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Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe

D.W. Stahle^{a,*}, P.T. Mushove^b, M.K. Cleaveland^a, F. Roig^c, G.A. Haynes^d

^aDepartment of Geography, University of Arkansas, Fayetteville, AR 72701, USA

^bForest Research Centre, P.O. Box HG 595, Highlands, Harare, Zimbabwe

^cLaboratorio de Dendrochronologia, Avenida Ruiz Leal, Parque Gral. San Martín, C.C. 330, (5500), Mendoza, Argentina

^dDepartment of Anthropology, University of Nevada, Reno, NV 89557-0006, USA

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Abstract

Dendrochronological analyses indicate that *Pterocarpus angolensis* produces anatomically distinctive annual growth rings in the indigenous forests of western Zimbabwe. Annual growth rings in *P. angolensis* can be identified on highly polished cross-sectional surfaces on the basis of the semi-ring porous tree rings; the reasonably continuous band of initial parenchyma; and by smaller changes in vessel diameter, wood density, and color from the early-wood to late-wood portion of the growth rings. Together, four lines of evidence indicate that these growth bands are annual: *P. angolensis* is strongly deciduous and the phenology of this species is tightly synchronized with the seasonality of rainfall in western Zimbabwe; the growth rings are semi-ring porous; ring-width time series are highly correlated between trees at a single forest location, and between forests separated by >100 km; and also because the mean ring-width chronologies derived from these trees are significantly correlated with regional rainfall totals during the wet season from 1901–1990. *P. angolensis* is one of the most valuable timber species in south tropical Africa, and the discovery of exactly annual growth rings will allow detailed analyses of the growth and yield under different ecological and management settings. It may also be possible to develop centuries-long tree-ring chronologies from *P. angolensis*, which would be useful for the reconstruction of past climate and streamflow. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Pterocarpus angolensis*; Annual growth rings; Dendrochronology

1. Introduction

Dendrochronology, or tree-ring dating, has been widely applied to climatic, ecological and forestry problems in the temperate latitudes where strong

seasonality in temperature and day length induce winter dormancy and annual ring formation in many trees. Dendrochronology has not been widely applied in tropical forests due to the extreme rarity of species that produce anatomically distinctive growth rings each year. The rarity of annual growth rings in tropical species reflects the lack of strong seasonality in temperature and day length. The absence of clearly iden-

*Corresponding author.

E-mail address: dstahle@comp.uark.edu (D.W. Stahle)

tifiable annual growth rings has also severely complicated the derivation of growth functions for most timber species in the tropics. However, the dramatic seasonality of precipitation in many tropical climates does induce annual rhythms in the physiology of many tropical species (e.g. Borchert, 1991), and a few tropical species that produce reliable annual growth rings have been identified [e.g. *Tectona grandis* in Java and Thailand (D'Arrigo et al., 1994; Pumijumnong et al., 1995); *Pinus merkusii* and *P. kesiya* in Thailand (Buckley et al., 1995); *Abies religiosa* (Huante et al., 1991), *Taxodium mucronatum* in Mexico (Stahle et al., in press); *Vitex keniensis* and *Premna maxima* in Kenya (Stahle et al., 1995)]. Annual growth rings have been reported for a few tree species in tropical Africa (e.g. Mariaux, 1975; Gourlay and Barnes, 1994). Grundy (1996) demonstrated annual ring formation and a growth response to rainfall for *Brachystegia speciformis* in Zimbabwe. Grundy's results are promising, but it must be recognized that they are based on young coppice stems <15 years old. Dendrochronological experience with tropical hardwoods, limited though it is, indicates that growth rings can be reasonably apparent on young trees with relatively large rings, but the anatomical landmarks may not be sufficiently distinctive to allow reliable identification of ring boundaries or exact calendar dating in suppressed or senescent growth (e.g. Stahle, in press). This is particularly true when the ring anatomy includes false rings, discontinuous rings, multiple parenchyma banding, or other complexities which are typical of tropical hardwoods (e.g. Detienne, 1989).

In this paper, we document the formation of reasonably distinct and exactly annual growth rings in *Pterocarpus angolensis* D.C. from Sikumi and Mzola forests, two indigenous forests in western Zimbabwe. This report will also describe the ecology, the minute anatomy of the wood, the climatic response of radial growth, and the relationship between age and diameter of *P. angolensis* at the two study sites. The discovery of annual growth rings in *P. angolensis* should be useful for dendroclimatic reconstructions of past climate in southern Africa, and the methodology we describe for the identification of annual growth rings should have a wide application for the evaluation of the growth and yield of *P. angolensis* under differing ecological and management settings.

2. The natural distribution of *P. angolensis*

Pterocarpus angolensis DC. (*mukwa* or African bloodwood) is a canopy species found in miombo woodlands, comprising one of the most important and widely used timber species in all of southern tropical Africa (Coates Palgrave, 1983). The species can be found growing naturally from sea level (Mozambican coast) up to 1650 m asl in parts of Tanzania (Fig. 1). In Zimbabwe, *P. angolensis* is found virtually in all the ecological zones except parts of the lowveld (grassveld) in the extreme north and south of the country. Our two study sites are on Kalahari sands with the woody vegetation dominated by *Baikiaea plurijuga* (Zambezi teak), *Brachystegia spiciformis* and, to a lesser extent, *P. angolensis*. *P. angolensis* is also found throughout the miombo region (i.e. those central, southern and eastern African woodlands dominated by the genera *Brachystegia*, *Julbernardia* and/or *Isoberlinia*) extending from Tanzania and southern Zaire in the north to Zimbabwe in the south, and across the continent from Angola through Zambia to Malawi and Mozambique (Campbell et al., 1996).

Over most of its range, mature undisturbed miombo is a closed deciduous woodland that is classified with savanna ecosystems but grades into seasonal dry forest at >1200 mm mean annual precipitation (Frost, 1996).

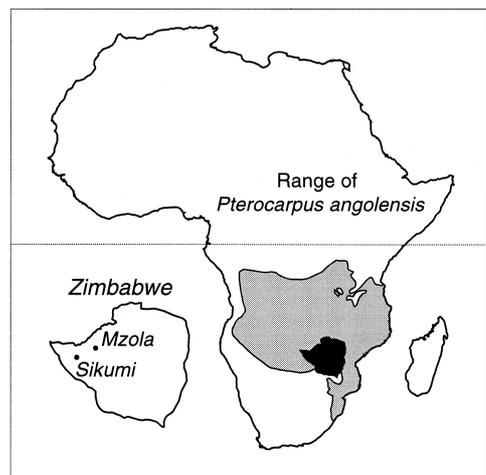


Fig. 1. The natural distribution of *P. angolensis* in southern Africa (after Coates Palgrave, 1983), and the location of the tree-ring chronologies from Sikumi and Mzola forests, Zimbabwe ($18^{\circ}32' S/26^{\circ}56' E$ and $18^{\circ}20' S/27^{\circ}40' E$, respectively).

More specifically, miombo woodlands fall within the southern sub-humid tropical zone of Africa receiving a mean annual precipitation of between 710 and 1365 mm and mean annual temperatures of 18.0°C to 23.1°C. More than 95% of annual rainfall occurs during a single 5–7-month wet season (October–April). Miombo woodland soils are generally acid, freely draining and have low cation exchange capacities, contain low nitrogen levels and little extractable phosphorus. Soil organic matter is also low except under densely wooded vegetation.

The miombo environment is quite stressful, and species such as *P. angolensis* have evolved distinctive adaptations to this setting. These include annual die-back-coppice cycles during an often protracted initial ‘suffrutex’ stage (i.e. the prolonged seedling stage with continuous root growth and annual shoot die-back, lasting an average of seven years; Boaler, 1966), and fire resistance after reaching the ensuing sapling stage. In fact, the conditions which control the composition of a miombo stand at any site are generally those that control the passage of plants from the suffrutex stage into the sapling stage. The suffrutex population in miombo woodland is often referred to as the ‘reserve forest’ because the proportion of suffrutices to larger plants of all the tree species is usually ca. 9 : 1.

The cause of seedling die-back in *P. angolensis* is not well explained, but it appears that this plant is investing more in underground growth during the early stages of life, like other miombo species of similar habit. This may ensure a large root system to exploit the scarce soil moisture resources. In general, it is postulated that, besides the large root system, the other major requirements for a suffrutex to graduate into a sapling include full light, absence of fire, absence of root competition, and adequate supply of mineral nutrients. Under favorable environmental conditions, *P. angolensis* can start flowering at the age of 20 years after reaching the sapling stage, and the trees can grow to 25 m in height and 1 m in diameter (Goldsmith and Carter, 1981).

3. Forestry and economic values of *P. angolensis*

As one of the canopy species of miombo and *Baikiaea–Burkea* woodlands on Kalahari sands,

P. angolensis possesses general indicator values. Because it is easy to work with, the wood is used for furniture, veneer, carving, joinery and as general purpose timber (Coates Palgrave, 1983). However, the importance of *P. angolensis* in Zimbabwe is in its use as a commercial timber species, well sought after by most logging concessions. The natural woodlands supporting adequate stocks of *P. angolensis* for industrial extraction are confined to the Kalahari sand areas of northwestern Zimbabwe and a few areas in north-central Zimbabwe. The growing stock has been diminishing as loggers increasingly harvest smaller trees in an attempt to satisfy expanding market demand. The distorted pricing of round timber and inappropriate inventory procedures are also acting against the sustainable management of *P. angolensis* populations throughout Zimbabwe.

4. Methods

Very large diameter cores (>5 cm in diameter) or partial cross sections with a transverse surface >5 cm are required for growth ring analysis of *P. angolensis* due to the complex anatomy and the occasional formation of extremely narrow or discontinuous growth rings. Wedge-shaped partial cross sections were obtained using ‘plunge-cuts’ with a chain saw from 14 living *P. angolensis* trees at Sikumi Forest in June 1996, and 39 cross sections were obtained at Mzola Forest from cut stumps and logs felled by a logging concession in March 1997. The Sikumi collection site was a single homogeneous stand of savanna-grown trees only covering some 5 ha. The Mzola collections were obtained from a much larger and ecologically more diverse area. All specimens were cut between 0.5 and 1.0 m above the ground level. These partial cross sections were generally 3–5 cm thick (in longitudinal dimension) and were allowed to air-dry prior to polishing. The cross-sectional surface of the specimens was mechanically sanded to an extremely high polish with progressively finer textures of sand paper (i.e. from 120, 240, 320, 400 grit, then finishing with 30, 15, and 9 µm sanding films). The polished surface was then buffed with 0000 steel wool to complete the preparation. The extremely fine polish achieved with these procedures is absolutely necessary in order to properly identify the anatomical features needed to

discriminate between annual growth rings in *P. angolensis*.

Standard dendrochronological techniques were used to cross-synchronize the time-series patterns of wide and narrow rings among trees at each collection site (i.e. cross-dating; Douglas, 1941; Stokes and Smiley, 1996). Ring-width cross-dating among separate trees at a single site, and across a larger region within a given climatic province, is a fundamental prerequisite for the development of tree-ring chronologies useful for paleoclimatic or ecological analysis. Cross-dating is possible only when some common macroenvironmental signal, such as seasonal rainfall, at least partially controls the radial growth of most trees in a particular forest or region.

Cross-dating is also a valuable tool for evaluating the possible annual nature of growth boundaries in tropical tree species because the multiple intra-annual bands—so common in many tropical species—are not necessarily synchronized with the seasonal cycle. Therefore, the variable widths of these intra-annual bands do not typically cross-synchronize in time among different trees. The existence of ring-width cross-dating among many trees for many years is a strong indication that the growth rings are indeed linked to the annual cycle. If cross-dating can be demonstrated, then the derived tree-ring chronologies can be compared with the annual records of climatic variability to help confirm the exact annual nature of the growth rings.

In this analysis, the polished sections of *P. angolensis* were cross-dated using the skeleton plot method (Douglas, 1941; Stokes and Smiley, 1996), and the dated ring widths were then measured on a stage micrometer with a precision of 0.001 mm. The measured ring-width time series (typically two radii per tree) were then submitted to the computer program COFECHA (Holmes, 1983) which uses correlation analyses to check dating and measurement accuracy. The exactly dated ring width time series were then submitted to the computer program ARSTAN (Cook and Holmes, 1985; Cook, 1985) in order to compute the tree-ring chronologies. The raw ring-width data are first standardized to remove long-term growth trend associated with the increasing size and age of the tree, and to remove differences in absolute growth rate due to micro-ecological and physiological differences among trees. In the standardization procedure, a

smooth growth curve is fitted with least-square criteria to the measured ring-width time series, and the standardized ring width indices are computed by dividing the measured ring-width value for each year by the value of the fitted curve for the same year [alternatives to division within the ARSTAN methodology include power transformation of the ring-width data before computing the indices as residuals from the fitted curve (Cook et al., 1992)]. The resulting time series of ‘standardized ring-width indices’ for each measured radius has a mean of ≈ 1.0 which is stationary over the entire length of the time series.

The ring-width indices of each radius from all trees can then be averaged together on a year-by-year basis to compute the mean index chronology for each study site (also called the final or standardized tree-ring chronology). A robust mean value function was used to compute the mean index chronology to minimize the influence of outliers on the derivation of the mean. The ARSTAN program also uses autoregressive modeling in order to compute a prewhitened or serially random mean index chronology [the ‘residual’ chronology, Box and Jenkins (1970), Cook (1985)], and a third mean index chronology with the average persistence structure of the component trees added into the prewhitened residual chronology [the so-called ARSTAN chronology, Cook (1985)].

Monthly rainfall totals have been compiled for a large climatically homogeneous region in southern and western Zimbabwe, northern South Africa, eastern Botswana and southern Zambia (i.e. ‘Region 60’, Nicholson, 1994). Correlation analyses between the Region 60 rainfall data and the mean index chronologies derived from Sikumi and Mzola were used both to demonstrate the exact annual nature of the growth rings in *P. angolensis* and to document the seasonality and strength of the climate response of this species.

5. Results

5.1. Annual growth rings in *P. angolensis*

There are four lines of evidence strongly indicating that the semi-ring porous growth bands evident on highly polished cross sections of *P. angolensis* are, in fact, annual growth rings. These four lines of evidence involve the phenology, ring anatomy, cross-dating,

and the correlation between the growth rings in *P. angolensis* and seasonal climatic data.

5.1.1. Phenology

P. angolensis is strongly deciduous during the annual dry season each winter (June–August). In fact, it is one of the most distinctly deciduous species in the entire miombo vegetation formation found in the unimodal rainfall region of south tropical Africa. The single wet season in Zimbabwe is associated with the southward migration of the Intertropical Convergence Zone (ITCZ) and the Zaire Air Boundary (ZAB) during the southern hemisphere summer (DJF; Tyson, 1986).

The phenology of *P. angolensis* is tightly synchronized with the seasonality of precipitation in western Zimbabwe (Coates Palgrave, 1983) and elsewhere (Boaler, 1963). Flowering and leaf flush occur during the spring (August–December). The distinctive circular seed pods are produced from summer into fall (January–April), and the leaves change color and are shed in late autumn and early winter (May–June). The fact that leaf fall begins earlier, and is more complete and prolonged, gives *P. angolensis* one of the strongest deciduous habits when compared to other species found in the dry forests of south tropical Africa.

This dramatic seasonality in flowering, leaf flush and leaf fall strongly suggests that radial growth is also restricted to the summer wet season (e.g. Borchert, 1991). This inference is supported by our observation that the growth ring corresponding to the 1995–1996 wet season was fully formed when the trees at Sikumi Forest were sampled on June 10, 1996, whereas the growth ring corresponding to the 1996–1997 wet season was not yet completely formed when the recently cut logs and stumps at Mzola were sampled at the beginning of March 1997.

Boaler (1963) also reported strict seasonality of radial growth for *P. angolensis* in Tanzania based on dendrometric studies over nearly three years. These inferences, concerning the seasonality of radial growth and annual ring formation, are strongly substantiated by the anatomical, cross-dating, and climatic evidence presented below, but the exact seasonal timing of radial growth in Zimbabwe and elsewhere should be further documented with dendrometers or other studies of cambial activity.

5.1.2. Ring anatomy

Growth ring boundaries in *P. angolensis* trees from Sikumi Forest are reasonably distinct (Fig. 2–Fig. 3(A)) and can be discriminated by the semi-ring porous structure of the vessels, a fine line of initial parenchyma, and by slight differences in vessel diameter, wood density, and color from the beginning to end of the growth band. The relatively large-diameter vessels that congregate near the beginning of the annual growth band are mostly solitary but less frequently are found in radial clusters of two to four cells (Figs. 2 and 3(A)). Additional details of the minute anatomy of *P. angolensis* are described in Fig. 3 (A–G).

Unfortunately, the initial vessels are not continuously present around the margin of the growth rings, which greatly complicates ring identification, particularly on small diameter increment cores (ca. 5-mm diameter). In fact, the growth rings in *P. angolensis* are often more easily identified at lower magnification (i.e. macroscopically at 10–20 \times) because of the discontinuous formation of large vessels in the early-wood. Another complication concerns the presence of smaller vessels in the late-wood which are often associated with discontinuous tangential bands of light-colored axial parenchyma cells, which are parallel to and mimic the true ring boundaries (Fig. 2). In spite of these complications, the semi-ring porous nature of the growth rings in *P. angolensis* is consistent with the anatomical structure of rings in other species known to produce annual growth bands in tropical and temperate forests.

5.1.3. Cross-dating

The fact that the patterns of wide and narrow growth rings can be cross-synchronized among all trees at Sikumi and Mzola forests over the entire life span of the tree (i.e. ‘cross-dating’) is very strong evidence that the growth rings are, in fact, distinctly annual. To further document this growth correspondence among trees, the visually cross-dated ring widths were measured precisely to 0.001 mm, and the time series of standardized ring widths were correlated among all trees at each site. The correlation matrix computed at Sikumi Forest indicates that the average correlation between ring-width time series from individual trees is $r = 0.56$, ranging from a low of $r = 0.40$ to a high of $r = 0.87$ (all are significant at $p < 0.05$). The average

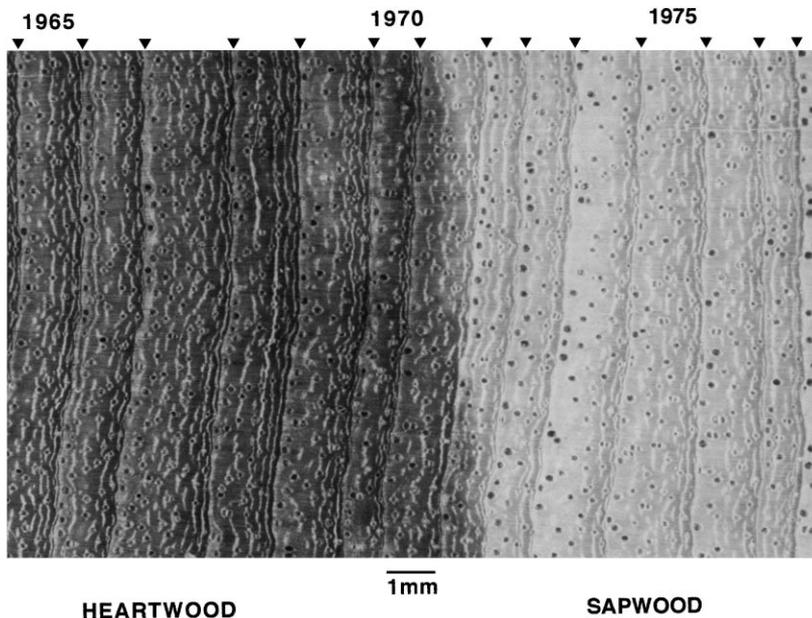


Fig. 2. The highly polished cross-sectional surface of a *P. angolensis* tree from Sikumi Forest (specimen SIK13A). This example dates from just before 1965 to 1978, and the annual ring boundaries are indicated by the marks above the photograph. Radial growth advanced from left to right, and the annual rings can be discriminated by the relatively large-diameter vessels which tend to concentrate near the beginning of the growth ring (i.e., semi-ring porous). A light-colored zone of initial parenchyma cells is also evident at the beginning of most growth rings, and, when coupled with the darker color and higher density of fibers in the late-wood zone, helps to identify the annual rings. This particular specimen exhibits rather open growth with good separation between the annual rings. However, the narrow growth rings of old or suppressed growth can be much more difficult to identify. The color change near the center of this image marks the heartwood : sapwood transition.

correlation among trees at Mzola forest is $r = 0.49$, with a range from $r = 0.23$ to 0.88 . The high degree of agreement between the ring-width time series from Sikumi Forest are illustrated in Fig. 4. The individual ring-width time series were averaged into a mean index chronology dating from 1876 to 1996 at Sikumi, and from 1873 to 1997 at Mzola (Fig. 5).

The ring-width correlation between trees provides strong evidence for the annual nature of the growth rings at Sikumi and Mzola forests because the radial growth banding in species not strongly synchronized to the annual cycle is rarely consistent around the circumference of the tree, and the widths of these bands are rarely correlated among different trees. The correlation of century-long ring width-time series between trees at both Sikumi and Mzola suggests that a common stand-wide environmental factor tied to the annual cycle is strongly influencing growth, probably regional climate variability. This inference is supported by the significant correlation between

the mean index chronologies derived at Sikumi and Mzola forests (Fig. 5), which are separated by over 100 km.

5.1.4. Correlation between tree growth and climate

To document the influence of regional rainfall on the radial growth of *P. angolensis*, monthly precipitation totals computed for the Nicholson (1994) 'Region 60' were correlated with the Sikumi and Mzola mean index chronologies for each month of a 24-month period straddling the *P. angolensis* growing season (Fig. 6). Sikumi and Mzola forests are not centrally located within Region 60, but this comparison is nevertheless sufficient to document the strong rainfall response of *P. angolensis*. Both the chronologies are significantly correlated with monthly rainfall only during the heart of the wet season (December–February, DJF), although the Mzola correlation with the month of February only achieves significance at the 0.10 probability level. Both the chronologies are also

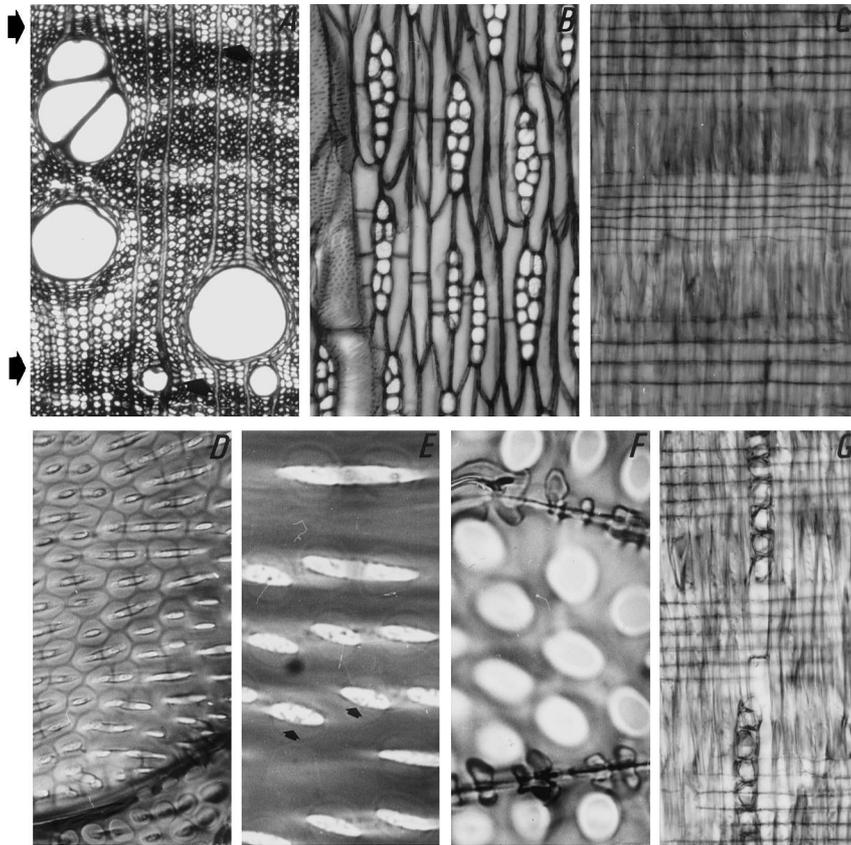


Fig. 3. The minute anatomy of *P. angolensis*. (A) This image illustrates one complete annual ring with early-wood near the bottom and late-wood near the top. Growth ring boundaries are indicated by a fine zone of initial parenchyma (see arrows in A), and by small changes in vessel diameter, wood density, and color. The semi-ring porous structure is often best imaged at low magnification (e.g. Fig. 2), and the vessels are mostly solitary or less frequently in radial clusters of up to four cells. The solitary vessels are round and outlined. (B) The tangential surface illustrating the uni- and biseriate rays with storied structure. (C) The radial surface showing heterogeneous rays composed of procumbent cells. (D) Alternate intervessel pits with polygonal shape. (E) Intervessel pits showing outgrowths (or vestures) in the pit cavity (arrows). (F) The pronounced nodular structure of the radial parenchyma end walls. (G) Short-chain prismatic crystals observed in the chambered axial parenchyma cells. The intervessel pits are alternate, round in outline, with elliptical included aperture, small and vested. Vessel-to-parenchyma pitting is distinctly bordered and similar in size and shape to the intervessel pits. No striations were observed on the walls of the vessel elements. Deposits were seen in the heart-wood vessels. An average of five vessels per mm² were counted. Perforation plates simple in the oblique-to-horizontal end walls. Fibers are thin-to-thick walled, short, with minutely bordered pits mainly distributed in the radial walls. Parenchyma is in tangential bands of three or more cells wide, and in terminal strings, which are distinct in cross section and sometimes on the tangential. Two parenchyma cells were observed per strand. The radial system includes heterogeneous and homocellular types. Rays are uniseriate, and rarely biseriate or locally biseriate, and are composed exclusively of procumbent cells. Rays are 0.15 mm high, and there are 12 or more rays per mm. All rays are storied.

significantly correlated with seasonalized rainfall totals for the wet season (DJF) in Region 60 for the period 1901–1990 [$r = 0.55$, $p < 0.001$ for Sikumi; $r = 0.34$, $p < 0.01$ for Mzola (see Fig. 7 for a scatter plot and Fig. 8 for a time-series plot of the Sikumi link to rainfall)]. These correlations for wet-season rainfall in Region 60 account for some 10–30% of the variance

in the Mzola and Sikumi chronologies, respectively, and other factors such as a fire, herbivory, and insect pests also influence the radial growth of *P. angolensis*. However, the strong coherence of growth among trees within and between sites (e.g. Figs. 4 and 5) indicates that the rainfall influence on growth is probably stronger than suggested by the correlations with

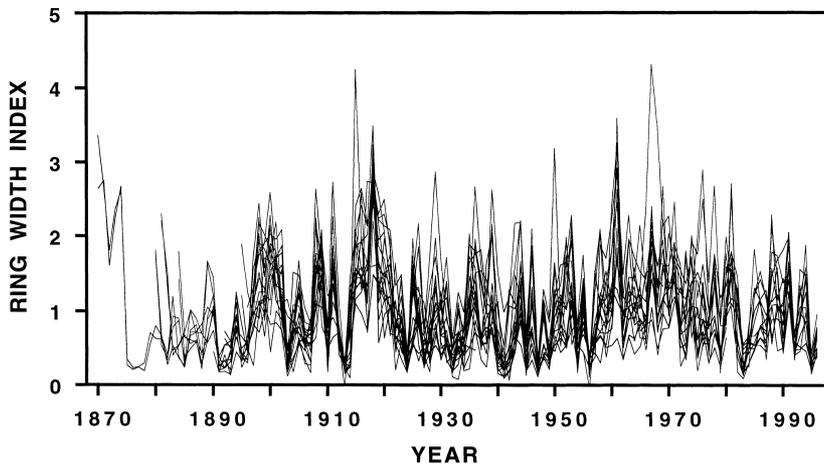


Fig. 4. Synchronized time series of annual ring width measurements of 10 exactly dated *P. angolensis* trees from the Sikumi Forest, Zimbabwe. These ring-width series have been detrended and standardized to remove trend in the mean due to the increasing age and circumference of the trees over time (Fritts, 1976). The striking correlation of ring-width variations between these trees provides strong evidence for the annual nature of the growth rings in this species, and reflects the common stand-wide influence of wet and dry years on the growth of these trees (e.g. Figs. 6–8).

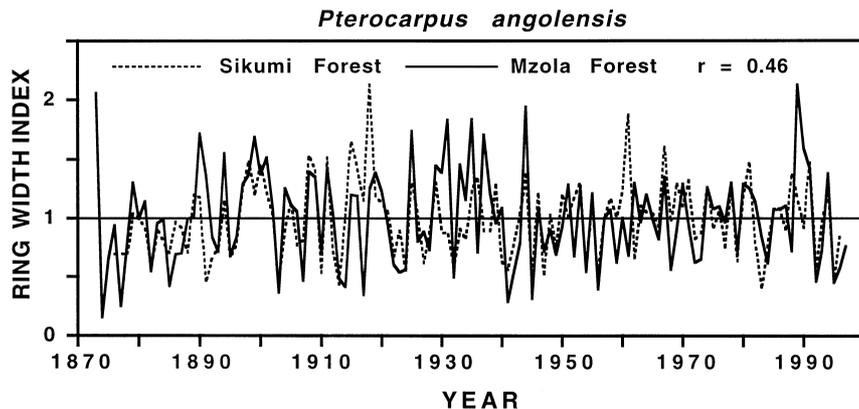


Fig. 5. The mean ring width chronologies of *P. angolensis* for Sikumi (1876–1996) and Mzola forests (1873–1997), computed as the robust mean value function of the detrended and standardized ring-width measurement time series (both series have been prewhitened to remove low-order autocorrelation). The two chronologies are significantly correlated over the 121-year common period ($r = 0.46$; $p < 0.0001$, for 1876–1996), even though they were derived from trees separated by more than 100 km.

Region 60 data, but this cannot be tested without representative rainfall data more proximate to the sample sites.

These analyses demonstrate that the radial growth of *P. angolensis* is significantly correlated with monthly rainfall amounts only during the wet season (DJF), which is entirely consistent with the phenological evidence for flowering and leaf flush from

August to December (before and during the onset of the rains), and for leaf fall in May–June (following the cessation of the wet season). These monthly rainfall correlations confirm the annual nature of the growth rings in *P. angolensis* and quite logically underscore the critical importance of wet-season rainfall amounts to the physiology and timber production of *P. angolensis* in western Zimbabwe.

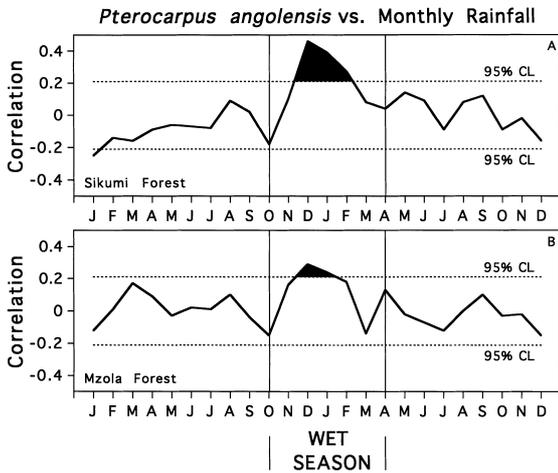


Fig. 6. Correlation coefficients computed between the *P. angolensis* tree-ring chronologies from the Sikumi (A) and Mzola (B) forests and monthly precipitation totals for the Nicholson (1994) Region 60, which covers much of Zimbabwe and portions of adjacent countries. Note the significant correlations with December, January, and February rainfall during the height of the wet season and concurrent with the formation of annual rings in *P. angolensis*.

5.2. Diameter growth of *P. angolensis*

In order to investigate diameter growth trends in *P. angolensis*, the cumulative ring-width data are plotted

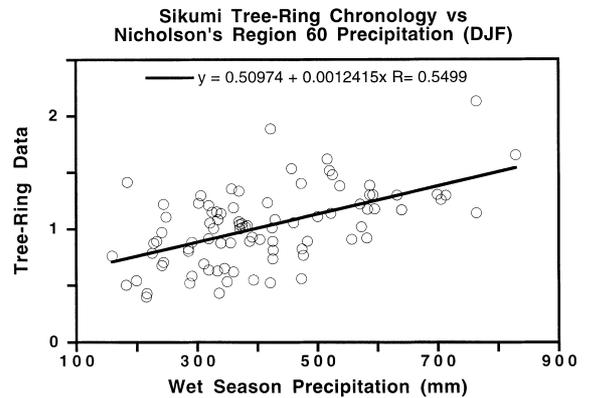


Fig. 7. Scatter plot comparing wet season (DJF) total precipitation for the Nicholson (1994) Region 60 with the tree-ring chronology of *P. angolensis* from Sikumi Forest for the period 1901–1990 ($r = 0.55$; $p < 0.0001$).

for 10 trees from the Sikumi Forest and 14 trees from Mzola Forest (Fig. 9(A and B)). In this analysis, the exact calendar dating of each growth ring is not important; instead, the ring-width data are accumulated—beginning with the pith ring and ending with last complete ring formed before bark. Therefore, the abscissa in Fig. 9 represents growth increments of the same physiological age for all available trees, and these radial growth curves (i.e. ‘cumulative stump

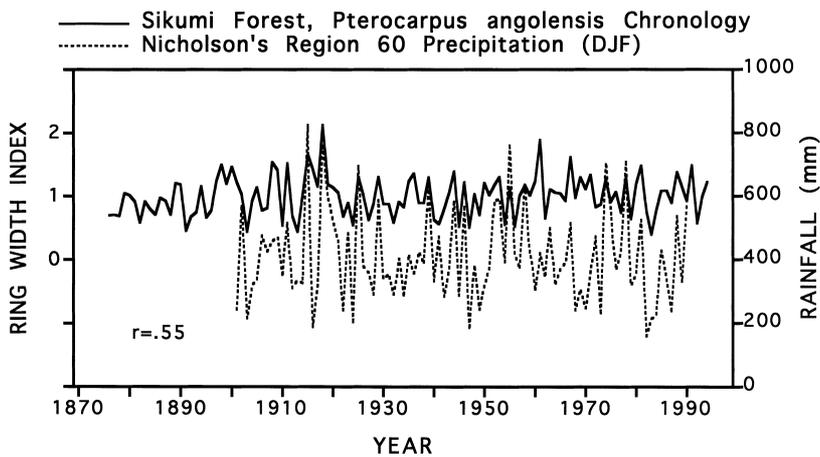


Fig. 8. The time-series correlation between the *P. angolensis* tree-ring chronology from the Sikumi Forest (solid line for 1876–1996; mean = 1.0) and wet season total precipitation for Nicholson’s (1994) Region 60 (dashed line for 1901–1990; mean = 409 mm). The calendar year for the tree-ring and rainfall data is designated at the end of the wet season (i.e. the 1995–1996 wet season and the growing season are both indicated as 1996). Note the reasonably strong agreement between this single *P. angolensis* chronology from western Zimbabwe and the large-scale average rainfall series.

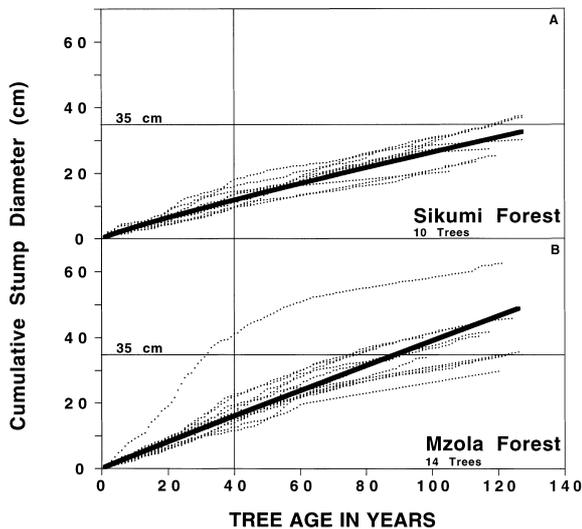


Fig. 9. The relationship between age and cumulative stump diameter for sample trees from the Sikumi and Mzola forests, Zimbabwe (see Eqs. (1) and (2)). Stump diameter refers to the stem diameter at ≈ 50 – 100 cm above the ground. The ring width data from a single radius per tree were first doubled to approximate diameter, and these diameter increments were then accumulated from the pith to the bark ring. The abscissa represents the same physiological age for each sample tree. In the few cases where the available cross section did not extend to pith, the true position of the pith ring and the width of the first five growth rings had to be estimated from the curvature and growth rate of the 10 innermost rings. The Zimbabwe Forestry Commission historically has set the minimum harvestable diameter of *P. angolensis* at 35 cm DBH, which would be achieved only after an estimated 137 years on average at Sikumi, and after 88 years on average at Mzola, once the saplings emerge from the suffrutex stage.

diameters') are described by the following power functions:

$$\text{Sikumi : } y = 4.7354(x^{0.873}); \quad R^2 = 0.90 \quad (1)$$

$$\text{Mzola : } y = 4.5072(x^{0.969}); \quad R^2 = 0.73 \quad (2)$$

where y is the cumulative stump diameter (mm) and x the tree age in years.

Fig. 9 provides an interesting insight into the radial growth of *P. angolensis* at these two locations, with important implications for timber management. First, the growth rate of *P. angolensis* is quite slow in the available trees from both these locations (the average stump diameter at 40 years of age was only 11.8 cm at Sikumi and 16.5 cm at Mzola, Fig. 9(a and b)). The more rapid growth rate at Mzola might partially reflect

the higher mean annual rainfall [some 700 mm compared with some 600 mm at Sikumi (Department of Meteorological Services, 1984)].

The minimum harvestable size of *P. angolensis* in Zimbabwe was set by the Forestry Commission early in the 20th century at ≥ 35 cm diameter at breast height (DBH), based on the size distribution of *P. angolensis* from a sample block in the Gwayi Forest Reserve. The power functions fit to the cumulative stump diameters indicates that on average it will take an estimated 137 years beyond the suffrutex stage to achieve this harvestable size for the 10 Sikumi trees, and some 88 years for the 14 Mzola trees. These results would suggest that the arbitrary 35 cm DBH size minimum requires a long rotation period, but has little to do with the age structure or stand dynamics of these indigenous *P. angolensis* forests in western Zimbabwe.

There is also appreciable variability in the growth rate of sample trees at both these locations, but particularly at the Mzola Forest where one tree achieved 35 cm DBH after only 32 years (Fig. 9(b)). At age 40, there was some 8 cm difference between the largest and smallest diameter trees in the Sikumi sample, and some 30 cm difference in the Mzola sample. If the single fast-growing individual at Mzola is omitted from this comparison, there is still a 12 cm difference in the stump diameters after 40 years at Mzola.

These observations of radial growth in the unmanaged *P. angolensis* samples suggest sizable differences in the microsite conditions and/or genetic potential of individual trees at Sikumi and Mzola. It should be noted that diameter-based selection (e.g. ≥ 35 cm DBH), coupled with highly variable growth rates, could result in preferential cutting of individuals with the highest rates of growth and may genetically impoverish the growing stock. Our results suggest that careful studies of tree age, size, and environmental conditions could produce useful volume and yield tables for specific ecological settings, and may lead to improved management of this important species.

From a dendrochronological perspective, Fig. 9 does not indicate any pronounced leveling-off of diameter growth with age, even though most trees exceed 100 years in age. This suggests that under natural conditions *P. angolensis* may live for 150 years or more (see also van Daalen et al., 1992). The Boaler

(1966) analyses suggested that *P. angolensis* may only live for ca. 100 years in his Tanzanian study area. But we have recently obtained a *P. angolensis* sample cut from a logging concession in western Zimbabwe that has 205 annual growth rings, suggesting that the longevity of this species may be quite dependent on ecological factors as well as human disturbance.

6. Managing disturbance in *P. angolensis* populations

As already pointed out, *P. angolensis* is a canopy species in miombo. There can be considerable heterogeneity in tree height, canopy cover, and herbaceous structure in miombo woodlands, thus reflecting the variation in soils and the impacts of fire, land use, herbivory, and other disturbances (Frost, 1996). Such episodic disturbances are capable of distorting what the plant demographer or forest manager may want to consider as the 'normal' size distribution patterns of different species. For instance, Mushove (1996) reported inverse-J size distribution curves for *P. angolensis* in Zimbabwe's Fuller and Mafungabusi forests but a bi-modal curve for the Gwayi Forest. In the 'anomalous' Gwayi curve the 'sapling' category (DBH interval of 2.6–15.0 cm) was not represented. Did that 'gap' in the curve mean that sometime in the history of that forest there had been an approximately 30-year period of zero germination (assuming an annual diameter growth rate of 4 mm)? Or could it be that there were years during which germination took place but the seedlings and/or saplings were completely or partially destroyed by fire, drought, or animals?

Dendrochronological evidence may provide clues to the mystery of the missing age group at the Gwayi Forest. Tree-ring data from the older trees in Gwayi could indicate drought years with very low growth and, therefore, poor germination or very low survival among the suffrutices. Exact dating of the time interval involved in the reproduction gap would also permit a rescheduling of the harvesting plan for Gwayi Forest in order to take into account the specific temporal gap in the growing stock.

Forest fires have historically constituted an important aspect of the ecosystem in many parts of the world. Species such as *P. angolensis* evolved under a

fire ecology and have developed adaptive strategies that provide direct protection against the negative effects of fire. During a fire, the extent of damage to the crown (i.e. the assimilating organ) will force the cambium to react in a particular way even if the fire occurred at a time when the cambium was 'dormant'. That cambial reaction is imprinted in the resultant tree-ring pattern. Extreme heating of the tree trunk often causes callus tissue or other traumatic growth reactions which can be identified in annual rings formed near the site of the trauma. In the case of *P. angolensis*, the red kino which gives the species its name (bloodwood) may be deposited in the vessels during the year of fire damage. The most obvious effects of damage by fire, however, are the scars that the fire creates when heat locally kills the cambium. In this way, dendrochronology can be used to date past forest fires (e.g. Madany et al., 1982) which can help determine the proper frequency of prescribed fire in forest management programs.

Traditionally, infestations by insects have been regarded primarily from the economic point of view because dying trees, reduced growth, increased risk of disease, and delays in producing new shoots all have adverse effects on profits. However, it is now realized that many of the so-called harmful insects play a part in the ecological cycle and they may have an important influence on forest structure and growth. A valuable contribution of tree-ring research to the forest entomologist is the dating and measurement of past insect impacts on forest growth (Swetnam and Lynch, 1989). Most defoliating insects do not develop in short, regular cycles, and even in a bad infestation not all trees of one species are attacked. Nevertheless, defoliation events can often be identified in the annual tree rings. If a comparison can be made with ring patterns in trees which have not been attacked (or with resistant varieties or species) it may be possible to attribute any reduction in growth in the host tree to insect damage.

Fungal infections find entry points whenever tree crown, trunk or roots are damaged. If an infection sets in, the tree normally begins to form a barrier to stop the infection from spreading (the process referred to as compartmentalization). Although the fungi may cause discoloration, the tree normally succeeds in minimizing damage by the blocking mechanism offered by annual ring boundaries, for instance. Through careful tree-ring studies, therefore, the phytopathologist can

identify and date fungal attacks. This technique may be relevant to the *P. angolensis* stands in Zimbabwe where *Fusarium* spp. have been singled out as one of the factors causing *P. angolensis* decline or die-back.

7. Conclusions

The identification of annual growth rings in *P. angolensis* from western Zimbabwe has important implications for the forest ecology and management of this valuable timber species, and for the reconstruction of past climate and streamflow. Annual growth rings provide a solid basis for age determination of *P. angolensis* growing under different ecological conditions, or under different management prescriptions. Accurate age data should allow development of improved growth and yield tables. The techniques for wood preparation and ring identification we outline require familiarity with wood anatomy in general, and with *P. angolensis* wood in particular. Tree-ring specimens with a cross-sectional surface of at least 5 cm are crucial for an exact dendrochronological analysis. But, once the anatomical features of the annual rings in *P. angolensis* are well known, it should be possible to obtain simple age estimates within 5 or 10 years of the true age from careful examination of highly polished 5-mm diameter cores obtained with a Swedish increment borer. These techniques are far simpler and less expensive than the radiometric methods outlined by van Daalen et al. (1992) for the age determination of *P. angolensis* in South Africa. However, we stress the vital importance of proper specimen preparation to allow accurate identification of the anatomical landmarks that separate the annual growth rings in *P. angolensis*. And when exact age determinations are required, there is no substitute for dendrochronology.

Tree-ring chronologies of *P. angolensis* have a simple response to total precipitation during the wet season which will be useful for the reconstruction of past climate and streamflow provided that longer chronologies can be developed. We have documented one *P. angolensis* over 200 years old from western Zimbabwe, and *P. angolensis* has been historically used for dugout canoes, implements, furniture, and construction throughout its native range. We are optimistic that future sampling of living trees and historic

wood will provide a valuable network of precipitation-sensitive tree-ring chronologies of *P. angolensis* covering south tropical Africa, useful for the reconstruction of past precipitation, streamflow, and the episodic impact of the El Niño/Southern Oscillation.

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