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ORIGINAL PAPER

# Dendrochronological potential of *Millettia stuhlmannii* in Mozambique

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**Abstract**

***Key message*** **This study demonstrates that *Millettia stuhlmannii* produces annual growth rings responsive to seasonal climate and should be useful for dendrochronology.**

*Abstract* *Millettia stuhlmannii* is a highly valuable and potentially overexploited timber species indigenous to southeastern Africa. It is of particular economic importance in Mozambique though relatively little is known about its growth rate or response to climate. This study investigates whether *M. stuhlmannii* is potentially useful for dendrochronology—that is whether this species forms annual growth rings that are responsive to external forcing such as climate. Five methods were used to determine whether *M. stuhlmannii* growth rings are indeed annual in nature, including analysis of ring anatomy, dating trees of known age, cambial wounding, classical cross-dating, and comparison of annual growth to climate variables. Growth rings of *Millettia stuhlmannii* are distinct and well formed, young trees from plantations of known age formed an appropriate number of distinct annual rings, trees showed distinct wood reaction to cambial wounding, adding exactly one complete ring in one calendar year, cross-dating within and between trees was somewhat successful, and annual growth is significantly correlated with wet season precipitation. Results of this study indicate that *M. stuhlmannii* is a potentially useful species for dendrochronology. These findings should allow a better understanding of this species' growth dynamics and ecology, as well as its response to climate variability in the past and potentially to future climate change.

**Keywords** *Millettia stuhlmannii* · Dendrochronology · Annual growth rings · Tropical forest · Mozambique · Panga-panga

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## Introduction

Tree rings have been widely used in temperate latitudes for the study of a variety of topics in forest ecology as well as for reconstructing the spatial and temporal variability of relevant climate factors. Until fairly recently, comparatively few dendrochronological studies have been carried out in tropical regions (e.g., Worbes 2002; Rozendaal and Zuidema 2011). In tropical Africa, only a handful of native species have been shown to form annual growth rings that are suitable for dendrochronology (e.g., Belingard et al. 1996; Stahle 1999; Fichtler et al. 2004; Trouet et al. 2001, 2006, 2010; Groenendijk et al. 2014), and to date only one species has been utilized for climate reconstruction (e.g., Therrell et al. 2006).

This study examines the dendrochronological potential of *Millettia stuhlmannii* (Taub.) a drought-deciduous tree that is abundant in Mozambique and portions of Tanzania, and can also be found in Zimbabwe and South Africa. *M. stuhlmannii* is a member of the Fabaceae family, Papilionoideae subfamily. It is also known as panga-panga

(Portuguese, English and French), jambirre (Portuguese), partridge wood (English), mpangapanga, and mpande (Swahili). It is a medium size tree (growing up to 20 m in height). Leaf drop occurs during the dry season (July–Oct), and leaf flush occurs immediately before flowering (Nov–Jan; Coates-Palgrave 2002).

The timber of this species is highly valued though not as widely available in the world market as the related species *M. laurentii* (Wenge). It is ranked as a *first class* commercial timber in Mozambique, where it is widely used for furniture, flooring, veneer and decorative construction (Marzolli 2007; Ali et al. 2008). In South Africa, panga-panga roots are commonly used by traditional healers for medicinal and for religious purposes (Tshisikhawe et al. 2011). Panga-panga, along with many other tropical timber species, is frequently overharvested in Mozambique and sustainable management of the species is urgently needed for the continued utilization of this resource (Mackenzie 2006). For example, overharvesting of *M. laurentii* has resulted in its classification as endangered by the IUCN (2012). Demonstrating that panga-panga produces annual rings will allow for long-term analysis of growth rates that can inform sustainable management of the species.

We used several basic methods to determine the nature of the growth rings of panga-panga including examining the microanatomy of ring formation; counting the number of rings on samples from plantation trees of known age; performing "cambial marking" experiments by wounding sample trees and then harvesting them 1 year later to study the formation of growth rings over that time; cross-dating the pattern of wide and narrow rings on multiple cross-sectional samples; and comparing a chronology of annual ring growth to climate factors such as monthly and seasonal precipitation.

## Materials and methods

### Study site

This study was performed at the Catapú forest concession, managed by TCT Dalmann Furniture Lda. The concession is located in the Sofala province, at S18°00′05″ and E35°08′13″, and extends over an area of ca. 25,000 Ha (Fig. 1). This concession has been operating in Mozambique since 1996, extracting about 2,300 $m^3$ of timber (primarily panga-panga) per year. It is one of the few Forest Stewardship Council certified logging concessions in Africa (FSC certification number SGS-FM/COC-2421), and currently the only one in Mozambique. The concession is located on the eastern side of the rift valley where elevation varies from 50 to 200 m above sea level. Soils in this region are generally developed in deep sands with occurrences of conglomeratic sandstones cemented by calcic-argillaceous rock (Mozambique National Directorate of Geology 2006).

The forest vegetation of the concession is classified into three major groups: dry deciduous forest, dry deciduous thicket and woodland. In addition to *M. stuhlmannii*, dominant tree species are *Adansonia digitata*, *Afzelia quanzensis*, *Balanites maughamii, Berchemia discolor, Bivinia jalbertii*, *Bombax rhodognaphalon*, *Celtis mildbraedii*, *Cordyla africana*, *Fernandoa magnifica, Milicia excelsa*, *Morus mesozygia, Sterculia appendiculata, Terminalia sambesiaca* and *Xylia torreana* (Coates-Palgrave et al. 2007).

The climate of the study site is tropical and is characterized by two distinct seasons, one warm and rainy with 80 % of the annual total rainfall, and the other relatively cool and dry. The rainy season lasts for about 4–5 months (November through March). Mean annual rainfall ranges from 700 to 1,400 mm, although from 2003 through 2007 rainfall barely exceeded 500 mm during the rainy season (Fig. 2). The maximum monthly rainfall normally occurs in January followed by February and December, with October being the driest month. The seasons differ in average temperature by ca. 7 °C.

### Sample collection and preparation

Partial cross-sections of panga-panga were collected from felled trees in both a plantation of known age trees as well as a mature forest during the logging seasons (ca. June) of 2007 through 2010. Cross-sections rather than increment cores were used due to the complex anatomy of tropical species and frequent occurrence of wedging and false rings (e.g., Stahle 1999; Worbes 2002; Brienen and Zuidema 2005). Partial cross-sections were obtained from about 0.25 to 0.5 m above the ground level using a chainsaw and all samples were then labeled and georeferenced to allow for FSC auditing. A total of twenty-five partial cross-sections were collected from the natural forest from mature trees of at least 40 cm diameter at breast height (DBH), which is the minimum legally allowable DBH for commercial harvest. Partial rather than full cross-sections were collected to facilitate transport.

### Anatomical analysis

All samples were processed using conventional methods (e.g., Hoadley 1990; Schweingruber 1996, 2007) and each ring boundary was marked under the microscope and counted from the outermost to the innermost ring to determine the age of each tree and allow cross-dating. To examine the ring microanatomy of *M. stuhlmannii*, microtomes were used to prepare micro-sections (ca. 20 µm

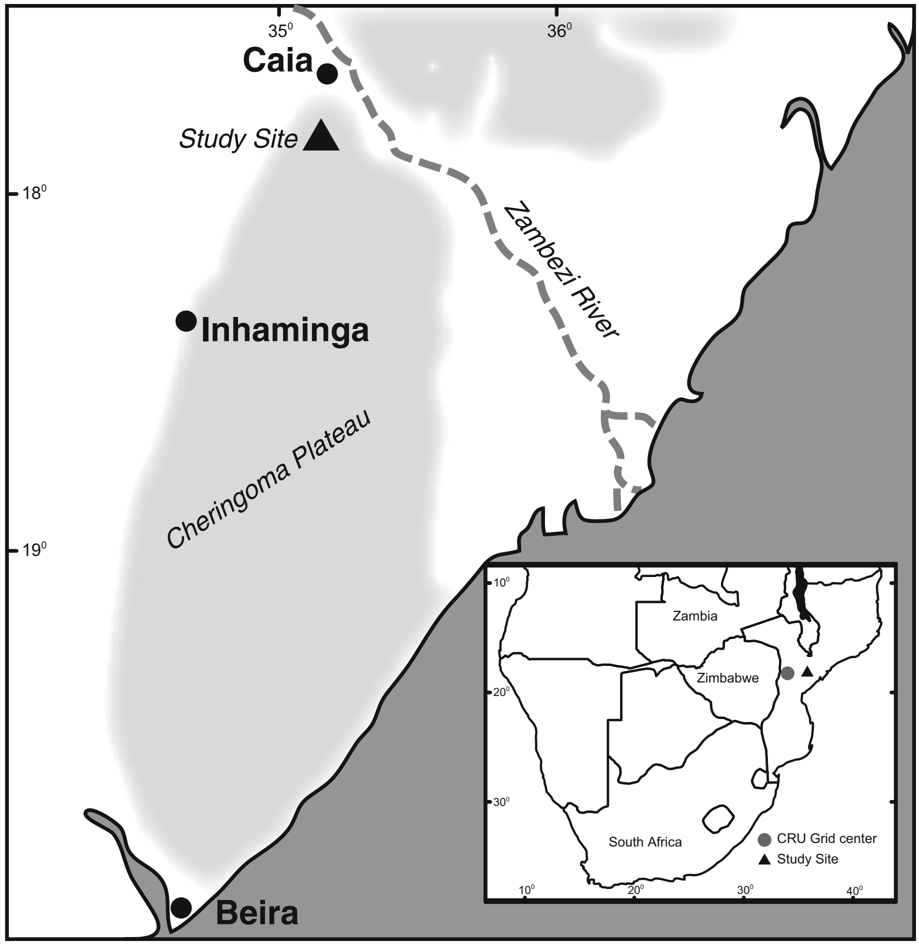


**Fig. 1** The study site is located about 150 m a.s.l. at the northern end of the Cheringoma Plateau in the Sofala province of Mozambique, about 30–40 km south of the Zambezi River. Floristically the study area falls within the Swahilian/Maputaland Regional Transition Zone. Forest and thicket in the study area form part of the Coastal Forests of East Africa Hotspot, one of 34 ecoregions of global conservation significance (Coates-Palgrave et al. 2007)

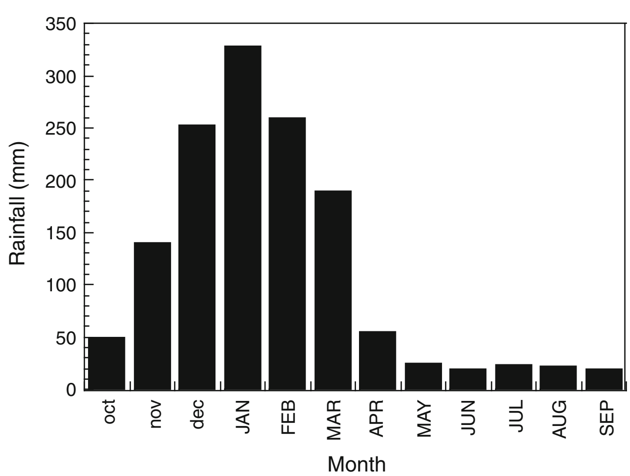


**Fig. 2** Average monthly rainfall totals from previous October to current September in central Mozambique obtained from grid point (S18°00′00″ and E33°45′00″) from 1901 to 1996 (*lower case letters* indicate months of previous calendar year). Over 80 % of annual rainfall typically occurs between November and March (Hulme 1992, 1994)

thick) of wood (1 × 1 × 1 cm—transversal, radial and tangential, respectively).

## Study of plantation trees

Ring counting of trees of known age is one method used to determine the annual nature of tropical tree rings (Worbes 1995). To use this method, it is necessary to obtain the exact date in which the trees were planted to accurately determine age. Twelve cross-sections were collected in June 2009 from the plantation site, which was planted in 1997 following a large forest fire. The plantation is located about 5 km from forest sample sites and plantation trees are planted approximately 2–3 m apart. Young plantation trees were used to prove the annual nature of panga-panga rings but were not included in the final chronology.

## Cambial wounding

The cambial wounding technique was first developed by Mariaux (1967) to study the cambial periodicity of

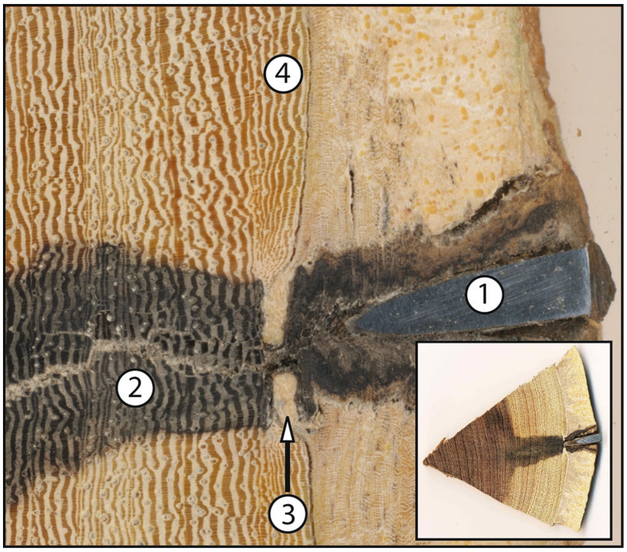


**Fig. 3** Photograph showing cambial wounding sample extracted from tree stem (*inset*) and enlarged area of wood reactions to pinning including: *1* pin (nail) used to mark cambium and wound canal, *2* area of wound compartmentalization indicated by oxidized sapwood parenchyma cells, *3* parenchymatous wound tissue, and *4* new xylem formed following pinning. Direction of growth is *left* to *right*

broadleaved species in Africa. This method consists of deliberately injuring the cambium by inserting a pin through the bark to the xylem and forcing a subsequent wound response in the tree that can be exactly dated (Mariaux 1967; Seo et al. 2007). A cambial wounding experiment was carried out on a total of nine mature panga-panga trees from the natural forest in June 2008 during the dry season when the cambium was dormant. Each tree was wounded by inserting a common nail at ca. 30 cm above the ground level. After 1 year (June 2009), all cambial wounding samples were collected by cutting wedge-shaped blocks from the living trees with a chainsaw prior to felling for harvest. Samples were dried naturally and small subsamples, 1 cm thick, were cut and sanded to make the wound visible (Fig. 3). Growth layers were counted from the wound tissue to the bark and each ring was measured to estimate the mean annual increment of trees after cambial disturbance.

Growth ring dating

All cross-section samples from mature trees were visually inspected and when possible, cross-dated by matching patterns of wide and narrow rings using the skeleton plot method (Douglass 1941; Stokes and Smiley 1968). After visual cross-dating, annual rings were measured on a Velmex "TA" stage micrometer to a precision of 0.001 mm. Cross-dating and measurement accuracy were verified using the dendrochronology program library (dplR) in the "R" software environment (Bunn 2008, 2010). The dplR was also used to detrend raw ring width measurements to remove non-climatic growth trends. Each series was double detrended using a negative exponential curve or linear regression of any slope. Detrended series were averaged together to form an index chronology for the site that was subsequently used for climate response analysis.

Climate and growth

Many studies have shown that climate influences tree growth in various regions of the tropics (Rozendaal and Zuidema 2011). Different factors can induce the formation of annual tree rings in the tropics: seasonal rainfall variation (Worbes and Junk 1999), seasonal day length variation (Borchert and Rivera 2001), temperature variations (Fichtler et al. 2004) and even annual flooding (Schöngart et al. 2006). In tropical regions, precipitation is most frequently the limiting climate factor for tree growth and dry periods of at least 2–3 months with precipitation of less than 60 mm per month induce stress on trees resulting in leaf drop and consequently cambial dormancy (i.e., ring boundary formation; Worbes 1995). Response function coefficients between the site chronology and monthly and seasonal rainfall were derived using the *bootRes* package (Zang and Biondi 2012) in the dplR library (Bunn 2008, 2010).

Monthly precipitation data based on a 2.5° × 3.5° grid were obtained from the CRU global gridded dataset (1900–1996; Hulme 1992, 1994; Fig. 1). Response function analyses were performed between the panga-panga chronology and monthly precipitation data from October ($t-1$) prior to the growth year to September ($t$) of the current year of growth. The previous October was chosen as the first month in the response function because panga-panga flushes around November and the rainy season in that particular region also begins around November, and lasts until March (Fig. 2). Gridded data were used because local meteorological records were quite short and highly discontinuous.

## Results and discussion

Several lines of evidence demonstrate that *M. stuhlmannii* produce annual rings: (1) analysis of ring anatomy; (2) ring counting in trees of known age; (3) cambial wounding; (4) successful cross-dating within and between trees; and (5) significant correlation between a ring width chronology and climate (monthly precipitation).

## Tree-ring structure and anatomy

At a macroscopic level, annual growth ring boundaries in all samples were slightly distinct and characterized by alternating bands of parenchyma and fiber vessels and by a thin line of marginal parenchyma. Rings were characterized by slight vessel size changes throughout the ring. Wedging and false rings were also common (e.g. Fig. 4).

Microscopic analysis (terminology follows Carlquist 2001; Schweingruber 1996) reveals that growth rings have a band of brown fibers without vessels at the beginning of each growth ring, and ring boundaries are marked by thin light cells of marginal parenchyma and were identified based on the size of the parenchyma cells. The rings are formed by alternating longitudinal bands of fiber cells and parenchyma cells, with an absence of helical thickening (polarized light), and libriform fibers with simple to minutely bordered pits. Vessels are mostly large and are randomly arranged throughout the ring with no discernible pattern of distribution. Some vessels occur in groups of two-to-three but mostly they are solitary and in contact with rays. Vessels are also normally surrounded by parenchyma cells. The perforation plates are simple and the inter-vessel pits are alternate, with relatively small ray-vessel pits. Paratracheal parenchyma varies from confluent (in tangential bands, surrounding many vessels) to aliform (surrounding one side of the vessels with a wing shape). Most vessels occurring throughout the ring are surrounded by wavy bands of parenchyma and fibers and have very thick walls. Rays are widely spaced and most are multiseriate although a few are biseriate (two rows of parenchyma cells). Rays are composed of one type of cell, oriented in one direction (homocellular rays). Ray cells are procumbent, and characterized by a horizontal rectangular shape (Remane 2013). Anatomical description of *M. stuhlmannii* can also be found in Richter and Dallwitz (2000).

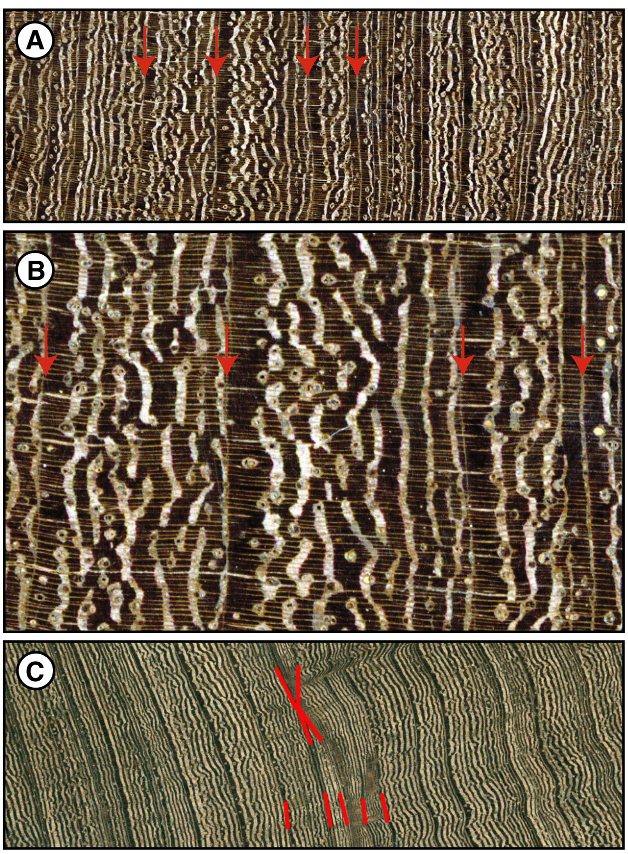


**Fig. 4** Photomicrographs of *M. stuhlmannii* tree rings in the darker heartwood portion of cross-sectional samples. Reasonably well-defined growth rings are shown in *A* and details of ring anatomy in *B* (ring boundaries marked by *red arrows*). It is possible to see fibers in each annual ring (*dark zones*) and the presence of paratracheal parenchyma surrounding the vessels (*light zones*). Vessels are distributed randomly in each annual ring. In *C* an example of a wedging ring is shown (ring boundaries marked by *red lines*). Direction of growth is *left* to *right* in each image

## Ring counting in plantation trees of known age

The plantation was established in 1997 and trees were felled in 2009. Exactly 12 distinct annual rings were formed (discounting pith). Ring boundaries of the young panga-panga were easy to identify macroscopically, and microscopy was only used to facilitate ring width measurement. Most of the plantation trees showed highly concentric growth but some have eccentric growth. Additionally, some wedging rings are present, especially in trees with irregular shape and during dry years (such as 2005). Mean ring width based on an average of 12 trees was also significantly correlated with rainy season mean precipitation from 1998 to 2009 ($r = 0.84$, $p < 0.001$; not shown).

## Cambial wounding

Panga-panga trees showed distinct wood reaction to pinning. A total of nine trees out of the nine sampled formed one complete ring 1 year after being pinned. As a response to pinning, sapwood parenchyma cells formed a black colored zone around the canal produced by the nail. This compartmentalization zone within the xylem contains high levels of extractives and is formed to protect the wound against pathogens and decay (Pearce 1996).

This compartmentalization zone was restricted to the sapwood and the size (depth) varied according to the pinning depth. During the healing process, cambial cells on the pinning canal formed dark colored anomalous parenchyma cells immediately adjacent to the wound and the adjacent cambial cells produced new xylem during the growing season (Fig. 3). In addition, callus tissue formed along the edge of the wound (Fig. 3) resulting from the differentiation of the parenchyma of xylem rays and phloem rays, respectively. Although callus tissue in most woody plants is produced by vascular rays, Trouet et al. (2012) found that in *Brachystegia spiciformis* Benth., cambium cells are responsible for callus tissue production and this process may continue even after the dormancy of the cambium.

### Visual and statistical cross-dating

Synchronization between tree-ring series for more than 50 years is one indication of seasonality of tree growth (Worbes 1995; Stahle 1999). In this work, we first attempted to visually cross-date each individual tree using the skeleton plot technique (Douglass 1941; Stokes and Smiley 1968) by plotting 2–4 radii per tree. Of 25 sampled trees, 6 were successfully cross-dated and the age of these individual samples varied from 84 to 155 years. Our success at cross-dating was limited by the frequent occurrence of wedging rings and missing rings (e.g., Fig. 4c), especially in the outer portion of sampled trees where growth was relatively slow resulting in narrow rings. Had we been able to sample younger forest-grown trees (legal harvest restrictions prevented us), these samples would likely have aided our chronology development given their expected more rapid growth and relatively wider rings (e.g., Detienne 1989; Stahle 1999). Additionally, full rather than partial cross-sections may have improved our ability to cross-date samples.

The average chronology based on six trees is 111 years in length. The mean sensitivity value is 0.806 indicating that tree growth is strongly limited by an exogenous environmental factor. Autocorrelation coefficients were relatively low for all series (0.008–0.424) hence the high mean sensitivity. Correlation between series was quite high for all trees (0.39–0.75). Analysis of chronology correlations for three 50-year segments with 25 years lag, 1900–1949, 1925–1974 and 1950–1999 were statistically significant ($r = 0.472$, $p < 0.0001$; $r = 0.513$, $p < 0.0001$ and $r = 0.676$, $p < 0.0001$, respectively) and the mean correlation was 0.50.

### Tree-ring response to climate

In this study, the exact year of the tree ring was assigned to the end of the rainy season (e.g., ring formation that starts in 1991 and ends in 1992 is assigned to the year 1992; e.g., Schulman 1956). Precipitation during the previous December ($r = 0.30$, $p < 0.05$) and current February ($r = 0.30$, $p < 0.05$) showed a significant influence on panga-panga tree-ring width (Fig. 5). Surprisingly, despite the fact that January typically has the highest monthly rainfall of the year, precipitation during this month was not significantly correlated with ring width. We are unaware of climatological or phenological mechanisms that would produce this result. However, such a finding has been reported elsewhere in tropical Africa (e.g., Hassan Khamisi 2014). We speculate that cloud cover associated with frequent rainfall in January may reduce photosynthetic activity, which is a mechanism that has apparently been observed in tree-ring studies from subtropical locations (e.g., Harley et al. 2012).

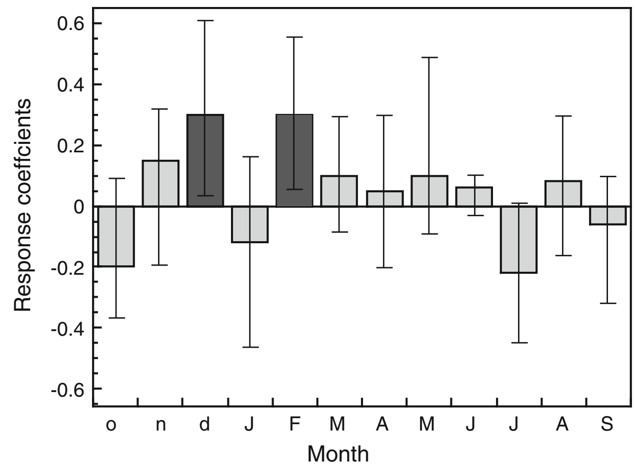


**Fig. 5** Response coefficients between the panga-panga tree-ring chronology and monthly precipitation data from October of the previous year (*lower case letters*) to September of the current year (*upper case letters*). Significant climate–growth relationships are represented by *dark gray bars* (December of previous year and February of current year) and 95 % confidence intervals

The strong correlation with previous December precipitation suggests that ring formation in panga-panga seems to start near the beginning of the rainy season. Comparison of annual ring width with rainfall over the entire rainy season (previous November through current March) explains around 43 % of panga-panga ring width variation (not shown). No significant correlation values are found between the chronology and rainfall in the months immediately following the rainy season (e.g., April–June), however, trees may still be responsive to the relatively small amount of rainfall in this season to produce stored energy for the next growing season. This is suggested by the phenology of panga-panga, which sheds leaves after May (fructification occurs during April–May (see Coates-Palgrave 2002). Slight negative correlations between the chronology and monthly rainfall during the dry season, especially in July ($r = -0.20$, $p > 0.05$) and October ($r = -0.13$, $p > 0.05$), are not likely to be biologically significant, not only because rainfall in this period is negligible, but also because samples from pinning experiments collected at the end of June show complete annual rings, which indicates that cambial activity had ended before late June.

## Conclusions

The microanatomy of *M. stuhlmannii* revealed that ring boundaries in all mature forest-grown trees and young plantation trees were somewhat distinct (young forest trees were not sampled). Plantation trees of known age show the expected number of distinct annual rings. The cambial wounding experiment was successful as suggested by the fact that sampled trees showed distinct wood reaction to wounding and one complete ring was formed over the course of one growing season. However, the only possible conclusion from this experiment is that panga-panga forms annual rings. Further studies to determine the onset and growing season length using this technique should be undertaken (e.g., Trouet et al. 2012). Despite frequent tree-ring anomalies (wedging rings, and missing rings), cross-dating between six series was successful and a pilot ring width chronology was developed, though we were only able to easily cross-date about 25 % of sampled trees. Additional collection of younger trees would likely have aided our cross-dating efforts as would collection of full as opposed to partial cross-sections, and future collections should include both samples from a range of tree ages and full cross-sections. Although based on a small sample, Panga-panga tree-ring width showed a strong response to inter-annual precipitation variability. Significant correlations between monthly precipitation and the chronology were found for the previous December and current February, but not with January, which is unexpected and warrants further study.

Although we were unable to sample young and medium age forest-grown trees because they do not meet minimum size thresholds for logging, future studies of this species should include sampling of this group to determine whether these also produce distinct annual rings and to aid in cross-dating. Other future research should include more precise determination of the onset of tree growth and length of the growing season.

Taken together, the results of our study indicate that *M. stuhlmannii* shows at least some dendrochronological potential, suggesting that this species may be useful for the study of past climate as well as long-term growth history, which will support the conservation and sustainable management of this commercially valuable timber species in Mozambique.

**Author contribution statement** I. Remane collected field samples, prepared and analyzed samples and data and wrote manuscript. M. Therrell collected field samples assisted with analysis and edited manuscript.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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