourne 416 pp.
- Amobi, C.C., 1973. Periodicity of wood formation in twigs of some tropical trees in Nigeria. *Annals of Botany* 376, 211–218.
- Anyamba, A., Eastman, J.R., 1996. Interannual variability of NDVI over Africa and its relation to El Niño/Southern Oscillation. *International Journal of Remote Sensing* 17, 2533–2548.
- Anyamba, A., Tucker, C.J., Mahoney, R., 2002. From El Niño to La Niña. Vegetation response patterns over East and Southern Africa during the 1997–2000 period. *Journal of Climate* 15, 3096–3103.
- Baillie, M.G.L., Pilcher, J.R., 1973. A simple cross dating program for tree-ring research. *Tree-Ring Bulletin* 33, 7–14.
- Belingard, C., Tessier, L., De Namur, C., Schwartz, D., 1996. Dendrochronological approach to the radial growth of Okoume (Congo). *C.R. Acad. Sci. Paris, Sciences de la vie* 319, 523–527.
- Berlage, H.P., 1931. Over het verband tusschen de dikte der jaarringen van djatiboomen (*Tectona grandis* L.f.) en den regenval op Java. *Tectona* 24, 939–953.
- Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree-ring analysis. *Oecologia* 146, 1–12, doi:10.1007/s00442-005-0160-y.
- 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. *International Journal of Climatology* 21, 973–1005.
- Campbell, B.M., 1996. The Miombo in transition: Woodlands and welfare in Africa. Bogor, Centre for International Forestry Research 266 pp.
- Carlquist, S., 1988. In: *Comparative Wood Anatomy – Systematic, Ecological and Evolutionary Aspects of Dicotyledon Wood*. Springer-Verlag, New York, USA 436 pp.
- Chidumayo, E.N., 1993. Responses of miombo to harvesting: ecology and management. Stockholm Environment Institute, Stockholm 110 pp.
- Chowdhury, M.Q., Schmitz, N., Verheyden, A., Sass-Klaassen, U., Koedam, N., Beeckman, H., 2008. Nature and periodicity of growth rings in two Bangladeshi mangrove species. *IAWA Journal* 29, 265–276.
- Cook, E.R., 1992. Using tree-rings to study past El Niño/Southern Oscillation influences on climate. In: Diaz, F.H., Markgraf, V. (Eds.), *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge University Press, Cambridge, pp. 203–214.
- Cook, E.R., Briffa, K., 1990. Data analysis. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology, Applications in the Environmental Science*. Kluwer Academic Publishers, Dordrecht, pp. 97–162.
- Couralet, C., Sass-Klaassen, U., Sterck, F., Bekele, T., Zuidema, P.A., 2005. Combining dendrochronology and matrix modelling in demographic studies: An evaluation for *Juniperus procera* in Ethiopia. *Forest Ecology and Management* 216, 317–330.
- D'Arrigo, R.D., Barbetti, M., Watanasak, M., Buckley, B., Krusic, P., Boonchirdchoo, S., Sarutanon, S., 1997. Progress in dendroclimatic studies of mountain pine in northern Thailand. *IAWA Bulletin* 18, 433–444.
- D'Arrigo, R.D., Jacoby, G.C., 1992. A tree-ring reconstruction of New Mexico winter precipitation and its relation to El Niño Southern Oscillation events. In: Diaz, F.H., Markgraf, V. (Eds.), *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*. Cambridge University Press, Cambridge, pp. 243–257.
- D'Arrigo, R., Wilson, R.J.S., Jacoby, G.C., 2006. On the long-term context for late 20th century warming. *Journal of Geophysical Research* 111, D03103, doi:10.1029/2005JD006352.
- Détienne, P., 1989. Appearance and periodicity of growth rings in some tropical woods. *IAWA Bulletin* 10, 123–132.
- Dünisch, O., Bauch, J., Sack, M., Müller, M., 1999. Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis*. *Aubl. Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg* 193, 79–96.
- Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt* 88, 230–250.
- Eshete, G., Stahl, G., 1999. Tree-rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. *Forest Ecology and Management* 116, 107–117.
- Esper, J., Cook, E.R., Schweingruber, F.H., 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* 295, 2250–2253.
- Esper, J., Frank, D.C., Büntgen, U., Verstege, A., Luterbacher, J., Xoplaki, E., 2007. Long-term drought severity variations in Morocco. *Geophysical Research Letters*, 34, doi:10.1029/2007GL030844.
- February, E.C., 2000. Archaeological charcoal and dendrochronology to reconstruct past environments of Southern Africa. *South African Journal of Science* 96, 111–116.

- February, E.C., Stock, W.D., 1998. An assessment of the dendrochronological potential of two Podocarpus species. *The Holocene* 8, 747–750.
- Fichtler, E., Clark, D.A., Worbes, M., 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree-rings and C-14. *Biotropica* 35, 306–317.
- Fichtler, E., Trouet, V., Beekman, H., Coppin, P., Worbes, M., 2004. Climatic signals in tree-rings of *Burkea africana* and *Pterocarpus angolensis* from semi-arid forests in Namibia. *Trees* 18, 422–451.
- Fritts, H.C., 1976. In: *Tree Rings and Climate*. Academic Press, London.
- Frost, P., 1996. The ecology of miombo woodlands. In: Campbell, B. (Ed.), *The Miombo in Transition: Woodlands and Welfare in Africa*. Center for International Forestry Research, Bogor, pp. 11–57.
- Gebrekirostos, A., Mitlöhner, R., Teketay, D., Worbes, M., 2008. Climate–growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. *Trees – Structure and Function* 22, 631–641, doi:10.1007/s00468-008-0221-z.
- Gourlay, I.D., 1995. The definition of seasonal growth zones in some African Acacia species – a review. *IAWA Journal* 16, 353–359.
- Grundy, I., 1995. Regeneration and management of *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin in miombo woodland, Zimbabwe: towards a sustainable management strategy. In: Mushove, P.T., Shumba, E.M., Matose, F. (Eds.), *Sustainable Management of Indigenous Forests in the Dry Tropics*, Proceedings of an International Conference in Kadoma, Zimbabwe. Forestry Commission, Harare, pp. 174–188.
- Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M.T., Guiot, J., 2006. Sensitivity of African biomes to changes in the precipitation regime. *Global Ecology and Biogeography* 15, 258–270.
- Hummel, F.C., 1946. The formation of growth rings in *Entandrophragma macrophyllum* A. Chev. and *Khaya grandifolia* C.DC. *The Empire Forestry Review* 25, 103–107.
- IPCC WGI, 2007. *Climate Change 2007: The Physical Science Basis*. IPCC Secretariat, www.ipcc.ch.
- Jacoby, G.C., D'Arrigo, R.D., 1990. Teak (*Tectona grandis* L.F.), a tropical species of large-scale dendroclimatic potential. *Dendrochronologia* 8, 83–98.
- Lindesay, J.A., Vogel, C.H., 1990. Historical evidence for Southern Oscillation–Southern African rainfall relationships. *International Journal of Climatology* 10, 679–689.
- Malaisse, F.P., Freson, R., Goffinet, G., Malaisse-Mousset, M., 1975. Litter fall and litter breakage in miombo. In: Golley, F.B., Medina, E. (Eds.), *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research*. Springer-Verlag, New York, pp. 137–152.
- Mariaux, A., 1967. Les cernes dans les bois tropicaux africains. Nature et périodicité. Peuvent-ils révéler l'âge des arbres?. *Bois et Forêts des Tropiques* 113 (3–14), 23–37 114.
- Mariaux, A., 1969. La périodicité des cernes dans le bois de Limba. *Bois et Forêts des Tropiques* 128, 39–53.
- Mariaux, A., 1970. La périodicité de formation des cernes dans le bois de L'Okoumé. *Bois et Forêts des Tropiques* 131, 37–50.
- Matarira, C.H., 1990. Drought over Zimbabwe in a regional and global context. *International Journal of Climatology* 10, 609–625.
- Millington, A.C., Critchley, R.W., Douglas, T.D., Ryan, P., 1994. In: *Estimating Woody Biomass in Sub-Saharan Africa*. The World Bank, Washington D.C.
- Nicholson, S.E., 2001. A semi-quantitative, regional precipitation data set for studying African climates of the nineteenth century, Part I. Overview of the data set. *Climatic Change* 50, 317–353.
- Nicholson, S.E., Entekhabi, D., 1986. The quasi-periodic behavior of rainfall variability in Africa and its relationship to the Southern Oscillation. *Journal of Climate and Applied Meteorology* 34, 331–348.
- Nicholson, S.E., Kim, J., 1997. The relationship of the El Niño–Southern Oscillation to African rainfall. *International Journal of Climatology* 17, 117–135.
- Priya, P.B., Bhat, K.M., 1998. False ring formation in Teak (*Tectona grandis* L.f.) and the influence of environmental factors. *Forest Ecology and Management* 108, 215–222.
- Richard, Y., Fauchereau, N., Pocard, I., Rouault, M., Trzaska, S., 2001. 20th century droughts in southern Africa: spatial and temporal variability, teleconnections with oceanic and atmospheric conditions. *International Journal of Climatology* 21, 873–885.
- Rinn, F., Jäkel, S., 1997. *TSAP, reference manual*. Heidelberg, Germany, 187pp.
- Ropelewski, C.F., Halpert, M.S., 1988. Precipitation patterns associated with the high index phase of the Southern Oscillation. *Journal of Climate* 2, 268–284.
- Rutherford, M.C., 1984. Relative allocation and seasonal phasing of growth of woody plant components in a South African savanna. *Progress in Biometeorology* 3, 200–221.
- Sass, U., Killmann, W., Eckstein, D., 1995. Wood formation in two species of Dipterocarpaceae in peninsular Malaysia. *IAWA Journal* 16, 371–384.
- Sass-Klaassen, U., Couralet, C., Sahle, Y., Sterck, F.J., 2008. Juniper from Ethiopia contains a large-scale precipitation signal. *International Journal of Plant Sciences* 169, 1057–1065, doi:10.1086/590473.
- Schöngart, J., Junk, W.J., Piedade, M.T.F., Ayres, J.M., Hüttermann, A., Worbes, M., 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Niño–Southern Oscillation effect. *Global Change Biology* 10, 683–692.
- Schöngart, J., Orthmann, B., Hennenberg, K.J., Porembski, S., Worbes, M., 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. *Global Change Biology* 12, 1139–1150.
- Schöngart, J., Piedade, M.T.F., Wittmann, F., Junk, W.J., Worbes, M., 2005. Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. *Oecologia* 145, 454–461.
- Stahle, D.W., Cleaveland, M.K., Haynes, G.A., Klimowicz, J., Ngwenya, P., Mushove, P.T., 1996. Preliminary tree-ring investigations of indigenous trees in Zimbabwe. In:

- Mushove, W.J., Shumba, E.M., Matose, F. (Eds.), Sustainable Management of Indigenous Forests in the Dry Tropics, Proceedings of an International Conference in Kadoma, Zimbabwe. Forestry Commission, Harare, Zimbabwe, pp. 57–61.
- Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* 124, 217–229.
- Stokes, M.A., Smiley, T.L., 1968. In: *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.
- Tarhule, A., Hughes, M.K., 2002. Tree-ring research in semi-arid West Africa: need and potential. *Tree-Ring Research* 58, 31–46.
- Therrell, M.D., Stahle, D.W., Ries, L.P., Shugart, H.H., 2006. Tree-ring reconstructed rainfall variability in Zimbabwe. *Climate Dynamics* 26, 677–685.
- Trenberth, K.E., 1997. The definition of El Niño. *Bulletin of the American Meteorological Society* 78, 2771–2777.
- Trenberth, K.E., Stepaniak, D.P., 2001. Indices of El Niño evolution. *Journal of Climate* 14, 1697–1701.
- Trouet, V., 2004. The El Niño Southern Oscillation effect on Zambezian miombo vegetation: proxies from tree-ring series and satellite-derived data. *Dissertationes de Agricultura*, 638, Katholieke Universteit Leuven, 252pp.
- Trouet, V., Haneca, K., Coppin, P., Beeckman, H., 2001. Tree-ring analysis of *Brachystegia spiciformis* and *Isobertia tomentosa*: evaluation of the ENSO-signal in the miombo woodland of eastern Africa. *IAWA Journal* 22, 385–399.
- Trouet, V., Coppin, P., Beeckman, H., 2006. Annual ring patterns in *Brachystegia* trees of the miombo woodland reveal climatic influence. *Biotropica* 38, 375–382.
- Trouet, V., Esper, J., Graham, N.E., Baker, A., Scourse, J.D., Frank, D.C., 2009. Persistent positive North Atlantic Oscillation mode dominated the medieval climate anomaly. *Science* 324, 78–80.
- Tyson, P.D., 1986. In: *Climatic Change and Variability in Southern Africa*. Oxford University Press, Cape Town.
- Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. *New Phytologist* 167, 425–435.
- Walter, H., 1940. Die Jahresringe der Bäume als Mittel zur Feststellung der Niederschlagsverhältnisse in der Vergangenheit, insbesondere in Deutsch-Südwest-Afrika. *Die Naturwissenschaften* 38, 607–612.
- White, F., 1983. *The Vegetation of Africa*. Natural Resources Research 20. UNESCO, Paris.
- Worbes, M., 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. *IAWA Bulletin* 10, 109–122.
- Worbes, M., 1995. How to measure growth dynamics in tropical trees – a review. *IAWA Journal* 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. *Journal of Ecology* 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., Staschel, R., Roloff, A., Junk, W.J., 2003. Tree-ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *Forest Ecology and Management* 173, 105–123.