

## **Towards Using Dendrochronological Proxy for Reconstructing Climate in Tropical Regions**

*C.M.P. William*<sup>1</sup>

### **Abstract**

There has been a controversial discussion on the use of dendrochronology as a proxy for reconstructing climate in the tropics. It is argued that the lack of seasonality in tropical regions constrains tree species growth formation and the resulting tree rings. Using Content Analysis (CA), and Relational Analysis in particular, and dendrochronology-laboratory practices at the University of Minnesota, the paper reviews the discussion on the use of tropical tree species in tree rings studies. The results show that tree species in *Pordocarpaceae* family and *Pterocarpus angolensis* growing in Tanzania and other parts of the tropics depict annually resolved tree rings so they may be useful proxy tropical tree species for reconstructing past climate. The challenges for practicing dendrochronology in the tropics relates to the diversity of rings formation and tree rings patterns in different species, and the lack of instrumental climatic records. We argue that tropical tree rings studies robustness may benefit from other climate proxies such as charcoal, stalagmites, pollens and spores, and fossil leaves.

### **Introduction**

Dendrochronology has widely been used as proxy for climate reconstruction in temperate regions. Seasonal weather patterns and response of some tree species to annual temperature and precipitation variations enable trees to form distinct annually resolved tree rings. This has not been the case in tropical regions because of the general lack of seasonality in the region (Jacoby, 1989). The argument that tropical tree species are unsuitable for dendrochronology experiments is controversial. This paper addresses this controversy by drawing from author's dendro-laboratory experiments and extensive review of literature on tropical dendrochronology. Pivotal to this study is emphasis on content analysis of the literature. We assume that this is a better way of understanding tree chronology work in the tropics because it is not possible to experiment each species of interest due to tropical species' spatial disparity, labour, time and financial constraints.

---

<sup>1</sup>Assistant Lecturer, Geography Department, College of Arts and Social Sciences, University of Dar es Salaam

Some tree rings studies perceive tree rings formation in tropics based on the conditions of the higher latitude climates and the resulting tree growth formation (Worbes, 2002). There must be a clear distinction of tree rings between tropical and temperate ecoregions. Temperature constrains tree growth in the temperate region, which is almost constant in the tropics. An important tree growth factor in the tropics that has always been underestimated is seasonal variations in annual precipitation (Jacoby, 1989).  
!!!

When mean annual precipitation for tropical areas is computed the mean annual precipitation value indicate that these areas are wet throughout the year. This generalization has obscured long-term variations experienced during the dry seasons of the year. As a result, there has been a very slight consideration of seasonality in tropical trees growth characteristics. The dominant thinking has been that many tropical tree species do not form distinct annually resolved rings and where rings distinctly form, they may not reflect annual growth. While this assertion may be true, it is currently being reconsidered (Worbes, 2002; Stahle et al., 1999; Verheyden et al, 2005 and Fitchler et al., 2004).

Yet the role of tropical forests tree species in maintaining, biodiversity, hydrological, ecological balance and supporting humans is of paramount importance. Sustainability of the tropical forests depend on a proper understanding of how these trees respond to environmental conditions such temperature and precipitation. Through studies of tree rings of some tree species in the tropics such as Tanzania the past climatic condition reconstruction is possible. Understanding past climate conditions informs not only the present plants ecology but may aid to model the future of tropical species.

Instrumental climate records may help in understanding contemporary dynamics of forest tree species but these records are either inconsistent or non-existent in most tropical countries. This renders the use of instrumental records in tropical regions difficult. Likewise, climate proxies such as charcoal (Thevenon *et al.*, 2003) stalagmites (Lundblas and Holmgren, 2005) pollen and spores (Dupont *et al.*, 2001) and fossil leaves (Jacobs and Henrendeen, 2004) contain weaknesses that make tree rings analysis (using some species) an avenue to understand better climate signals of the past.

### **Methods Used in Tropical Dendrochronology**

In principle methods used for dendrochronology work in the tropics is not different from methods in higher latitudes. However, development of a theory on seasonal tree formation (Baillie, 1995) started in higher latitude climates as early as the 19<sup>th</sup> century. Similar investigation was going on in

## *Towards Using Dendrochronological Proxy for Reconstructing Climate*

the tropics (Worbes, 2002) during the same period. To side with one of the arguments remains controversial. The controversy on tropical trees growth formation comes from a number of reasons. First, the controversy relates to the number of specific observations of inconsistent behaviour of different tree species shedding off their leaves in an area. Second, the contention results from the observation of the differences in shedding off leaves of the different tree branches on a tree species. Third, it also relates to a continuous growth of roots of the tree species in a particular location (Worbes, 2002).

A fourth incongruity that led to the controversy relates to the results of experimentation with trees from tropical and temperate climates. Tropical tree species were grown in higher latitudes and similarly trees from the high latitudes were experimented in the tropics. These experiments resulted in unexplained processes of tree growth. One of the reasons for lack of explanations relates to exclusion of testing for the influence of temperature and precipitation to rhythms of plant growth (Worbes, 2002).

In the early 1900, Dutch scientists had started studying tree rings in Indonesia (Worbes, 2002). Based on minute details of the trees and microscopic descriptions of the same, researchers concluded that there was apparent link between seasonal precipitation and tree growth. In a monsoon dominated east, trees showed annually resolved trees rings but in the west where the climate is wet throughout the year tree rings were indistinct. This research, laid a platform for similar studies in the 1920s.

Coster in 1920s investigated tree growth forms using a mix of methods and techniques (Worbes, 2002). He widened the scale of phonological observations and merged it with trees' anatomical experiments. He classified growth zone structures based on the arrangement of vessels, parenchyma and fiber of the trees. Later the method was applied easily to most of the tropical tree species with secondary wood growth. Worbes (2002) argues that Berlage in 1931 adopted Coster's method and constructed the first tropical tree ring chronology, which refutes assertion by Therrell *et al.* (2006) that they were the first to present tree rings reconstruction of rainfall in the tropics. Much was appreciated of Coster's contribution to tree chronology of the tropics but the scientific community did not notice his work because it was kept in German (Worbes, 2002) where it was not accessible to many scholars. However, tropical dendrochronology continued developing through the 1960s.

In 1967, 1969, and 1970 Mariaux worked on tropical timber species in different West African countries. He tried to develop better ways of verifying trees annual seasonal growth. He suggested a 'Cambial wounding

with Mariaux's windows' method. He, however, unsuccessfully used radiodensitometry in detecting ring boundaries. He was constrained by the fact that within a year angiosperm trees develop complex structure and multiple seasonal variations in density. The search for better ways of dendrochronology work in tropics continued and it is still our current concern (Worbes, 2002). We may argue that the contemporary development in tree chronology is a result of long time efforts and experimentation.

The method that Coaster developed set a standardized way of doing tree rings investigation (Baillie, 1995, Worbes 2002) only that efforts focused on improving the methods. In 1980, for example, Stuiver and other scientists proposed that altering radiocarbon concentration in the atmosphere would be a better and unnatural way to mark time in a tree. The underlying assumption was that tree rings reflect air radiocarbon in particular year. Hence, by altering of atmospheric radiocarbon we induce a signal that will be marked in a tree ring. Mozzerto experimented with radiocarbon alteration in the atmosphere and mathematically was able extrapolated age. He based his assumption on constant tree growth that conflicted with concepts in dendrochronology. Later Worbes and Junk (1989) blend the radiocarbon analysis with investigation of the anatomy of the trees. They measured radiocarbon content in each tree growth zone along a radius to attest whether the rings of the tree formed yearly. They established that the rings formed annually. Dendrochronology investigations in the tropics use these techniques to date. We may argue that contemporary tropical dendrochronology has benefited from advancement in technology.

Schöngart *et al.* (2006) employed a traditional method from Coster, and Worbe to microscopically analyze tree ring structure and classify ring boundaries of the samples cored from the different West Africa tree species. They delineated ring boundaries based on the parenchyma bands, where fiber and parenchyma tissues alternate, and where the distributions of vessels vary. Whenever necessary, they combined all the features in order to define a ring boundary. They measured ring width to the nearest 0.01mm using a LINTAB digital devise followed by cross-dating of each tree series using a visual and statistical t-test. A Time Series Analysis and Presentation (TSAP) computer program performed tree rings analysis. With evolution in analysis software technology tree rings chronology is even much faster and efficient.

Unlike the previous methods Fitchler, *et al.* (2004) sampled full stem discs. These were finely polished after being dried in open air, a standard procedure. Similar to Schöngart *et al.* (2006), Fitchler, *et al.* (2004) the authors used LINTAB digital device to measure ring width. A stereo-

## *Towards Using Dendrochronological Proxy for Reconstructing Climate*

microscope with low magnification was used to analyze tree ring structure and cross-dating was visually and statistically done. Verheyden *et al.* (2004) and Stahle *et al.* (1999) use this similar standard of data collection and analysis. The standard procedures in dendrochronology have remained unaltered despite of the changes in computer statistical programs. For example, the University of Minnesota (Department of geography) dendrochronology laboratory widely use the preceding methods and techniques.

Generally one may argue that there has been a tremendous improvement in technology and analytical methods for dendrochronology in the tropics since the early 1930s. Currently, existing methods in tropical dendrochronology has improved our understanding of the use of tropical species for dendrochronology. There is still need for innovations in methods and techniques in dendrochronology research in order to address problems associated with tree rings work using tropical tree species. This is because tree growth forms in the tropics and temperate climates differ.

### **Spatio-temporal Distribution of Dendrochronology Work in the Tropics**

Table 1 shows some of the dendrochronology work in tropical climates in different areas at different periods. Dendrochronology works in the tropic dates back about 100 years and involves investigations in more than twenty tropical countries (Worbes, 2002). The list provided in Table 1 is not exhaustive but a representation of a bulk of dendrochronology works in this tropical climate region.

This paper does not refer to a time that actual field investigation started in each of the area named in Table 1; rather the paper uses time of the publications to provide a relative time when scientists did a particular tree rings scientific inquiry. This paper, therefore, is presenting a relative picture of a spatial and temporal distribution of dendrochronology works in the tropics.

We may argue that different areas in the tropics are differentiable by the microclimates in each. Climatic conditions in a country are not spatially evenly distributed nor are similar over time. Climatic conditions affect edaphic factors and similarly the species that grow in these areas. Investigations of tropical tree species need to consider this variation as it is pivotal to growth forms in each tree species.

**Table 1: Selected Areas in the Tropics where Dendrochronological Work has been Done (2008).**

Area	Region	Site publication
Zimbabwe	Africa	Therrell and Stahle(2006) Stahle <i>et al.</i> (1999)
Namibia	Africa	Fitchler <i>et al.</i> (2004)
Tanzania	Africa	Bryant (1968)
Kenya	Africa	Verheyden <i>et al.</i> (2005)
Ethiopia	Africa	Eshete and Stahl (1999)
Ivory coast	Africa	Schöngart <i>et al.</i> (2006)
Nigeria	Africa	Amobi (1973)
Benin	Africa	Schöngart <i>et al.</i> (2006)
Indonesia & Thailand	Asia	Poussart <i>et al.</i> (2003)
Malaysia	Asia	Sass and Eckstein(1995)
India	Asia	Chowdhury (1939, 1940)
Elsalvador	Central America	Hastenrath (1963)
Puerto Rico	Central America	Drew (1998)
Brazilian Amazon	South America	Worbes (1989) Ash (1983a, 1983b, 1983c)
Bolivia	South America	Brienen and Zuidema (2005)
Tropical Australia	Australia	Ash (1986) Ogden (1981)

Further, it indicates that different scientists have worked in tropical climates at different periods and with different tree species. What is clear is that they have used standard dendrochronology procedures that dendrochronology laboratories elsewhere use. Statistical manipulations vary with the type of species used and the major question(s) the researcher is investigating. Nevertheless, the advancement in statistical analysis packages is diverse and each scientist uses software that he or she is comfortable using. The results from each of the different investigations remain robust provided there is use of standard dendrochronology procedures and analytical rigor.

### Useful Species in Tropical Dendrochronology

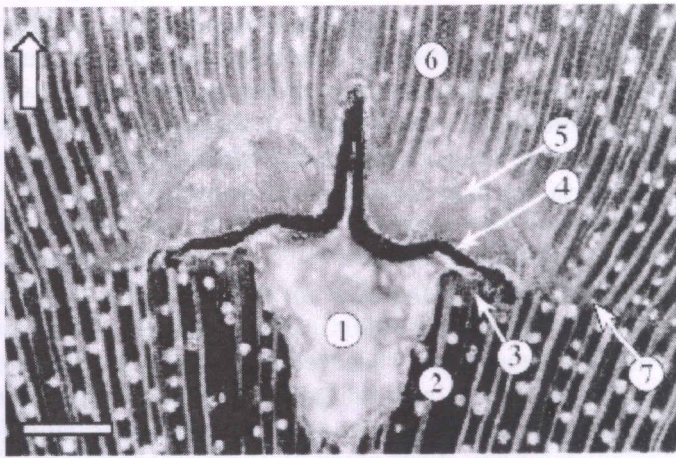
#### *Species type and its geography*

The variable nature of the tropical climate and the concomitant edaphic factor render all tree species in the tropics not ubiquitously distributed. This necessitates tree rings studies to use different tree species in different locations in the tropics. Different scholars have investigated the number of tree species in the tropics. While this paper attempts to identify these tropical tree species, through a literature review and attesting some of these species with laboratory experiments, the paper may not be able to name all tree species studied. In this paper, the focus is on a few tree species that have been of interest in tree rings studies. The next section of this paper pays attention on tree rings studies in Africa.

## *Towards Using Dendrochronological Proxy for Reconstructing Climate*

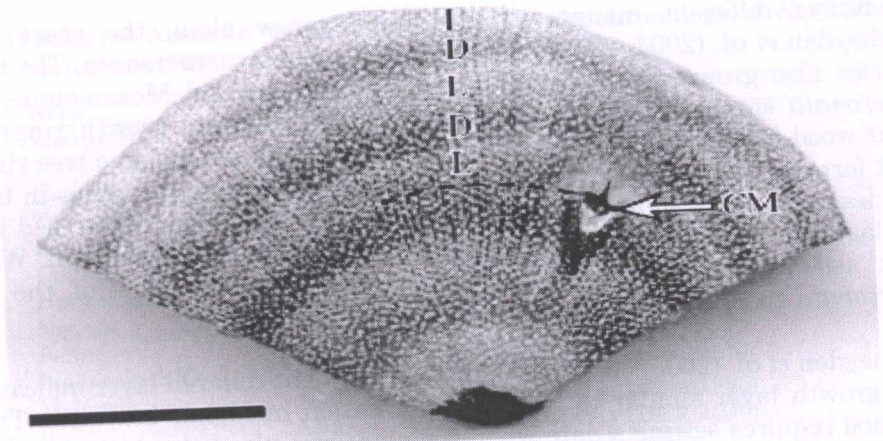
In Kenya different mangrove tree species grow along the coast but Verheyden *et al.* (2004, 2005) investigated *Rhizophora mucronata*. The tree species also grows along coastal areas of Tanzania and Mozambique. *R. mucronata* species is widely documented to lack annual growth rings in their wood formation, which may be due to attempts to analogue tree rings that form in tree species in temperate climates with rings that grow in tree species such as *R. mucronata*. Verheyden and other researchers used the analogue of alternating collared layers as rings of the *R. mucronata*. With that assumption, they were able to establish growth rates of the *R. mucronata* species (Verheyden *et al.*, 2004).

Verheyden *et al.* (2005) observed that a dark or light collared layer indicated one growth layer similar to tree rings formation in higher latitudes. This method requires setting a date when the plant was planted, which means it is suitable for planted *R. mucronata* species. For *R. mucronata* in their natural habitat a mix of methods is required. In this case, a cambial marking method fits most. The approach involves injuring a cambium of the tree forcing the tree to respond to the injury over time. The injured tree grows for two to five years. Later when the tree is harvested, the observed callus tissue that develops in response to the cambium injury becomes a time marker (Figure 1a, 1b) that enables studying a tree growth formation for a particular time.



**Fig.1a: Microphotograph of the cambial mark**

Notes: 1 puncture canal; 2, oxidized wood; 3, fibres with incomplete cell wall thickening; 4, layer of crushed cambial derivatives; 5, parenchymatous wound tissue; 6, restored wood structure; 7, local parenchyma band indicating the position of cambial initials at the time of pinning (see text for more detailed explanation). Scale bar = 500  $\mu$ m; the arrow indicates the direction of growth. Source: Verheyden *et al.* (2004).

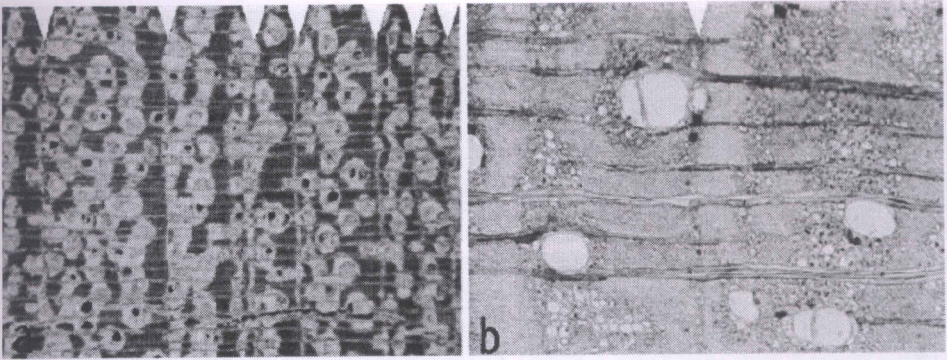


**Fig. 1b:** Polished *R. mucronata* wood section showing five growth layers  
**Notes:** (D = dark; L = light) produced since the cambial marking (CM) of November 1999. Scale bar = 1 cm. Source: Verheyden *et al.* (2004)

Therrell *et al.* (2006) and Stahle *et al.* (1999) researched on *Pterocarpus angolensis* (African bloodwood) tree rings in Zimbabwe. The tree species grows in some parts of Tanzania at altitude of 1650m. It is almost ubiquitous in the tropics except in Madagascar and Australia (Therrell *et al.* 2006). This tree species form realistic tree rings that depict annual growth (Stahle *et al.*, 1999). It is clear that semi-ring permeable growth bands of the *Pterocarpus angolensis* are tree rings. A thorough investigation of the phenology, ring anatomy, cross-dating and correlation of growth rings and seasonal climatic data confirm formation of annually resolved rings in *P. angolensis* species.

*Burkea Africana* (Red Syringa) grows in different altitudes in different habitats in Africa (Fitchler *et al.*, 2004). Using species found in Namibia Fitchler and other researchers observed that *Burkea Africana* like *Pterocarpus angolensis* forms annual growth patterns. The tree species contain a marginal parenchyma strip at the edge of the ring (Figure 2). Wedging rings exist although this one corrects the problem through analysis of different radii. The problem of missing rings was absent in *B. Africana* (Fitchler *et al.*, 2004). Taking all samples of the *B. Africana* and cross-dating the width of the rings of the samples the authors concluded observed rings were periodical.



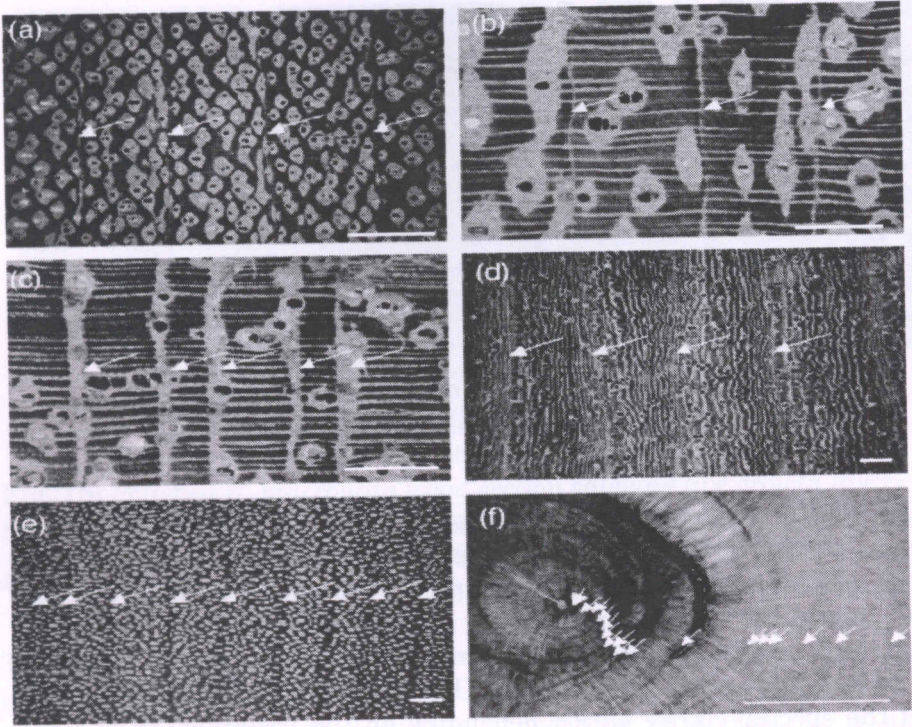


**Figure 2: *Burkea africana* macroscopical (a x16) and microscopical (b x25)**

**Note:** White triangles indicate ring boundaries. Source: Fitchler *et al.*, 2004.

Brienen and Zuidema (2005, 2006) studied tree rings of *Amburana cearensis*, *Cedreia odorata*, *Cedrelinga catenaeformis* and *Peltogyne heterophylla*. All are timber species that produce annual growth formations. Growth zone in the species varied among species. In *Cedreia odorata* species growth zone were very clear. Parenchyma bands at the margins characterized the species growth zone (Brienen and Zuidema, 2006). The rest of the species' clarity varied depending on the variations in density, vessel distribution, recurrence of patterns of parenchyma bands and fiber bands. Brienen and Zuidema (2005) argue that *Cedreia odorata* is suitable for tree rings studies. It is possible to identify accurately annual tree rings in *C. odorata* even though it experiences low rates of growth due to variations in rainfall and edaphic factors.

In West Africa, Schöngart *et al.* (2006) investigated *Daniellia oliveri*, *Azelia Africana*, *Anogeissus leiocarpus*, *Pterocarpus erinaceus*, *Isobornia doka*, and *Diospyros abyssinica* tree species. The species' wood structure of the growing cells enable the formation of delineated tree rings. Other variations in tree rings relate to the species' ring width and how often a tree species sheds off leaves. Parenchyma stripes at the end of the rings are a characteristic feature of the *Daniellia oliveri*, *Azelia Africana*, and *Isobornia doka* species (figure 3). In some cases two rings formation exists in the species, therefore, the two rings constitute a single ring. For the *Pterocarpus erinaceus* it is possible to identify the rings but tissues tend to become smaller towards the boundary of the ring tissues. Tree rings are less visible in *Diospyros abyssinica* and *Anogeissus leiocarpus* tree species. Although observing wide rings is not a problem, as width of the rings decrease it becomes difficult to identify the rings.



**Figure 3: Growth zones in wood of tree species from tropical West Africa**

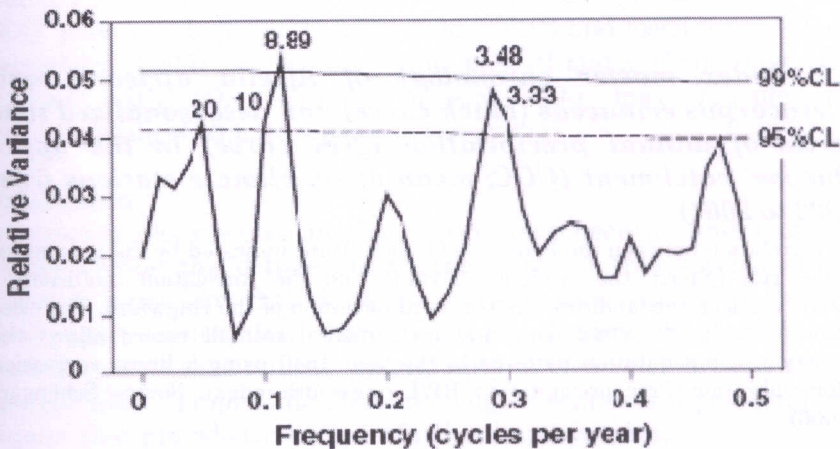
**Notes:** Growth boundaries delimited by marginal parenchyma bands: (a) *Isoberlinia doka*, (b) *Afzelia Africana*, and (c) *Daniellia oliveri* showing crystalline substances in the terminal parenchyma band (all Caesalpiniaceous). – Growth boundaries characterized by variations in the vessel distribution: (d) *Pterocarpus erinaceus*, and (e) *Anogeissus leiocarpus* (Combretaceae). Growth patterns with alternating bands of fiber and parenchyma tissues: (f) *Diospyros abyssinica* (Ebenaceae), sample with fire scars in three consecutive years. Flashes indicate tree ring boundaries; white horizontal bars have a length of 1 mm. Source: Adopted from Schöngart *et al.* (2006)

Studies conducted in Africa and other tropical areas refute the argument that tree species in the tropics are not suitable for tree rings analysis and using them as proxy for studying past climatic conditions (Jacoby, 1989). However, dendrochronology laboratory attestation of tropical species indicate that tropical trees form annual rings (Worbes, 2002, Schöngart *et al.*, 2006, Brienen and Zuidema, 2005, 2006, Fitchler *et al.*, 2004, Stahle *et al.*, 1999, Verheyden *et al.*, 2005, Verheyden *et al.*, 2004, 2005 ). Tropical tree rings formation is not necessarily similar to tree rings formed in temperate environment due to differences in temperature and precipitation regimes of the tropics and the higher latitudes and the concomitant edaphic

factors. As indicated by the experimentation of the tropical species clarity of the rings differ with the species in question, this is not a constraint because similar problems are common with tree species in temperate regions. What is evident here is the avenue for doing dendrochronology in the tropics such as Tanzania. Refute

### **Application of Tropical Tree Rings Analysis**

The assertion of indistinct annual ring formation in tropical trees led to the argument that there was little application of dendrochronology in the tropics (Poussart *et al.* 2003; Verheyden *et al.*, 2004, 2005; Therrell *et al.*, 2006). Tree rings chronology in the tropics has a wide range of applications. Therrell *et al.* (2006) use tree rings to understand rainfall variability in Zimbabwe over time. They were able to establish how El Niño Southern Oscillation (ENSO) significantly influence rainfall in the country (figure 4). They also indicate that there is a strong potential of using tree rings reconstruction for estimating crops performance and tree growth, Therrell *et al.* (2006).



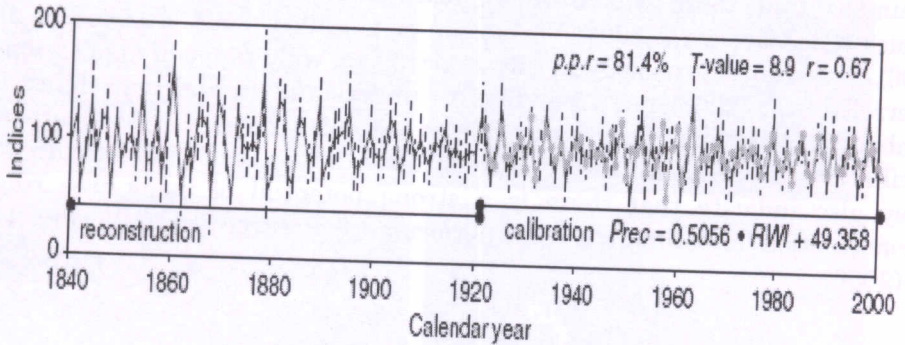
**Figure 4: Spectral analysis of the rainfall reconstruction**

**Notes:** The figure indicates that significant spectral power is concentrated at periods of 20, 8–10 and ~3.4 years. The 3.4-year peak may reflect the influence of ENSO. Source: Therrell *et al.* (2006).

Nevertheless, tree rings chronology helps in determining trees age (Verheyden *et al.* (2004), in estimating timber yields (Brienen and Zuidema, 2006) and informing decision-making in forest management as a whole (Stahle *et al.*, 1999). Tree rings studies, therefore, play a crucial role in

providing information on forest dynamics, which are central for sustainable management of forest ecosystems.

Furthermore, dendrochronology aid in establishing a relationship between climatic conditions and trees growth (Schöngart *et al.* 2006). In addition, long time climatic reconstructions (figure 5) have benefited from tree rings investigation (Poussart *et al.*, 2003, Schöngart *et al.* 2006, Ward, 1987).



**Figure 5:** *Index master chronology of Afzelia africana and Pterocarpus erinaceus (black curve) and deseasonalized time series of annual precipitation (grey curve) in the upper Oue'me' catchment (UOC; mean of six climate stations from 1922 to 2001).*

**Notes:** The correlation between the two curves is significant indicated by the percentage of parallel run (p.p.r.), the student's T-value and the correlation coefficient  $r$  ( $P < 0.0001$ ). Vertical lines indicate the standard deviation of the ringwidth. The close correlation between the chronology and instrumental rainfall record allows the reconstruction of precipitation patterns to the year 1840 using a linear regression model for calibration (Prec, precipitation; RWI, ring-width index). Source: Schöngart *et al.* (2006).

We can argue that there is valuable contribution from dendrochronology in understanding not only natural spatio-temporal processes but also socio-economic aspects. This way dendrochronology presents a framework for understanding a bigger picture of nature-society interactions.

### Challenges in Tree Rings Studies in the Tropics

Different tropical tree species at a coarser resolution share similar climatic conditions. This argument points to possible comparisons between studies of the same tree species in different places. Existence of microclimatic conditions and edaphic factors that are spatially variable may lead to

## *Towards Using Dendrochronological Proxy for Reconstructing Climate*

different growth forms of the same species. Comparisons of dendrochronology of same species from different areas of the tropics may lead to flaws. Thus, we need to treat dendrochronology work in the tropics with caution.

Moreover, scientists have done plausible dendrochronology work in the tropics using different methods and techniques. There are complexities of methods in some investigations unlike others. Establishing tree rings pattern in tree species that form alternate dark to light colours require complex techniques as opposed to tree species whose annual rings are distinctively identifiable. Likewise, the fact that in most tropical countries contemporary climatic records lack (Terrel *et al*, 2006) calibration of tree ring records is difficult. It is important that other methods and techniques develop to address problems aforementioned (Worbes, 2002).

Despite of the constraints in tree rings work in tropical climates opportunities for enriching tree rings data with data from other climate proxies in areas where these data exist may improve the robustness of the dendrochronology work in the tropics. Scientists have used such proxies as charcoal (Thevenon, et al. 2003), stalagmites (Lundblas and Holmgren, 2005), pollen and spores (Dupont et al., 2001) and fossil leaves (Jacobs and Herendeen, 2004) in reconstructing past climate. Combining tree rings analysis with other climate proxies data may provide a better understanding of climate signals of the past.

### **Conclusion**

Dendrochronology works in the tropics have been a subject of long time inquiry. While the debate on whether tropical tree species are suitable lingers it is evident that there are suitable tree species for that purpose. This paper argues that there is ample dendrochronology research on tropical species that refutes unsuitability of tree rings proxies for studying past climates. Tropical dendrochronology research is a perpetual scientific enquiry that provides avenue for further improvement.

Tree species in the *Pordocarpaceae* family and *Pterocarpus angolensis* tree species may be useful for dendrochronology in Tanzania. Further researches will improve our understanding of other local species that exist, for example, in the Eastern Arc Mountain ranges, in view of the species or a close family studied elsewhere in the tropics. Needless to mention, dendrochronology in the tropics is plausible and has established a strong foundation future investigation may be built upon.

References

- Amobi, C.C. 1973. Periodicity of Wood Formation in Some Trees of Lowland Rainforest in Nigeria. *Ann. Bot.* 37: 211–218.
- Ash, J. 1986. Growth Rings, Age and Taxonomy of *Dacrydium* (Podocarpaceae) in Fiji. *Aust. J. Bot.* 34: 197–205.
- 1983a. Growth Rings and Rainfall Correlations in a Mangrove Tree of the Genus *Diospyros* (Ebenacea). *Aust. J. Bot.* 31: 19–22.
- 1983b. Tree rings in tropical *Callitris macleayana* F. Muell. *Austr. J. Bot.* 31: 277–281.
- 1983c. Growth Rings in *Agathis robusta* and *Araucaria cunninghamii* from Tropical Australia. *Aust. J. Bot.* 31: 269–275.
- Baillie, M.G.L. 1995. *A Slice Through Time: Dendrochronology and Precision Dating*. London: B.T. Batsford Ltd.
- Bryant, C.L. 1968. The growth rings of *Pterocarpus angolensis* are Annual. *Silv. Res. Note, Silv. Sect. For. Div. Lushoto*, 4 (3).
- Brienen, J.W.R., & A.P. Zuidema. 2006. The Use of Tree Rings in Tropical Forest Management: Projecting Timber Yields of Four Bolivian Tree Species. *Forest Ecology and Management*, 226: 256–267.
- Brienen, J.W.R., & A.P. Zuidema. 2005. Relating Tree Growth to Rainfall in Bolivian Forests: A Test for Six Species Using Tree Ring Analysis. *Oecologia*, 146: 1–12.
- Drew, A.P. 1998. Growth Rings, Phenology, Hurricane Disturbance and Climate in *Cyrilla racemiflora* L., Rain Forest Tree of the Luquillo Mountains, Puerto Rico. *Biotropica*, 30: 35–49.
- Dupont, L.M., B. Donner, R. Schneider, G. & Wefer, 2001. Mid-Pleistocene Environmental Change in Tropical Africa Began as Early as 1.05 Ma. *Geology*, 29: 195–198.
- Eshete, G., & G. Stahl. 1999. Tree rings as Indicator of Growth Periodicity of Acacias in the Rift Valley of Ethiopia. *Forest Ecology and Management*, Number 116, 107–117.
- Fitchler, E., V. Trouet, H. Beeckman, P. Coppin, & M. Worbes. 2004. Climatic Signals in Tree Rings of *Burkea africana* and *Pterocarpus angolensis* From Semiarid Forests in Namibia. *Trees*, 18: 442–451.
- Hastenrath, S. 1963. Dendrochronologie in El Salvador. *Meteorol. Rundschau*, 4: 110–113.
- Jacoby, G.C. 1989. Overview of Tree-ring Analysis in Tropical Regions. *IAWA Bulletin*, 10: 99–108.
- Jacobs, B.F., & P.S. Herendeen. 2004. Eocene Dry Climate and Woodland Vegetation in Tropical Africa Reconstructed from Fossil Leaves from Northern Tanzania. *Paleogeography, Paleoclimatology, Paleocology*, 213: 115–123.

*Towards Using Dendrochronological Proxy for Reconstructing Climate*

- Libby, L.M. 1983. *Past Climates: Tree Thermometers, Commodities, and People*. Austin: The University of Texas Press.
- Lundblad, K., & K. Holmgren. 2005. Paleoclimatology Survey of Stalagmites from Coastal Areas of Tanzania. *Geografiska Annaler*, 87A: 125–140.
- Marchant, R., & H. Hooghiemstra. 2004. Rapid Environmental Change in African and South American Tropics Around 4000 years Before Present: A Review. *Earth Science review*, 66: 217–260.
- Ogden J, 1981. Dendrochronological Studies and Determination of Tree Ages in the Australian Tropics. *Journal of Biogeography*, 8: 405–420.
- Poussart, P.F., M.N. Evans, & D.P. Schrag, 2003. Resolving Seasonality in Tropical Trees: Multi-decade, High-resolution Oxygen and Carbon Isotope Records from Indonesia and Thailand. *Earth and Planetary Science Letters*, 218: 301–316.
- Sass, U., W. Killmann, & D. Eckstein. 1995. Wood Formation in Two Species of Dipterocarpaceae in Peninsular Malaysia. *LAWA Journal*, 16: 371–384.
- Schongart, J., B. Orthmann, K.J. Hennenberg, S. Porembski, & M. Worbes. 2006. Climate-Growth Relationships of Tropical Tree Species in West Africa and Their Potential for Climate Reconstruction. *Global Change Biology*, 12: 1139–1150.
- Stahle, D.W., P.T. Mushove, M.K. Cleaveland, F. Roig, G.A. Hyanes. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management*, 124: 217–229.
- Therrell, M.D., & D.W. Stahle. 2006. Tree-ring Reconstructed Rainfall Variability in Zimbabwe. *Climate Dynamics*, 26: 677–685.
- Thevenon, F., D. Williamson, A. Vincens, M. Taieb, O. Merdaci, M. Decobert, G. Buchet. 2003. A Late-Holocene Charcoal Record from Lake Masoko, SW Tanzania: Climatic and Anthropogenic Implications. *The Holocene*, 13: 785–792.
- Verheyden, A., F. De Ridder, N. Schmitz, H. Beeckman, & N. Koedam. 2005. High-resolution Time Series of Vessel Density in Kenyan Mangrove Trees Reveal a Link with Climate. *New Phytologist*, 167: 425–435.
- Verheyden, A., J.G. Kairo, F. De Ridder, H. Beeckman, & N. Koedam. 2004. Growth Ring Formation and Age Determination in the Mangrove *Rhizophora mucronata*. *Annals of Botany*, 94: 59–66.
- Ward, R.G.W. 1987. *Applications of Tree Ring Studies: Current Research on Dendrochronology and Related Subjects*. Oxford: BAR.
- Worbes, M. 2002. One Hundred Years of Tree-ring Research in the Tropics - A Brief History and an Outlook of Future Challenges. *Dendrochronologia*, 20: 217–231.
- . 1989. Dating Tropical Trees by Means of  $^{14}\text{C}$  from Bomb Tests. *Ecology*, 70: 503–507.