

Dendrochronology in the dry tropics: the Ethiopian case

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Abstract Dendrochronology is developing outside temperate and boreal regions. Over the past decade substantial progress has been made in Mediterranean and wet tropical regions. However, research in dry tropical regions, notably those of sub-Saharan Africa, has remained fragmentary. Here, we try to identify the unique challenges and

opportunities of dendrochronology in the dry tropics. First, we briefly review the status of dendrochronology outside temperate and boreal regions with an emphasis on sub-Saharan Africa. Subsequently, we focus upon one of those areas where dendrochronology in the dry tropics is at the forefront of scientific advance: Ethiopia. A detailed review of tree ring studies in the lowlands and highlands highlights the complexity of ring formation and made us identify four major types of growth ring expression: anatomically not

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distinct rings, multiple rings per year, annual rings and multiple missing rings. This complex tree growth behaviour is associated with large-scale variations in precipitation regime (unimodal to multimodal) and relatively small-scale variations in tree sensitivity to water availability. Literature results are used to develop a scheme that can be used to predict differences in growth ring formation along gradients in these two factors. Because of the exceptional growth sensitivity of and the importance of local site conditions (topography, biological factors, etc.) for most trees sampled, those growing at the limits of their ecological amplitude are prone to possess multiple rings per year or multiple missing rings. In such circumstances, site selection should not always take place at the limits of the ecological amplitude of a species, but may sometimes have to be diverted to more mesic environments. Successful studies are now appearing, such as those reporting correlations between tree ring chronologies and Blue Nile river flows.

Keywords *Acacia · Juniperus procera · Ring formation · Tree rings · Wood anatomy*

Introduction

To date, the application of dendrochronology has mostly been limited to temperate and boreal regions, because of their marked climate seasonality that induces the periodic formation of growth rings with clear wood-anatomical boundaries in trees. Strong annual cycles in temperature and light availability in temperate and boreal regions force trees into dormancy (no cambial activity) during winter, causing the formation of distinct annual rings (Fritts 1976). With decreasing distance to the equator, these annual cycles weaken. However, less seasonally defined cycles in water availability occur, but those are prone to cause the formation of indistinct non-annual rings (Worbes 2002). These conditions provide major challenges to the development of dendrochronology in Mediterranean and tropical regions and have been subject of many scientific papers (reviewed by, e.g. Cherubini et al. 2003; Stahle et al. 1999; Worbes 2002).

Recently, major progress has been made to the development of dendrochronology in highland environments of the Mediterranean basin (e.g. Esper et al. 2007; Touchan et al. 2008, 2010; Trouet et al. 2009), the Middle East (e.g. Pourtahmasi et al. 2007; Touchan et al. 1999) and Asia (e.g. Bräuning and Mantwill 2004; Shao et al. 2010; Treydte et al. 2006), where cold winters cause cambial dormancy. Even in lowland-Mediterranean and wet tropical regions considerable progress has recently been achieved (e.g. Brienen and Zuidema 2005; Buckley et al.

2010; Cherubini et al. 2003; D'Arrigo et al. 2010; Jones et al. 2009), but in sub-Saharan Africa dendroclimatology is still facing considerable methodological problems.

Other high-resolution records that can be employed as proxies for climate reconstruction (e.g. ice cores and historical documents) are also exceptionally scarce in sub-Saharan Africa (Verschuren 2004) and the need to improve this situation has been noted by various authors (Gasse 2000; Olago and Odada 2004; Umer et al. 2004; Verschuren 2004). In Ethiopia the situation is particularly critical, because it is one of the economically least developed countries in the world and the main source area of the River Nile providing almost 90% of Egypt's freshwater. At the same time, research on climate change and its economic consequences in Ethiopia has been limited and fragmentary so far (Conway and Schipper 2010). Ethiopia is one of the few countries in sub-Saharan Africa where dendrochronology in its classical definitions may be feasible (Briffa and Russell-Smith 1986; Verschuren 2004).

This paper reviews dendrochronological research in Ethiopia as an example of dendrochronology in the dry tropics of sub-Saharan Africa.

Dendrochronology outside temperate and boreal regions

Recent reviews have established two branches of dendrochronology outside temperate and boreal regions: tropical (Worbes 2002) and Mediterranean (Cherubini et al. 2003) dendrochronology. In lowland tropical environments tree ring formation tends to depend on periodic droughts or floods (Worbes 2002), whereas in Mediterranean environments both winter cold and summer drought can be conditional (Cherubini et al. 2003).

Highland and dry tropical environments, like most of Ethiopia, present an intermediate case. Though the tropics experience only minor temperature variations over an annual cycle, their diurnal temperature range can be high. In highland tropical environments, low temperatures (even below freezing) may occur every night. The timing of droughts may be more irregular and less confined to certain seasons in dry tropical regions as a whole. Incidental frost and drought can cause air to fill water-conducting cells (cavitation), which blocks the water conduits (embolism), and hence reduces the hydraulic conductance of the tree (Bréda et al. 2006). By increasing water stress, this reduces plant productivity. Similarly, increasing drought will reduce plant productivity. Hence, both events can cause ring boundary formation.

The complexity of tree ring formation in dry tropical environments is exacerbated by three features of tree

growth behaviour. First, tree rings are often discontinuous along the circumference of the tree (partial rings), which requires the obtaining of multiple cores per tree or even stem discs (Worbes 2002). Second, the response to environmental conditions tends to vary strongly between species and individual trees, depending on variability in, e.g. wood anatomical structure, habitat, nutrient availability, rooting depth and growth history (Cherubini et al. 2003). Third, and most profoundly, many trees do not experience true dormancy (no cambial activity), but rather varying degrees of quiescence (reduced cambial activity), in which the (highly variable) degree of quiescence determines ring distinctness (Cherubini et al. 2003; De Luis et al. 2007).

Many techniques have been developed to assess the periodicity of observed tree rings in dry tropical environments. Worbes (1995) gives an overview of these techniques, many of which require monitoring of cambial activity. Robust *post mortem* techniques include ring counting in trees of known age (e.g. Couralet et al. 2005) and radiocarbon dating during the second half of the twentieth century when the atmospheric ^{14}C concentration was elevated dramatically by extensive bomb testing (e.g. Worbes and Junk 1989). Recently, high-resolution stable isotope ratio measurements have revealed seasonal cycles that may be employed to date tree samples as well (e.g. Anchukaitis et al. 2008; Verheyden et al. 2004a). It has been shown that crossdating alone cannot prove the annual nature of tree rings if the correlation between the ring width series is low (Wils et al. 2009). Crossdating tends to be particularly difficult in young trees due to weak ring distinctness and in old trees, due to frequent occurrence of false and partial rings (Wils et al. 2010a).

Successful studies in sub-Saharan Africa outside Ethiopia report mean inter-correlations between crossdated ring width series of 0.24 (Trouet et al. 2006) to 0.63 (Therrell et al. 2006). Most studies are concerned with climatology (e.g. Fichtler et al. 2004; Schöngart et al. 2006; Therrell et al. 2006; Trouet et al. 2006, 2010), but tend to be complicated by low numbers of samples, short chronologies and/or low correlations between the chronologies and instrumental climate data. Only Therrell et al. (2006) have been able to develop a climate reconstruction, spanning AD 1796–1996 and based on widths of tree rings in *Pterocarpus angolensis* D.C. from Zimbabwe. Other studies deal with silvicultural applications of dendrochronology (Therrell et al. 2007; Worbes et al. 2003).

Dendrochronology in Ethiopia

Ethiopia is a mountainous country in the Horn of Africa. The lowlands are characterised by a hot, (semi-)arid climate, whereas the highlands are cooler and receive ample

rainfall due to orographic forcing of air masses. Three seasons are recognised: the major wet season (May–September), the minor wet season (February–May) and the dry season (October–January). The nature and length of the seasons and the amount of rainfall vary spatially (Fig. 1). The western highlands are the most important source area of the River Nile.

Lowlands

In the lowlands of Ethiopia, dendrochronological work has been concentrated in the Rift Valley south of Addis Ababa. Sampled trees have been mostly drought-deciduous *Acacia* species [*Acacia senegal* (L.) Willd., *Acacia seyal* Del., *Acacia tortilis* (Forsk.) Hayne (Gebrekirstos 2006; Gebrekirstos et al. 2008, 2009) and *Acacia etbaica* Schweinf. (Eshete and Ståhl 1999)], but Gebrekirstos (2006) and Gebrekirstos et al. (2008, 2009) also studied the co-occurring evergreen species *Balanites aegyptiaca* (L.) Del. Trees have been sampled at the Abernosa woodlands (R in Fig. 1) (Gebrekirstos 2006; Gebrekirstos et al. 2008, 2009), Alagae, Ziway and Awasa plantations, and the Langanoo woodlands (all between R and V in Fig. 1) (Eshete and Ståhl 1999).

Ring boundaries in African *Acacia* species are delimited by long calcium oxalate crystal chains and often marginal parenchyma cells (Fig. 2) (Gourlay 1995a, b; Nicolini et al. 2010). X-ray density measurement of *Acacia* samples has not allowed or aided the identification of ring boundaries, due to high wood density, the presence of gums and a complex wood anatomy (Eshete and Ståhl 1999; Gourlay 1995a). In *Balanites aegyptiaca*, ring boundaries are delimited by vessels surrounding a narrow band of marginal parenchyma cells (Gebrekirstos et al. 2008). The number of growth rings per year depends on the number of wet seasons, and on the severity of the dry seasons experienced at the tree stand (Eshete and Ståhl 1999; Gourlay 1995b).

Tree rings have been successfully identified in samples from Ethiopian *Acacia* species and *Balanites aegyptiaca* by Eshete and Ståhl (1999) and Gebrekirstos et al. (2008), though all core and many stem-disc samples had to be discarded [87% by Eshete and Ståhl (1999) and 20% by Gebrekirstos et al. (2008)] as unsuitable for dendrochronological work. In these samples, tree rings could not be identified or crossdated, due to potentially missing rings, deviating responses to environmental factors and, particularly, human disturbance. Most of the stem discs obtained from an enclosed ranch, where human disturbance is negligible, could be crossdated (Gebrekirstos et al. 2008). Radial growth variations of crossdated trees studied at the Abernosa woodlands suggested that *Acacia tortilis* and *Balanites aegyptiaca* are more tolerant to drought, but less

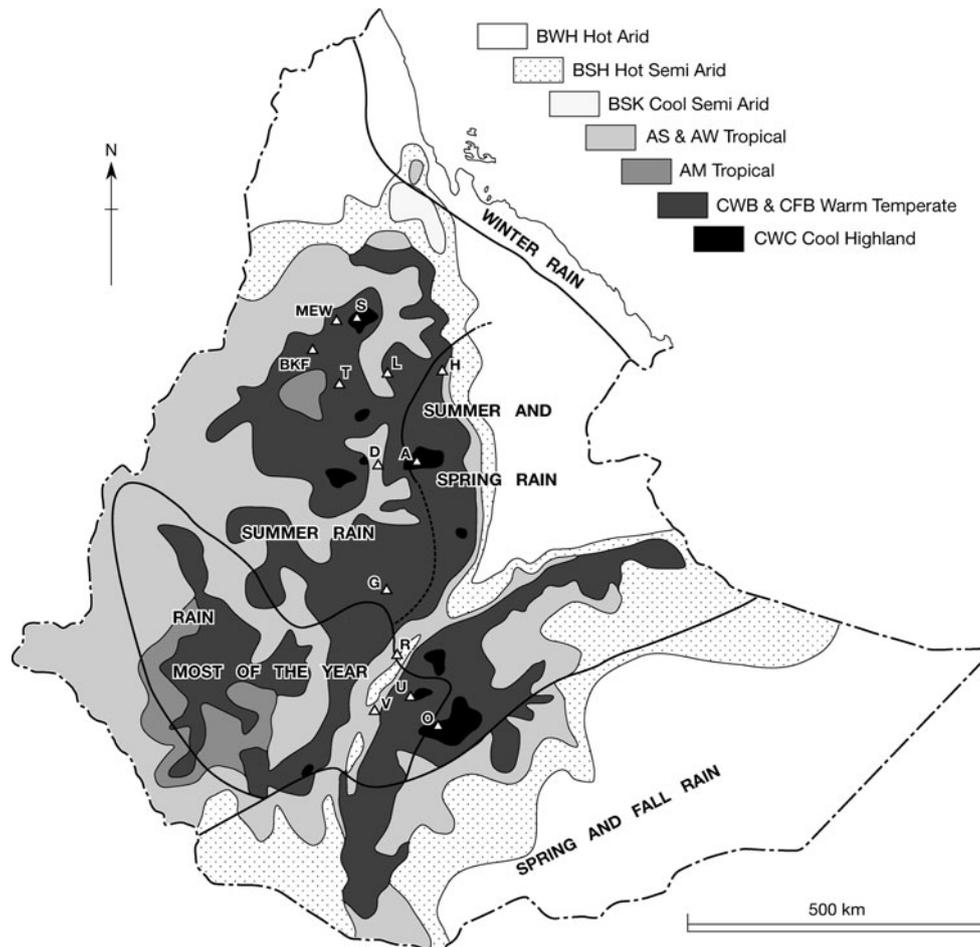


Fig. 1 Climate and rainfall patterns in Ethiopia and Eritrea (after EMA 1988; Wils et al. 2009). Study sites of various researchers are indicated: Abernosa woodlands (R), Shashemene plantation (V), Menagesha-Suba forest (G), Adaba-Dodola forest (O), Semien Mountains (S), Taragadem forest (T), Doba forest (A), Denkoro forest (D), Gomia-Mariam forest (M), Debre Kidane-Mihret forest (E), Woken-Woybila-Mariam church (W), Kuskum church (K), Debrebirkan Selassie church (B), Hugumburda forest (H), Lalibela forest (L), Fasiledes bath (F) and Munessa forest (U). Gebrekirstos (2006) and Gebrekirstos et al. (2008, 2009) sampled trees at site R. Eshete and Ståhl (1999) sampled trees at four sites (Alagae, Ziway

and Awasa plantations, and Langano woodlands) between sites R and V. Couralet (2004), Couralet et al. (2005, 2007) and Sass-Klaassen et al. (2008a) sampled trees of known age at site V and trees of unknown age at sites G and O. Conway et al. (1997, 1998) sampled trees at sites G, S and T. Wils (2007, 2009), Wils and Eshetu (2007) and Wils et al. (2008, 2009, 2010a, b) sampled trees at sites A, D, M, E, W, K and B. Eshetu (2006) sampled trees at site H. Z. Eshetu sampled trees at site L (not published). M. Koprowski sampled trees at site F (not published). Krepkowski et al. (2010) are currently monitoring tree growth at site U

vigorous under wetter conditions than *Acacia senegal* and *Acacia seyal* (Gebrekirstos et al. 2008), supporting findings by Gebrekirstos et al. (2006, 2010).

A ring width chronology spanning 68 years was developed for the Abernosa woodlands (Gebrekirstos et al. 2008). It correlated with total precipitation during the wet season ($r = 0.61$, $p < 0.01$, 67-year overlap). Pointer years [conspicuous growth rings replicated in several series (Schweingruber et al. 1990)] characterised by narrow rings corresponded to years of drought and famine reported by Degefu (1988) and El Niño years, and spectral analysis revealed cycles at periodicities characteristic of the El Niño-Southern Oscillation (ENSO) phenomenon

(2–8 years). The strong correlation between the chronology and climate data was interpreted as a convincing indication that the tree rings were annual in nature (Gebrekirstos et al. 2008).

Gebrekirstos et al. (2009) measured carbon isotope ratios ($\delta^{13}\text{C}$) on tree rings of *Acacia* species from the Abernosa woodlands at an annual resolution. The individual series were combined into a master $\delta^{13}\text{C}$ chronology. This chronology correlated with total precipitation during the wet season ($r = -0.82$, $p < 0.01$, 30-years overlap) and with the Abernosa ring width chronology ($r = -0.77$, $p < 0.01$, 30-year overlap), suggesting a strong response to water availability (Gebrekirstos et al. 2009, 2010).

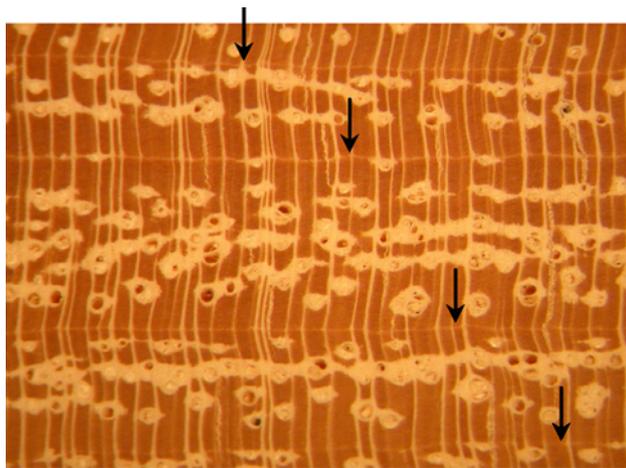


Fig. 2 Growth rings in a *Acacia tortilis* disc sample from the Abernosa woodlands (R) (after Gebrekirstos 2006; Gebrekirstos et al. 2008). Boundaries of annual rings are indicated by arrows

Highlands

In the highlands of Ethiopia, exploratory expeditions by Briffa and Russell-Smith (1986) and Conway et al. (1997, 1998) identified *Ekebergia capensis* Sparrm. and particularly *Juniperus procera* Hochst. ex Endlicher as potential candidates for dendrochronology. Subsequent research has been focused on *Juniperus procera*, though Wils and Eshetu (2007) also hypothesise that growth rings in *Prunus africana* (Hook f.) Kalkman are annual in nature. Trees have been sampled in Afromontane Forests and church compounds under various rainfall regimes. Locations are plotted in Fig. 1: various forests in the Semien Mountains (S), Taragadem forest (T), Menagesha-Suba forest (G), Adaba-Dodola forest (O), Shashemene plantation (V) (Conway et al. 1997, 1998; Couralet 2004; Couralet et al. 2005, 2007; Sass-Klaassen et al. 2008a), Doba forest (A), Denkoro forest (D), Gomia-Mariam forest (M), Debre Kidane-Mihret forest (E), Woken-Woybila-Mariam church (W), Kuskum church (K), Debrebirkan Selassie church (B) (Wils 2007, 2009; Wils and Eshetu 2007; Wils et al. 2008, 2009, 2010a, b), Hugumburda forest (H) (Eshetu 2006), Lalibela forest (L) (Z. Eshetu, not published) and Fasiledes bath (F) (M. Koprowski, not published).

Juniperus procera is an irregularly growing, evergreen conifer, which can achieve a relatively high age. The wood is resistant to decay and has therefore been used extensively for building purposes. Though widespread cutting has reduced forest cover in Ethiopia, many *Juniperus procera* trees have been protected on lands owned by the Ethiopian Orthodox Church (Wassie et al. 2009).

Ring boundaries in *Juniperus procera* can be identified from the alternation of small, flattened and thick-walled tracheids in the darker latewood and large, round and

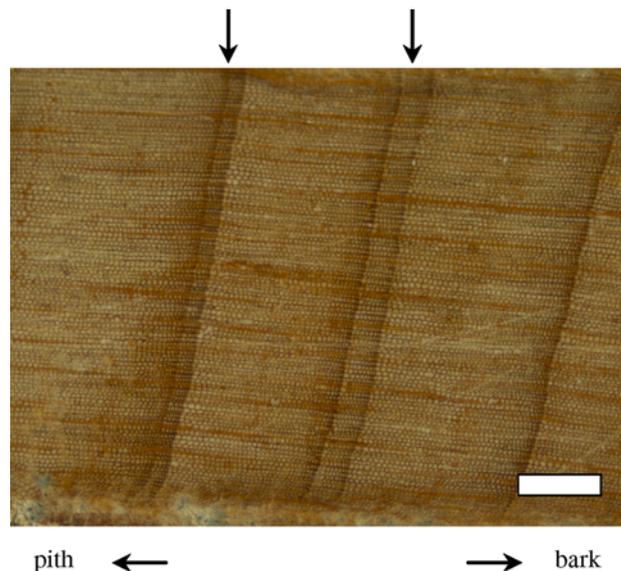


Fig. 3 Growth rings in a *Juniperus procera* core sample from Gomia-Mariam forest (M) (Wils et al. 2010a). False rings are indicated by arrows at the top. Growth is from left to right, magnification is 4× and scale bar is 500 μm

thin-walled tracheids in the lighter earlywood (Fig. 3). Similar to *Acacia* species, the number of growth rings per year is variable and seems to depend on the number of wet seasons and the severity of the dry seasons experienced at the tree stand (Jacoby 1989; Wils et al. 2009).

Growth rings have been identified at all sites, but could only be crossdated successfully at sites G, O, V (stem discs) (Couralet et al. 2005, 2007), M, E, W, K and B (cores) (Wils et al. 2010a). The annual nature of the growth rings was confirmed by ring counting in plantation trees [site V (Couralet et al. 2005, 2007)] or AMS radiocarbon dating (Wils et al. 2010b). On the other hand, growth rings at sites A and D were neither annual nor synchronous in nature (Wils 2009; Wils et al. 2009) and studies at sites S, T, H, L and F have remained inconclusive so far (Conway et al. 1998; Eshetu 2006). Mean annual radial growth varied considerably in relation to site conditions (1.5–4.0 mm/year), whereas age trends were not apparent in the ring width series (Couralet et al. 2005; Wils 2009).

Ring width chronologies were developed for sites G, O [southern sites (Couralet et al. 2005, 2007; Sass-Klaassen et al. 2008a)], M, E, W, K and B [northern sites (Wils 2009; Wils et al. 2010b)], varying from 61 (E) to 290 (B) years in length. The southern ring width chronologies correlated with total precipitation during the wet season ($r = 0.33$ (G) and $r = 0.49$ (O), $p < 0.02$, 53-year overlap) (Sass-Klaassen et al. 2008a). The northern ring width chronologies display correlations with Blue Nile river flow during the preceding dry season (up to $r = 0.63$ (W vs. December flow), $p < 0.01$, 90-year overlap) (Wils et al. 2010b).

The first stable isotope measurements on *Juniperus procera* wood were made on trees from Kenya (δD) and could be related to variations in the level of Lake Victoria (Krishnamurthy and Epstein 1985). Recently, Wils (2009) measured carbon isotope ratios on tree rings of four *Juniperus procera* trees from Kuskuum church (K) at an annual resolution. From the $\delta^{13}C$ and ring width data from sites W, K and B a preliminary reconstruction of Blue Nile baseflow could be developed, spanning the period AD 1836–2006 (Wils et al. 2010b). This reconstruction explained 56% of the variance in mean Blue Nile river flow during December and January of the preceding dry season ($r = 0.75$, $p < 0.01$, $EPS = 0.85$, 91-year overlap) (Wils et al. 2010b). It captures years of drought and famine reported in 1837, 1845, 1858, 1875, 1889, 1899 and 1914 (Degefu 1988; Nicholson 2001) and a period of declining flow during the 1960s coincides with reported drought from 1964 to 1966 and in 1969 (Degefu 1988).

Synthesis and discussion

Though the Conway et al. (1997, 1998) exploratory expedition was initially species-oriented, its results and subsequent research indicated that it is not only the species that determines whether a tree forms annual growth rings or not. Regardless of species, a high percentage of the samples obtained from the lowland sites Langanu (between R and V) and Abernosa (R) woodlands, and all samples obtained from Alagae, Ziway and Awasa plantations (between R and V) were discarded, as they displayed either more or less growth rings than would be expected if the rings were annual (Eshete and Ståhl 1999; Gebrekirstos et al. 2008). In the highlands, annual growth rings were observed in many *Juniperus procera* samples, but notably not at all sites. Doba (A) and Denkoro forests (D) yielded samples with, respectively, more and less growth rings than expected if annual (Wils 2009; Wils et al. 2009). Two out of seven trees sampled at Kuskuum church (K) could not be crossdated as well, probably because of multiple missing rings (Wils et al. 2010a). A few individual cores from the northern sites contained ring width patterns that were too different to crossdate with confidence (Wils 2009).

In the lowlands, the distinction between suitable and unsuitable samples could be attributed to plant-level access to water, the degree of human disturbance and the availability of stem discs rather than cores (Eshete and Ståhl 1999; Gebrekirstos et al. 2008). In the highlands, this distinction could be primarily attributed to differences in precipitation regime (Fig. 1) and groundwater flow. Doba (A) and Denkoro (D) forests are located at the border of two relatively dry rainfall regimes and experience not only low but also highly erratic precipitation during the minor

wet season. Doba forest, located at the top of a mountain ridge, is well-drained; hence, trees respond to multiple dry spells per year (Wils et al. 2009). On the other hand, Denkoro forest, located on a slope, receives groundwater flow more continuously; hence, ring formation occurs rarely (Wils 2009). Additional variability may be caused by the incidence of mist (Kerkfoot 1964) and frost at night (Cherubini et al. 2003). Variability within sites, notably within Doba forest (A) where ring patterns were not even synchronous, and also at Kuskuum church (K), may be related to differences in tree vitality, growth history, age, habitat and anthropogenic pressure from wood harvesting (Cherubini et al. 2003; De Luis et al. 2007; Martín-Benito et al. 2008; Wils 2009; Wils et al. 2009). Some individual cores could not be crossdated, because of the irregular radial growth of *Juniperus procera*, yielding many partial [either wedging or partially indistinct (Worbes 1995)] rings. Note that the samples that could be crossdated contained multiple false and indistinct growth rings (Fig. 3) as well, but those could be identified as such during crossdating (Wils et al. 2010a).

In summary, four major types of growth ring periodicity can be identified: anatomically not distinct rings [e.g. D, as is typical of many trees growing in the tropics (Worbes 2002)]; multiple rings per year [e.g. A, as is typical of certain tree species growing in the Mediterranean (Cherubini et al. 2003)]; annual rings (as is typical of trees growing in temperate and boreal regions); and multiple missing rings [e.g. two trees at K, as is typical of trees growing in arid regions (Sass-Klaassen et al. 2008b)]. The type of periodicity is associated with large-scale variations in precipitation regime (unimodal to multimodal) and tree sensitivity to water availability (sensitive to complacent). The latter factor is highly variable in space and time, depending on water availability (precipitation, evapotranspiration, mist, soil type, relief, rooting depth, plant interactions), biological factors (vitality, growth history, age, faunal pressure, species, phenology, nutrient availability), frost damage and anthropogenic disturbance. In Table 1 the situation is summarised for each (group of) study site(s) discussed in this review.

Based on the studies reviewed, a scheme was developed that can be used to predict the occurrence of the various types of periodicity from the prevailing precipitation regime and local tree sensitivity (Fig. 4). Multimodal rainfall regimes are expected to increasingly cause missing rings in sensitive trees at dry locations, as the wet seasons will often be too short to initiate tree growth. In complacent trees at wet locations, rings are expected to be increasingly indistinct under multimodal rainfall regimes, as the dry seasons will often be too short and/or wet to retard or stop growth (e.g. site D). Multiple rings are expected to occur in sensitive trees at intermediate to dry locations experiencing

Table 1 Dominant type of growth ring periodicity, precipitation regime and tree sensitivity to water availability for the study sites discussed in this review

Area and sites	Dominant type of growth ring periodicity	Precipitation regime	Tree sensitivity to water availability
Southern Rift Valley lowlands			
Sites RV	Various, including annual rings	Rains from March to September, though dry spells may occur from March to June	Intermediate
Northwestern highlands			
Sites BKMEW	Annual rings	Rains from June to September	Intermediate to sensitive
Site A	Multiple rings	Small rains from March to May, main rains from July to September, though small rains can be discontinuous or continue until main rains	Sensitive
Site D	Anatomically not distinct rings	Rains from March to September, though dry spells may occur from March to June	Complacent
Sites TSL	Inconclusive	Rains from June to September	Inconclusive
Site H	Inconclusive	Small rains from March to May, main rains from July to September, though small rains can be discontinuous or continue until main rains	Inconclusive
Southern highlands			
Sites GO	Annual rings	Rains from March to September, though dry spells may occur from March to June	Intermediate

Tree sensitivity to water availability and causative growth ring periodicity may vary strongly within sites

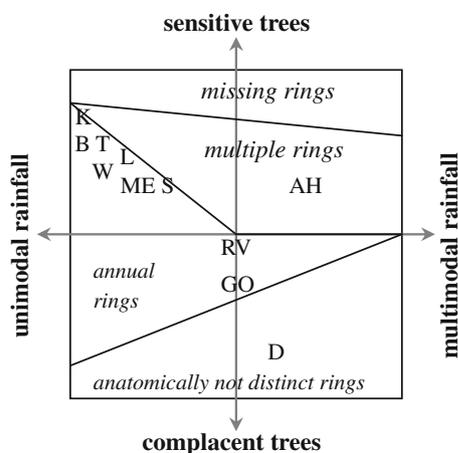


Fig. 4 Scheme indicating various types of growth ring periodicity along gradients in rainfall regime (unimodal to multimodal) and tree sensitivity to water availability (sensitive to complacent). Although conditions may vary strongly within sites, the approximate average positions of the study sites discussed in this review are indicated by their corresponding letters. The conditions at those study sites are hypothetical for the inconclusive sites *S*, *T*, *H* and *L*, while the conditions at the other sites constitute the empirical basis of the scheme. For more information, see Table 1

multimodal rainfall regimes (e.g. site A). Annual rings are expected to be formed if every year conditions are wet enough to allow growth during the major wet season and potential minor dry seasons, whilst dry enough to substantially retard or stop growth during the major dry season.

Figure 4 essentially displays a set of empirically founded hypotheses that can be tested by monitoring tree growth under various rainfall regimes and well-documented local conditions. Such studies should be combined with the collection and routine examination of parallel meteorological and hydrological measurements, and with mechanistic modelling of tree growth (Vaganov et al. 2010). Quantitative observations of tree growth, cambial activity, tree physiology and phenology can be made by dendrometer measurements (Couralet et al. 2010; Deslauriers et al. 2007), cambial sampling (Rossi et al. 2006) and pinning (Verheyden et al. 2004b), quantitative wood-anatomical analysis (De Luis et al. 2007; Fonti et al. 2009), growth experiments (Heinrich and Banks 2006), phenological measurements (Lavender 1991; Leblanc et al. 2005) and comparative assessment of rooting depth.

As growth ring formation in dry tropical regions (like Ethiopia), as opposed to temperate and boreal regions, can be more sensitive to conditions that are generally less predictable and more variable, trees growing at the limits of their ecological amplitude are prone to possess multiple rings per year (e.g. site A) or multiple missing rings (e.g. two trees at site K). The latter problem was also observed by Fritts (1976) at the extreme upper edge of the timberline. The principle of site selection at the limits of the ecological amplitude of a species should therefore be applied with care everywhere, but in dry tropical regions the problems are such that the principle seems invalid. Hence, site selection in dry tropical regions for dendrochronological studies

should not always take place at the limits of the ecological amplitude of a species, but may sometimes have to be diverted to more mesic environments.

The proven opportunity to identify and crossdate annual tree rings in Ethiopian trees and the strong correlation of growth ring variables with environmental variables demonstrate that dendrochronology can be applied successfully in Ethiopia, particularly in regions experiencing a unimodal rainfall regime. These results in combination with those from other dry tropical regions, particularly Zimbabwe (Therrell et al. 2006), indicate that dendrochronology in the dry tropics is now developing beyond potential.

Recommendations

An improved understanding of the processes governing growth ring formation can be achieved by an extension of the network of sites and by intensive monitoring of tree growth in relation to environmental factors. Recently, a study combining dendrometer measurements and cambial sampling has been started in Munessa forest (U in Fig. 1) (Krepkowski et al. 2010).

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