

Annual Growth Ring Patterns in *Brachystegia spiciformis* Reveal Influence of Precipitation on Tree Growth¹

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ABSTRACT

The availability of exactly dated tree-ring chronologies is limited in tropical regions. However, these chronologies could contribute widely to studies of the influence of natural and human-induced factors on tropical forests. We examine the potential for building a chronology based on three sites in the miombo woodland of western Zambia. *Brachystegia spiciformis* Benth., a dominant species from this vegetation type, is used. Response of the chronology to several climatic factors is examined. All specimens showed very clear growth rings, and cross-dating between radii of a tree was successful for all trees. Site chronologies could be constructed after cross-dating of growth ring series of individual trees. The mean growth ring curves of the three sites were significantly similar, allowing for the construction of a regional chronology. Correlation function analysis between the tree-ring chronology and regional climatic variables revealed that climate at the core of the rainy season, in December and January, has an explicit influence on tree growth. Where precipitation and relative humidity in these months influence tree growth positively, temperature correlates in a negative way. Some 20 percent of the variance in the *B. spiciformis* tree-ring chronology is accounted for by wet season rainfall. The successful cross-dating and correlation between a tree-ring chronology and climate demonstrated in this study indicate annual ring formation in *B. spiciformis* trees and sensitivity to climatic conditions.

Key words: *Brachystegia spiciformis*; dendroclimatology; dry tropical forest; miombo; tree rings; woodland; Zambia.

BASIC KNOWLEDGE OF THE RELATIONSHIPS between environmental variables and tree growth is crucial for predicting future vegetation growth responses to climatic variation (Pumijumnong 1999) and to low frequency climatic phenomena such as the El Niño Southern Oscillation (ENSO; Cook 1992). Tree-ring analysis is widely used in temperate, arctic, high mountainous, and arid zones to study these relationships, to reconstruct the periodicity and intensity of climatic phenomena, and to study the growth, structure, and production of forests (Fritts 1976, Schweingruber 1988, Wimmer & Vetter 1999).

Tree rings are induced by seasonally alternating favorable and unfavorable growth conditions. Temperature is the limiting factor for tree growth in temperate regions, but in tropical regions (except for mountainous areas) temperature and photoperiod are relatively constant throughout the year. Seasonally occurring stress factors in the tropics can be drought and flooding (Worbes 1995). These climatic stress factors can induce cambial dormancy in tropical trees and, in consequence, growth zones in the wood.

The existence and annual nature of tree rings has been investigated and verified for a large number of tropical trees ranging from dry zones (Gourlay 1995) to humid zones (Fichtler *et al.* 2004)

and mangroves (Verheyden 2004). For tropical African species, the appearance and nature of tree rings has been described by Walter (1940), Mariaux (1967, 1969, 1970), Amobi (1973), Détienne (1989), Eshete and Stahl (1999), and Tarhule and Hughes (2002), among others.

Poor infrastructure and low socioeconomic development in major parts of southern Africa render the region vulnerable to climate anomalies and extreme weather events (Janowiak 1988). Due to this high vulnerability, interannual climatic variability and low frequency climatic changes can lead to extreme negative impacts on societies. As in many other tropical regions, time series of climatic data, necessary to study interannual climatic variability, are scarce, and other methods of examining the climatic record are required. Regional rainfall data sets within southern Africa do not extend over more than 100 yr and register relatively short oscillations of climate (Tyson 1986). Moreover, for most parts of Africa, the network of climate stations is not dense enough to provide a coherent spatial picture of climatic variability (Anyamba & Eastman 1996). Tree-ring data, if they have a fixed annual resolution and can produce absolute time series (Cook 1992), offer a potential solution. Despite the strong potential of tree-ring analysis in the tropics for applied research, as shown in the above-mentioned studies, applications are relatively rare. The number of exactly dated, long tree-ring chronologies for tropical regions is limited. Berlage (1931) constructed the first tree-ring

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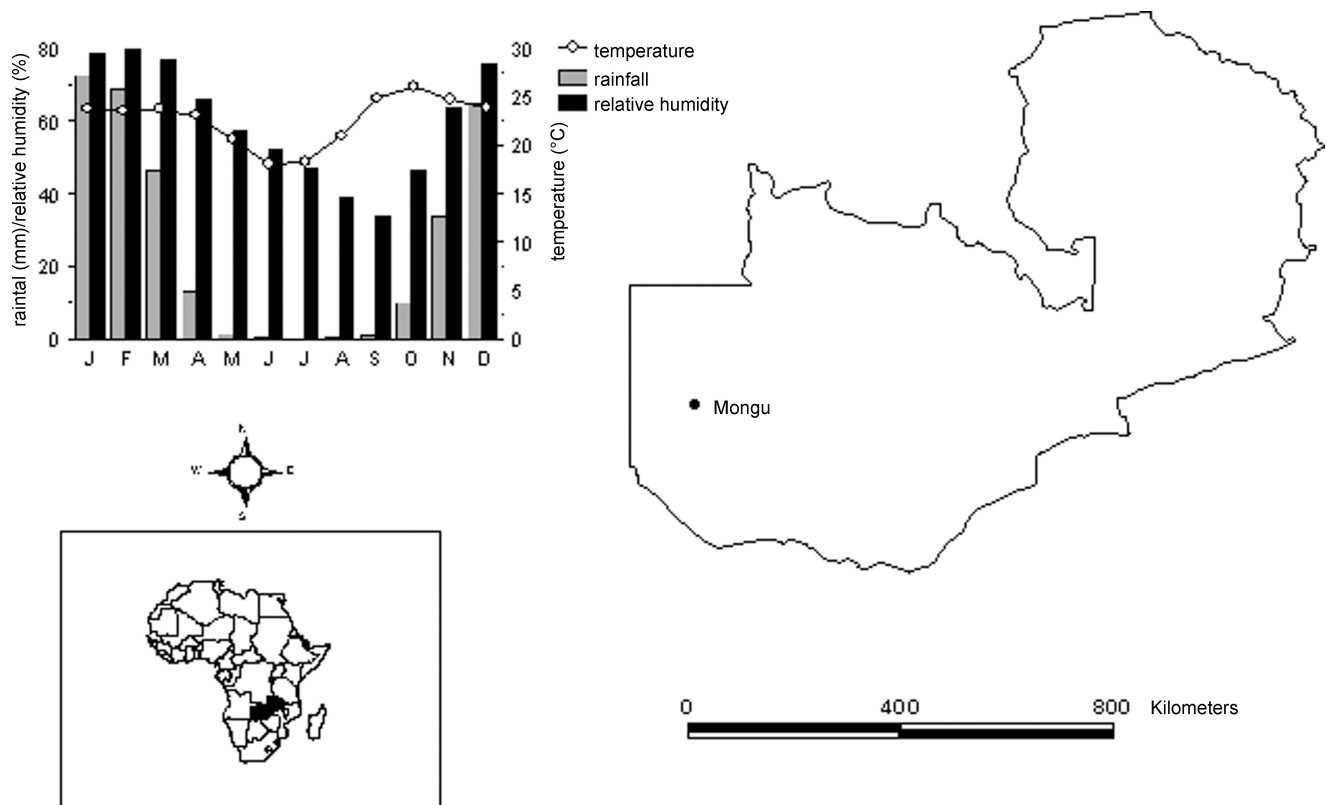


FIGURE 1. Geographical location and climate diagram for Mongu, Zambia.

chronology in the tropics. The over 400-yr-long chronology for teak (*Tectona grandis* L.f.) from Java was later revised by Jacoby and D'Arrigo (1990). For the Amazon basin, a more than 200-yr-long, ENSO-sensitive chronology of *Piranhea trifoliata* Baill. was presented by Schöngart *et al.* (2004). The only exactly dated chronologies for tropical Africa were developed by Stahle *et al.* (1999). The 200-yr-long chronologies of *Pterocarpus angolensis* from the seasonally dry forests in Zimbabwe showed strong correlation with wet season precipitation.

Miombo woodlands are the principal vegetation type in southern Africa, covering over 2.8 million square km in the region (White 1983). Miombo woodland is dominated by three genera of the family Fabaceae (subfamily Caesalpinioideae): *Brachystegia*, *Julbernardia*, and *Isoberlinia*. Most miombo trees, including the dominant species, are deciduous, shedding their leaves during the dry season. Several miombo species have previously been examined for dendrochronological purposes, including *Brachystegia spiciformis*, *Julbernardia globiflora* (Benth.) Troupin (Grundy 1995), *P. angolensis* DC (Stahle *et al.* 1999, Fichtler *et al.* 2004), and *Isoberlinia tomentosa* (Harms) Craib *et al.* (Trouet *et al.* 2001); however, so far no chronology is available for the miombo region.

This study examines the potential for building a chronology based on *B. spiciformis* trees from three sites in the miombo woodland of western Zambia. *B. spiciformis* is one of the dominant species of miombo woodland (White 1983). We examine annual tree-ring

formation in *B. spiciformis* and assess the influence of climate on tree growth.

METHODS

STUDY SITES.—The study was performed at three sites within a 25-km radius of the meteorological station at Mongu (15°15'S, 23°09'E) in western Zambia (Fig. 1). Site 1 was 30 km south of sites 2 and 3, which were 1 km apart. The miombo vegetation at all of the study sites is part of the drier miombo zone (mean annual rainfall <1000 mm), but its structure and species composition are influenced by specific edaphic conditions, and soils are generally poor as they derive from deep (30 m) Kalahari sands. The vegetation is defined as *B. spiciformis* Kalahari woodland (Jeanes & Baars 1991). The sites were located on flat terrain adjacent to the Zambezi River flood plain. The tree canopy at all sites is dominated by *B. spiciformis*, and then in order of decreasing importance, *Burkea africana* Hook., *Guibourtia coleosperma* (Benth.) J. Léonard, *Brachystegia bakeriana* Burt Davy *et al.* Hutch, and *Ochna pulchra* Hook. Sites 2 and 3 were sampled in August 2000 and site 1 in October 2002. All sites had been subjected to logging earlier on in the sampling year and samples were taken from recently cut tree stumps.

SAMPLES.—Disks were cut from between 15 and 18 stumps at each site (Table 1). The last growth rings were formed in the growing

TABLE 1. Descriptive statistics of the *Brachystegia spiciformis* chronologies for three sites near Mongu and the raw and detrended tree-ring series contributing to the chronologies.

Descriptive statistics	Site 1	Site 2	Site 3
Number of specimens sampled	18	16	15
Number of samples analyzed	18	15	13
Number of samples used in chronology	16	15	13
Age (min. 4 trees) (yr)	57	38	27
Range in ages (yr)	23–63	17–48	17–31
Time-span (yr)	1940–2002	1953–2000	1970–2000
Raw data			
Mean ring width (mm)	2.44	2.62	3.25
Standard deviation (mm)	1.56	1.5	1.66
Mean sensitivity	0.41	0.39	0.49
Autocorrelation	0.64	0.51	0.49
Detrended data			
Correlation between trees	0.24	0.29	0.26
Variance explained by first eigenvector (%)	32	28	31

season of 1999–2000 for sites 2 and 3 and in 2001–2002 for site 1. Full stem disks were collected, as these have proven more suitable than increment cores for tree-ring analysis in Africa (Eshete & Stahl 1999, February 2000). The occurrence of wedging rings (rings that do not cover the whole circumference of the tree or are locally absent) makes the use of increment cores risky. Wedging rings appear more frequently near the stem base (Lamarche *et al.* 1982) and therefore samples were taken from as near to breast height (1.3 m) as the height of existing stumps would allow (range = 0.7–1.3 m). All samples are lodged in the Xylarium of the Royal Museum for Central Africa in Tervuren, Belgium (accessions Tw56575 to Tw56670).

Transverse surfaces of all disks were sanded and polished (sand paper grain 80 to 1200). All stem disks were first analyzed microscopically to identify the presence of any wedging rings. Growth ring widths were then measured to the nearest 0.01 mm using LINTAB equipment and TSAP software (Rinn & Jäkel 1997) along four perpendicular radii per sample disk.

CLIMATE DATA.—Rainfall data from Mongu meteorological station were available from 1941–2000. In addition, the Mongu rainfall data were averaged with data from two nearby stations (Senanga and Kalabo) over the common interval from 1941–1984. Averaging precipitation records from separate stations can decrease small-scale noise and improve statistical relationships between tree growth and meteorological data (Blasing *et al.* 1981).

Mean monthly relative humidity and temperature data were derived from the IPSL ClimServ data set (Centre National de la Recherche Scientifique, Laboratoire de Météorologie Dynamique, <http://climserv.lmd.polytechnique.fr>) and were available for the period 1948–2000. The mean annual rainfall for Mongu was 885 mm/yr, mean annual relative humidity was 56.3 percent, and

mean annual temperature was 21.5°C (Fig. 1). Monthly, seasonal, and annual climatic data were used for the correlation analysis with tree-ring data. Annual data corresponded to the growth year, partly covering two calendar years (August ($n - 1$) to July (n)), whereas seasonal data were calculated over the rainy season (November to March; RS) and over the transition months between dry and rainy season (September, October and April, May; TM). The date of the calendar year in which the growing season ended was assigned to all climatic data.

STATISTICAL ANALYSIS.—Cross-dating consists of the exact dating of a tree-ring curve of unknown age by comparing it to a dated reference tree-ring chronology (Stokes & Smiley 1968, Schweingruber 1996). For most tropical regions (including southern Africa), no exactly dated reference chronologies are available, and cross-dating consists of comparing growth curves visually and statistically to bring ring-width series in a synchronous position (Pilcher 1990, Worbes 1995). Successful cross-dating indicates the influence of an external growth factor on tree growth in a region (Eckstein *et al.* 1981). After visually comparing the ring-width series, statistical measures are used to identify problems in measurement and to verify the cross-dating result.

By cross-dating, we combined the tree-ring series of four radii of a tree (using TSAP software) to give a mean growth curve per tree. Before average growth ring series of different trees of the same site were cross-dated, long-term growth trends associated with increasing trunk radius were removed from each individual curve (Cook & Kairiukstis 1990), by division by a one-sided (backward) moving average over 5 yr (Rinn & Jäkel 1997).

Mean curves per site (chronologies) were obtained by averaging cross-dated and detrended curves of individual trees. Mean sensitivity values were calculated for all chronologies to provide a measure of between-ring variability (Schweingruber 1988):

$$\bar{S} = \frac{\sum_{i=1}^{n-1} |S_i + 1|}{n - 1} \quad \text{with} \quad S_i = \frac{(x_i - x_{i-1}) \cdot 2}{(x_i + x_{i-1})}$$

where x is tree-ring width and n the total number of rings in a specimen.

The success of the cross-dating of individual series was investigated using the cross-correlation algorithm developed by Baillie and Pilcher (1973). Student's t -values are calculated for all positions of overlap of two series:

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

where r is the sample Pearson's correlation coefficient and n is the length of the ring-width series.

In addition to the t -test, the *Gleichläufigkeitskoeffizient* (GLK) is used in dendrochronology to investigate the success of cross-dating. Gleichläufigkeit is a measure of the year-to-year agreement between the interval trends of two chronologies based upon the sign of agreement, expressed for two curves by the following equations (Eckstein & Bauch 1969):

$$\Delta_i > 0 : G_{ix} = +\frac{1}{2}$$

$$\Delta_i = (x_{i+1} - x_i) \quad \text{when} \quad \Delta_i = 0 : G_{ix} = 0$$

$$\Delta_i < 0 : G_{ix} = -\frac{1}{2}$$

for two curves x and y $G_{(x,y)} = \frac{100}{n-1} \sum_{i=1}^{n-1} |G_{ix} + G_{iy}|$

where G is Gleichläufigkeit, n is number of values, x, y are series, and Δ_i is the difference in tree-ring width between two consecutive years. The t -value expresses the degree of affinity of two time series, while incorporating the number of observations (Baillie & Pilcher 1973). GLK is a nonparametric method for analysis of concordance. Combining the two concepts optimizes the cross-dating process. The ultimate cross-dating test, however, remains the visual and personal judgment (Cook & Kairiukstis 1990). Successfully cross-dated ring-width series of individual trees were averaged to build site-specific mean chronologies. A master chronology combining all site-specific chronologies was obtained in the same way.

Tree-ring series and meteorological series are compared as a basis for the construction of statistical models linking tree rings and climate (Schweingruber 1988). Correlation function analysis is used prior to a response function analysis as a preliminary interpretative guide to document seasonality and strength of tree growth response (Blasing *et al.* 1981). Correlation functions consisted of a series of Pearson's correlation coefficients between a tree-ring chronology and each of several sequential climatic variables.

RESULTS

DISTINCTIVENESS OF GROWTH RINGS.—All *B. spiciformis* specimens showed clear growth rings (Fig. 2a). Growth ring boundaries were marked by terminal parenchyma, a common characteristic for the subfamily Caesalpinioideae (Worbes 1989, Höhn 1999). Terminal parenchyma bands are commonly composed of maximum five rows of parenchymatous cells forming a continuous layer that is often visible on the transverse surface as a fine light-colored band. Ring wedging (the occurrence of locally absent rings; Fig. 2b) tended to occur more frequently toward the outer parts of the stem discs, where annual diameter expansion was lower. Additionally, older trees with slower growth showed more ring wedging. In some specimens growth ring formation was distinct, but cross-dating between radii of the tree was hampered by excessive ring wedging. These specimens were excluded from the data set, as well as specimens showing excessive wound formation (possibly caused by fires; Table 1).

CROSS-DATING.—Cross-dating between four radii of a tree was successful for all nondiscarded trees at all three sites, which confirmed strong growth symmetry and the absence of missing rings and measuring errors. It was possible to mutually cross-date 16 out of 18 *B. spiciformis* trees from site 1 (Table 1). Trees contributing to the chronology of this site varied in age from 23–63 yr. The mean growth ring series for this site (with a contribution of minimum

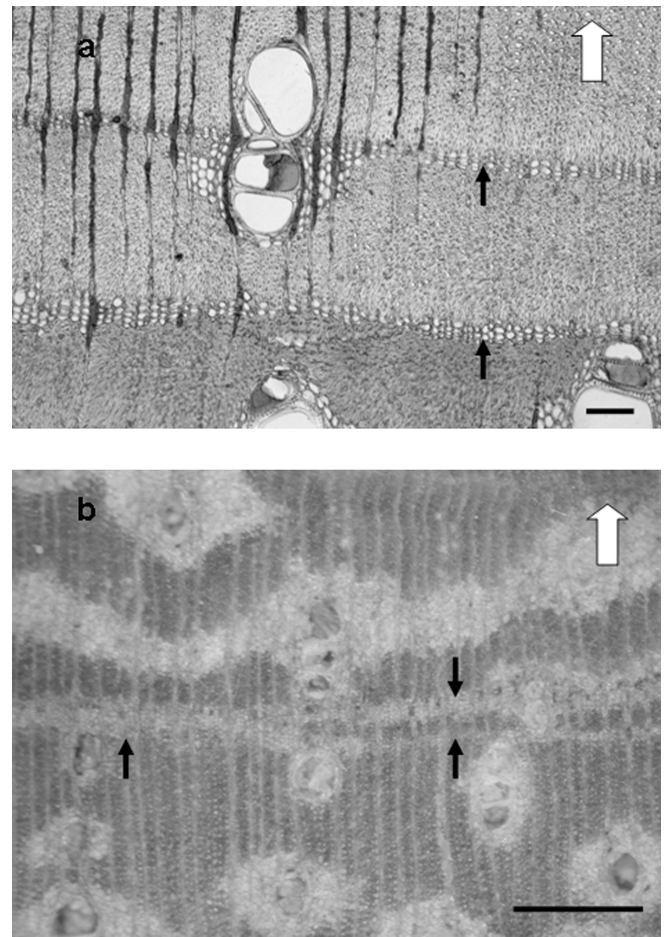


FIGURE 2. Growth ring (a) and ring wedging (b) in *Brachystegia spiciformis*. Growth ring boundaries consisting of marginal parenchyma are indicated by black arrows. The two ring boundaries shown on the right-hand side of (b) wedge into one ring boundary on the left-hand side of the picture. The white arrows indicate the growth direction. Scale-bar: (a) 100 μm and (b) 1 mm.

four trees) covered 57 yr and was characterized by a mean sensitivity of 0.41. At site 2, cross-dating was possible for all analyzed trees ($N = 16$). Ages of individual trees varied between 17 and 48 yr, resulting in a mean growth ring series of 38 yr with a mean sensitivity of 0.39. The mean growth curve of the third site was based on all measured *B. spiciformis* trees ($N = 15$), aged between 17 and 31 yr. This mean growth curve spanned 27 yr and showed a relatively high mean sensitivity of 0.49.

Growth rates were highest at site 3 (3.25 mm/yr), whereas comparable growth rates were found at the two other sites (2.44 and 2.62 mm/yr). The variation of the individual tree-ring widths around this mean (presented by the standard deviation) was relatively low and comparable for the three sites, indicating the ecological homogeneity of the sites (Schweingruber 1988). Mean sensitivity values were higher for site 3 than for both other sites, indicating that the growth of individual species on this site experienced the strongest influence of environmental factors. Time-series autocorrelation

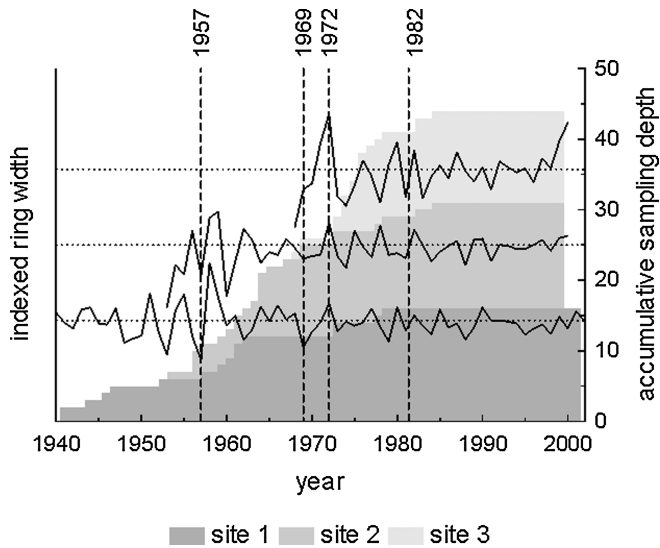


FIGURE 3. Mean growth ring curves (left axis) and accumulative sampling depth (right axis) for *Brachystegia spiciformis* at site 1, site 2, and site 3.

coefficients were high at all sites, but considerably higher at site 1 compared to the other two sites (0.64 compared to 0.49 and 0.51). High time-series autocorrelation coefficients reflect a strong influence of growth in the preceding year on growth in the year under investigation. A significant growth trend was thus present in the samples of all sites and detrending was necessary. Correlation coefficients of the detrended series, a measure of the homogeneity of the site, were highest at site 2. The variation held in common among the series may also be assessed by the percentage of variation explained through the first eigenvector of the correlation matrix of the tree-ring series. The variance explained by the first eigenvector was moderately high and varied around 30 percent at all sites. The chronologies constructed for the three sites and the number of samples contributing to them are depicted in Figure 3.

Cross-dating between sites was successful, allowing the construction of a regional chronology (Table 2). The chronologies of all three sites showed a similar pattern of positive and negative peaks (Fig. 3), and correlations between all three sites were significant ($P < 0.05$). Correlation was strongest between site 1 and site 2 ($t = 2.8$, $df = 94$), correlations between both sites and site 3 were slightly lower ($t = 2.3$ and $t = 1.6$, $df = 64$). GLK-values, however,

TABLE 2. Gleichläufigkeitskoeffizient (GLK), t -value and Pearson's correlation coefficient (R-value) for cross-dating of tree-ring chronologies from three sites near Mongu.

	GLK	t -value	R-value
Site 1 and Site 2	65	2.8 ^a	0.4 ^a
Site 1 and Site 3	71	1.6	0.35 ^a
Site 2 and Site 3	76	2.3 ^a	0.35 ^a

^a $P < 0.05$.

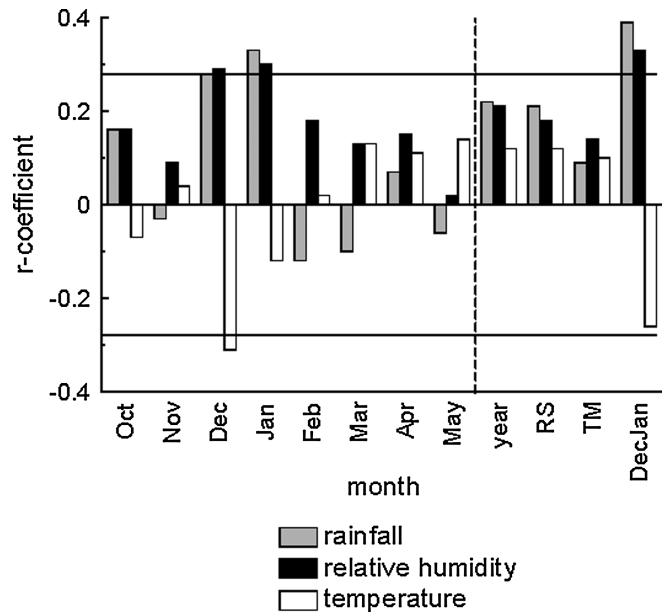


FIGURE 4. Correlations between the Mongu tree-ring chronology and rainfall, relative humidity, and temperature data for Mongu. Climate data used are monthly (October [Oct] to May), annual, and seasonal (rainy season [RS], transition months [TM], and December to January [DecJan]). Significance levels ($P < 0.05$) are indicated as solid horizontal lines.

were higher for the latter correlations (76% and 71%, respectively, and as compared to 65%), indicating a stronger agreement between interval trends.

RESPONSE TO CLIMATE.—A correlation analysis was performed for each climatic data set separately, using the mean chronology of the three sites. The correlation analysis covered 56 yr for the Mongu precipitation data set (1945–2000) and 52 yr for relative humidity and temperature (1949–2001). The influence of climate on tree growth appeared to be strongest at the core of the rainy season. This is demonstrated by the correlations found between the chronology and climate variables for the months of December and January (Fig. 4). Where rainfall and relative humidity affected tree growth positively in both months ($r = 0.28$ and $r = 0.32$, $P < 0.05$ for rainfall; $r = 0.29$ and $r = 0.3$, $P < 0.05$ for relative humidity), the influence of December and January temperature was negative ($r = -0.31$, $P < 0.05$ and $r = -0.12$). Based on these significant correlations for single month climatic data, the sum (for rainfall data) or average (for relative humidity and temperature data) of December and January (DecJan) was added to the climatic data set. Summing (in case of rainfall) or averaging (in case of relative humidity), the data for both months increased correlation coefficients. The correlation between December and January precipitation and the tree-ring chronology is illustrated in Figure 5.

Rainfall data of December and January showed no correlation with relative humidity or temperature data for the same month. Relative humidity and temperature, however, were strongly negatively

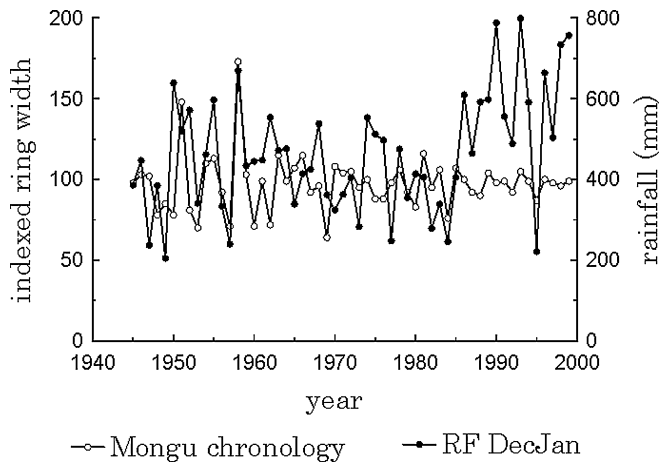


FIGURE 5. Time-series (1945–1999) correlation between the *Brachystegia spiciformis* chronology for Mongu and summed December and January precipitation for Mongu.

correlated ($r = -0.44$ to $r = -0.91$, $P < 0.05$). A principal component analysis was applied on the relative humidity and temperature data series of December and January to reduce potential multicollinearity effects and to emphasize the common variance between the data sets (Thacker 1996). The first component resulting from this analysis explained 76 percent of the total variance for the four time series. This first component showed a strong positive correlation to the tree-ring chronology ($r = 0.33$, $P < 0.05$), confirming the earlier results of the correlation function analysis (Fig. 4).

When comparing the tree-ring chronology to regionally averaged precipitation data, correlations appeared to be stronger for the regional data than for single-station data. This was the case for precipitation in December ($r = 0.3$, $P < 0.05$), in January ($r = 0.33$, $P < 0.05$), and for the summed precipitation in these months ($r = 0.44$, $P < 0.05$).

DISCUSSION

Brachystegia spiciformis showed clear growth rings, delimited by fine bands of marginal parenchyma. These parenchyma bands are typical for many trees of the Fabaceae family (Gourlay 1995) and have been presented as reliable delimitations of growth zones by Walter (1940). As in *Acacia karroo* Hayne (Gourlay & Barnes 1994), another member of the family of the Fabaceae, the terminal parenchyma bands in *B. spiciformis* can be distinguished from intraseasonal aliform parenchyma bands by their fineness and evenness of appearance (Fig. 2a,b). The dendrochronological potential of the Caesalpinioideae subfamily in general has previously been noted and emphasized by several authors (Maingi 1998, Tarhule & Hughes 2002). *Brachystegia spiciformis* in particular has been examined for dendrochronological purposes by several authors. Stahle *et al.* (1996) mentioned vague growth ring banding in *B. spiciformis* from Zimbabwe and assigned a low dendrochronological potential to the

species. Bolza and Keating (1972), however, found distinct growth rings in the species, and Grundy (1995) demonstrated annual ring formation and a growth response to rainfall for young coppice *B. spiciformis* trees (less than 15 yr old) in Zimbabwe.

The difference in dendrochronological potential credited to the species can be related to the humidity level of the bioclimatic regions where samples were taken and the associated differences in growth rate. The *B. spiciformis* trees studied by Stahle *et al.* (1996) were sampled in the Hwange National Park in Zimbabwe (mean annual rainfall 560 mm), whereas the samples used for this study were taken in the dry miombo woodland of western Zambia (mean annual rainfall 880 mm). As pointed out by Stokes and Smiley (1968), ring wedging occurs primarily under very dry conditions, when growth rates are low. Since conditions are drier and growth rates lower in Zimbabwe compared to western Zambia, growth ring anomalies are bound to occur more frequently. Excessive growth ring anomalies can hamper cross-dating between radii and between trees, and can impede the use of a sample for tree-ring analysis. Sampling in mesic areas rather than dry areas may avoid the problem of excessive occurrence of growth ring anomalies.

Growth ring anomalies were found to appear more frequently toward the perimeter of old stems, where radial growth rates are lower. A similar phenomenon occurs in other Caesalpinioideae species from western Africa (Tarhule & Hughes 2002). This pattern might explain why Grundy (1995) found distinct growth rings in young coppice *B. spiciformis* trees from Zimbabwe, whereas older trees from the same ecoclimatic region showed low dendrochronological potential (Stahle *et al.* 1996). 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 anomalies (Tarhule & Hughes 2002).

The annual character of the growth rings found in the *B. spiciformis* specimens used for this study was confirmed by successful cross-dating. Ninety to 100 percent of the sampled trees at any site showed a comparable pattern, leading to successful cross-dating and indicating a common stand-wide influencing factor. Moreover, cross-dating of site-specific chronologies was also successful, allowing for the construction of a regional chronology for the Mongu area and suggesting a common influence on tree growth at a regional scale. A correlation function analysis between the tree-ring chronology and regional climatic variables revealed that climate could be this common influencing factor. More particularly, climate at the core of the rainy season, in December and January, seems to have an explicit influence on tree growth (Fig. 3).

The positive effect found for precipitation at the core of the rainy season has previously been described by Stahle *et al.* (1999) for *P. angolensis* trees from miombo woodland in Zimbabwe and by Fichtler *et al.* (2004) for *B. africana* trees (a species also occurring in miombo woodland) of Namibia. This study shows that some 20 percent of the variation in the *B. spiciformis* chronology was accounted for by wet season rainfall, a number corresponding to the results of Stahle *et al.* (1999) for Zimbabwe and Schöngart *et al.* (2004) for the Amazonian Basin. Fires, insect attacks, herbivory, and human factors could contribute to additional variance.

Stronger correlations were found for regionally averaged precipitation data as compared to single-station data. Single-station data are often subject to small-scale noise (Blasing *et al.* 1981) due to microclimate conditions and measurement errors. This noise can be reduced and statistical relationships can be improved by averaging data over a larger region.

In addition to the previously recognized influence of wet season rainfall on tree growth in miombo species (Stahle *et al.* 1999, Fichtler *et al.* 2004), this study reveals an influence of relative humidity and temperature for the same period. The positive effect on tree growth of an increase in relative humidity can be explained by its direct impact on photosynthetic activity via stomatal conductance. Only high stomatal conductance (linked to high relative humidity) enables high CO₂-uptake and high assimilation rates (Ball *et al.* 1987). Relative humidity appears to have its greatest influence during the core of the rainy season, when the highest portion of the yearly assimilation takes place. A negative effect of temperature on tree growth was demonstrated by Fichtler *et al.* (2004) for two miombo species in Namibia. This can be explained by an increase in plant respiration with increasing temperature, resulting in a higher loss of assimilated carbon (Fitter & Hay 1981).

The successful cross-dating and correlation between a tree-ring chronology and climate, demonstrated in this study, indicate annual ring formation in *B. spiciformis* trees and sensitivity to climatic conditions. The species therefore shows a strong dendroclimatic potential. *Brachystegia spiciformis* is widespread and locally dominant throughout the miombo region, allowing the future construction of a dense and broad tree-ring network based on this species.

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