DENDROCLIMATOLOGY USING TROPICAL BROAD-LEAVED TREE SPECIES – A REVIEW

Esther Fichtler

With 5 figures and 1 appendix
Received 16 April 2015 · Accepted 10 October 2015

Summary: Global change has led to the warming of the atmosphere and oceans, the diminishment of snow and ice, while the sea level is rising. These changes have widespread impacts on human and natural systems on all continents and across the oceans. In tropical regions, ecosystems and socio-economic cultures become more and more affected by the high vulnerability to extreme climate events, deforestation and population growth. Therefore long term climate records from these regions are needed to better understand the natural climate variability and to simulate the magnitude of human-induced factors on climate change. However, climate records from tropical regions are scarce in time and space. Whenever tree growth is limited directly or indirectly by climate variables that can be quantified and dated, dendroclimatological methods can be used to reconstruct past environmental conditions - dendroclimatology examines the relationship between tree growth and climate with an annual resolution. Dendroclimatology in the tropics still remains in an early stage, although paleoclimatic records from tropical regions are essential to our understanding of past changes in the Earth's climatic system, equator-to-pole linkages, and the prediction of sensitivity of tropical regions to future climate change. This review gives an overview on different aspects of tropical dendroclimatology on classical ring width studies in broad-leaved species, looking at two tropical biomes, moist broadleaf and dry broadleaf forests. It points to technical aspects of tropical dendrochronology and refers to a multitude of successful tree-ring studies of tropical species related to climate. This demonstrates that tropical dendroclimatology is undergoing a promising development; however, tropical tree-ring studies mainly take place in the dry tropics, while studies in the wet tropical forests are still the exception.

Zusammenfassung: Der globale Wandel führt zur Erwärmung der Atmosphäre und der Ozeane und der Abnahme von Schnee und Eis, während der Meeresspiegel steigt. Diese Veränderungen haben weitreichende Auswirkungen sowohl auf die Ökosysteme auf allen Kontinenten sowie der Weltmeere. In tropischen Regionen werden Ökosysteme und sozioökonomischen Kulturen mehr und mehr durch die hohe Anfälligkeit für extreme Klimaereignisse, Entwaldung und das stetige Bevölkerungswachstum beeinflusst. Für ein besseres Verständnis der natürlichen Klimaschwankungen und um den Einfluss des Menschen auf den Klimawandel besser simulieren zu können, sind langfristige Informationen zum Klima aus tropischen Regionen erforderlich. Es fehlen allerdings instrumentelle Messungen und Aufzeichnung gerade aus diesen Gebieten, sowohl in zeitlicher wie auch in räumlicher Hinsicht. Wann immer das Baumwachstum direkt oder indirekt von Klimavariablen abhängig ist, die quantifiziert und datiert werden können, ist es möglich, frühere Klimabedingungen mit Hilfe dendroklimatologischer Methoden zu rekonstruieren: die Dendroklimatologie untersucht die Beziehung zwischen Baumwachstum und Klima mit einer jährlichen Auflösung. Dendroklimatologie in den Tropen steckt noch immer in den Anfängen, obwohl paläoklimatische Datensätze aus tropischen Regionen dringend benötigt werden. Dieses Review gibt einen Überblick über die verschiedenen Aspekte der tropischen Dendroklimatologie basierend auf klassischen Ringbreiten-Studien in Laubbaumarten aus zwei tropischen Biomen, immerfeuchten Laub- und trockenen Laubwälder. Es verweist auf die technischen Aspekte der tropischen Dendrochronologie und auf eine Vielzahl erfolgreicher dendroklimatologischer Studien mit tropischen Laubbaumarten. Die tropische Dendroklimatologie durchläuft eine vielversprechende Entwicklung; allerdings finden klimatologische Jahrringstudien vermehrt in den trockenen Tropen statt, während Studien in den immerfeuchten Tropen noch immer die Ausnahme sind.

Keywords: Tree-rings, tropical dendroclimatology, moist broadleaf forest, dry broadleaf forest, climate-growth relationship

1 Introduction

The latest IPCC (Intergovernmental Panel on Climate Change) report (2014) indicates the unequivocal warming of the climate system since the 1950s clearly due to the human influence on the climate system with the highest anthropogenic emissions of greenhouse gases in history. This leads continuously to the warming of the atmosphere and oceans, the retreat of snow and ice, as well as a rise in sea level. These recent climate changes have had widespread impacts on human and natural systems on all continents and across the oceans.

https://doi.org/10.3112/erdkunde.2017.01.01 ISSN 0014-0015 http://www.erdkunde.uni-bonn.de

Forests play a vital role in climate change mitigation and contribute to soil and water conservation in many fragile ecosystems (FAO 2014). Tropical forests include four biomes: moist broadleaf, dry broadleaf, coniferous and mangrove forests (Olson et al. 2001). They fulfil important functions including the production of timber, fuel wood and non-timber forest products as well as social functions by providing subsistence for local populations and cultures (Montagini and Jordan 2005). Other important aspects are the diverse environmental functions of tropical forests, such as the influence on global hydrological cycles - evapotranspiration from tropical forests contribute to precipitation at higher latitudes as well as within the tropics (Avissar and Werth 2005). Tropical ecosystems are areas of great global biodiversity and contain over half of all globally described species (Groombridge and Jenkins 2003). Moreover, tropical forests play a key role in the global carbon cycle (Bonan 2008; Clark 2004), accounting for 32% of the net terrestrial carbon stocks and primary productivity (Dixon et al. 1994; Field et al. 1998). In tropical regions, ecosystems and socio-economic cultures are more and more affected by a high level of vulnerability to extreme climate events, deforestation and population growth. Therefore, long term climate records are needed, especially in tropical regions where proxy data are scarce in order to better understand natural climate variability. This is especially important if we are to accurately simulate the magnitude of human-induced factors on climate change (Schöngart et al. 2006).

Trees are long living organisms that record environmentally relevant information in their growth rings. Basically, a tree-ring represents a record of survival (Smith 2008), with the tree reacting as a filter (Fritts 1976): changes in environmental conditions are leading to physiological and metabolic reactions, which produce ring structures of different qualities and widths. Radial tree growth is the result of various internal and external factors. Therefore, dendrochronology defines ring width as a predictor of tree performance (Schweingruber 1996) in a changing environment. Abrupt changes are of special interest in dendrochronological studies, as these can be used to date and analyse the impact of certain incidents, such as extreme climatic events (Schöngart et al. 2004).

Essentially, dendroclimatology examines the relationship between tree growth and climate on the basis of annually resolved increments. Through the measurement of annual growth rings of several individuals of a tree species, continuous growth chronologies can be constructed. Whenever tree growth is limited directly or indirectly by climate variables, which can be quantified and dated, dendroclimatological methods can be used to reconstruct past environmental conditions. Tree-rings have unique advantages compared to other proxies (e.g. ice cores, lake sediments, etc.) as trees have a wide geographical distribution; their rings preserve a continuous record with an annual resolution and can consequentially be dated by ring counting (Managave and Ramesh 2012).

Currently, major research gaps exist concerning the dynamics of tropical forests, their resilience to drought and their status as carbon sinks. Interactions between climate and disturbances, such as fires, aerosols, and reactive gases and the effects of small-scale deforestation on cloud formation and precipitation are key unknowns (Bonan 2008). Projections concerning the effects of global change on forests remain highly uncertain (Clark and Clark 2011). Evidence of climate change in the tropics is difficult to verify by instrumental records, because they are limited spatially and temporally; long term climate data is often non-existent (Ramirez and Del Valle 2012). An effective way to extend such a time series backwards is by analyzing tree-rings over the full lifetime of trees, easily spanning over a century (Zuidema et al. 2012).

In the last 45 years dendrochronological methods for tree species of temperate zones have become increasingly sophisticated (overviews in Schweingruber 1996; Vaganov et al. 2006). Tree–ring chronologies from trees of these zones have been used in many ways to reconstruct diverse aspects of past climates (extensive overview in Hughes 2002). Thus the relevance of dendrochronology in global change studies is obvious. Excellent examples are the use of Northern hemisphere tree-ring data in reconstructions of temperature (e.g. Mann et al. 2003; Esper et al. 2002), or precipitation (e.g. Trouet et al. 2009; Büntgen et al. 2011). In contrast, tropical trees have long been considered impractical due to the supposed lack of annual growth rings in tropical trees. However, studies over the last two to three decades have unanimously shown that many tropical tree species develop annually visible rings, that dendrochronological methods could be effectively applied (extensive overviews in Worbes 2002; Rozendaal and Zuidema 2011). Nevertheless, the vast majority of tree-ring studies have so far been carried out in extra-tropical regions, and the analysis of tropical trees is still regarded as a challenging task

(Bräuning 2011). Therefore, dendroclimatology in the tropics remains at an early stage of development, although paleoclimatic records from tropical regions are essential for our understanding of past changes in the Earth's climatic system.

This paper aims to give an overview of different aspects of tropical dendroclimatology based on broad-leaved species. However, this is limited to a certain extent as the field of dendrochronology is split into many sophisticated sub-disciplines. This review concentrates on classical ring widths studies, which form the basis for developing an annually dated time series, necessary for most sub-fields. Furthermore, considering all tropical habitats would go beyond the scope of a journal paper. For this reason, this review focusses on two tropical biomes, i.e. moist broadleaf and dry broadleaf forests. Technical aspects of tropical dendrochronology will be treated, as well as the recent achievements of tropical tree-ring studies in relation to climate. Finally, this review will address the strengths and future challenges for dendroclimatology in the tropics.

2 State of the art methods in tropical dendrochronology

For over more than 100 years the existence of tropical tree-rings has been reported (for extensive historical overviews see Worbes 2002). In the last three decades, many studies have proven the annual nature of rings in broad-leaved tree species of tropical regions from arid zones (Gourlay 1995; Stahle et al. 1999; Fichtler et al. 2004; Trouet et al. 2006), humid zones (Fichtler et al. 2003; Couralet et al. 2010), inundation forests (Worbes 1985; Schöngart et al. 2002), mangroves (Menezes et al. 2003; Verheyden et al. 2004) and swamps (Callado et al. 2001). Analyzing a tree-ring time series provides information not only on the relative growth rates of trees over time, as well as the time needed to accumulate the biomass for single trees, but also on long term species performance, stand history as well as possible relationships to climate variability. In this way, annual tree-ring patterns of tropical tree species provide a reliable basis that can be used in various ways, namely to gain information on forest dynamics (e.g. Worbes et al. 1992; Brienen and Zuidema 2006a), tree age (e.g. Worbes and Junk 1999; Fichtler et al. 2003), growth rate (e.g. Worbes et al. 2003), to help develop climate reconstructions (e.g. Worbes 1999; Schöngart et al. 2004), to develop management criteria (e.g. Brienen and Zuidema 2006b; Schöngart 2008), and to estimate changes in the C-stocks of above-ground coarse wood biomass (Schöngart et al. 2010).

In contrast to temperate zones, relatively few applications have been developed for tropical regions (e.g. Worbes et al. 2003, Schöngart et al. 2004; 2006; Brienen and Zuidema 2006a, 2006b; Zuidema et al. 2011; Pumijumnong and Eckstein 2011). This is caused by limited technical facilities and financial resources in tropical countries themselves, but also due to the inaccessibility of stands. Additionally, low sampling replication can be a problem because of the enormous diversity of species that comes along with the low abundances of individuals of any particular species in most tropical forests. Standard non-destructive methods like coring are not suitable for most tropical broad-leafed species, as anatomical wood inspection and reliable tree-ring detection require a certain wood surface beyond those of a standard tree core.

2.1 Tree-ring detection

The basic requirement for the successful use of tropical dendroclimatology is the presence of annual ring structures in the wood. Trees all over the world face periodically unfavorable growing conditions and consequentially respond with reductions in cambial activity or with cambial dormancy. Parameters responsible for this behaviour are annual variations of precipitation (drought stress), low temperatures (frost) or flooding (water stress). Accordingly, radial growth is slowed down or interrupted for days or months. This results in different anatomical wood structures that appear as ring boundaries in the cross-section of the stem. These rings are annual if the triggering climate factors, such as a dry or rainless period (in most parts of the tropics), occur once a year (Worbes 1995). Macroscopically apparent growth structures become visible as rings in cross-sections of different zones or bands on sanded discs. In most cases, different colors within one growth zone can be traced back to the variation in wood density, where dark zones show a higher density. This is attributed to fiber cells with shortened radial diameters and thickened walls (Fig. 1). This is not only visible in coniferous wood, but also often observed in several broad-leaved families from the tropics (Worbes and Fichtler, 2010).

The high diversity of tropical woody species, however, is reflected by a high structural diversity of growth zones formed of different vessel, fiber, and

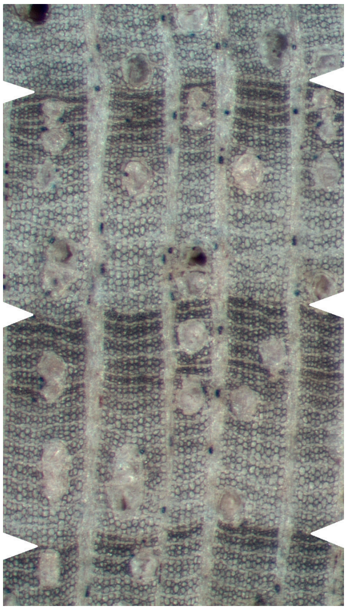

Fig. 1: *Duguetia sp.* from an inundation forest, Brazil, showing variation in wood density; dark zones show a higher density, which is attributed to fiber cells with shortened radial diameters and thickened walls.

parenchyma characteristics that can be classified by four basic tree-ring types (Fig. 1 and Fig. 2; Worbes 1985; Worbes and Fichtler 2010). The most common feature is a tree-ring boundary, consisting of either one or several rows of fibers with shortened radial diameters and thickened walls. This results in the above mentioned density variations. Also common, especially in the large family of Fabaceae, are boundaries with uni- or multi-rowed marginal bands of axial parenchyma cells, often filled with substances that are very light in appearance. The third type is characterized by periodically recurring parenchyma and fiber bands of different widths, resulting in a certain pattern delineating the boundary of the ring. The fourth type, often described for temperate tree species, but also occurring in tropical species, is characterized by a varying frequency of vessels and different diameters within a ring. The characteristics of these four types often occur in various combinations (Worbes and Fichtler 2010). It should be noted, however, that different rings within the same individual can show extremely dissimilar characteristics. The high variation of possible ring boundaries and the high plasticity within and between rings complicates tree-ring detection in tropical species. To use growth patterns for climatological tree-ring studies, a successful determination of tree-ring boundaries throughout a sample is required. To detect all boundaries, it is therefore essential to consider changes in the general pattern of the growth structure rather than searching for one specific character delineating tree-rings within a species (Worbes and Fichtler 2010). Further complications for the detection of tree-rings in tropical trees can arise due to the fact that in some species the visibility of tree-ring boundaries changes with ontogenetic development. Furthermore, very narrow rings sometimes consist of single cell rows and are hard to distinguish. Wedging rings are a common feature in many tropical species (Fig. 3). This is due to the failure of cambial activity at certain positions of the stem, which lead to ring boundaries merging. Some species may show ring boundaries that tend to gradually disappear or break-off (Worbes and Fichtler 2010). Dendrochronological investigations in those species would require the analysis of stem discs instead of cores to ensure the exact detection of all rings.

Currently, no techniques are available to substitute the immense skill of experts on wood anatomy, wood formation, and tree physiology necessary for the detection of tree-rings in tropical species. So far the high plasticity of the anatomical wood structures and, consequently, of tree-ring patterns have prevented technical innovations for automatic tree-ring detection in tropical species.

2.2 Building chronologies

Dendroclimatology focusses on tree-rings as natural archives of past climates. The field of dendroclimatology has matured in the last four decades since the first international workshop on dendroclimatology in 1974, and has evolved from a potentially interesting technical method of high-resolution paleoclimatology to an important source of evidence for policy-relevant decision making (cf. Hughes, 2002). The IPCC makes extensive references to the work on proxy records (Houghton et al. 2001), including tree-rings, and the field of dendroclimatology has experienced a huge increase in interest regarding discussions on climate change. In addition, within dendroclimatology itself, the climate change debate has gained interest.

The first step in dendroclimatology is to collect samples from a set of trees, whose growth is supposed to be limited by one or more climatic factors. It should be noted, however, that rarely one factor alone is responsible for tree growth. To develop a site chronology, individual series have to be cross dated and standardized (removal of age effects; Briffa 1999). On the basis of different site chro-

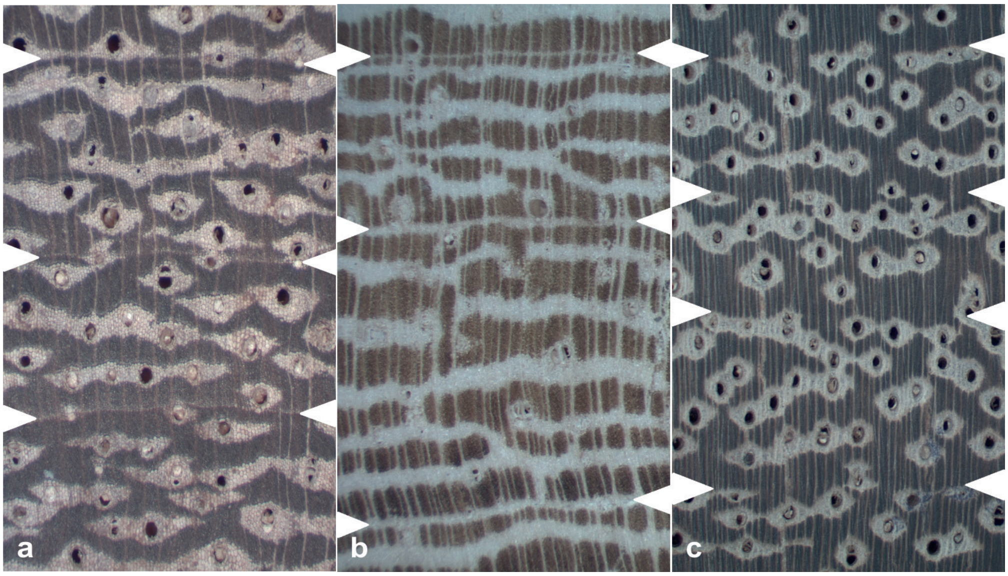

Fig. 2 a-c: Three different types of tree-ring structure (from left to right) *Tabebuia barbata* from inundation forests, Brazil; showing uni- or multi-rowed marginal bands of axial parenchyma cells, often filled with substances, of a very light appearance. *Lonchocarpus nelsii* from tropical dry forest, Namibia, showing periodically recurring parenchyma and fiber bands of different widths resulting in a certain pattern delineating the boundary of the ring. *Hymenolobium mesoamericanum* from a humid lowland rainforest, Costa Rica, showing a varying frequency of vessels exhibiting a vague band without vessels at the beginning of each ring. White triangles indicate tree ring boundaries; growth direction is from the bottom to the top.

nologies from a certain region, a tree-ring network can be built. Using statistical analyses the relation between tree-ring time series and instrumental climate data sets of recent periods should be established, thus leading to a calibration set for the tree-ring sequence of periods for which no meteorological data exist (Fritts 1976). Once such a relationship is established, it can be used to reconstruct climatic information for the whole time covered by the tree-ring data set. A full account of the methods of dendroclimatology and paleoclimate reconstruction from tree-ring analyses is given in sources of literature (e.g. Fritts 1976; Cook and Kairiukstis 1990; Briffa 1999; Esper et al. 2002). A dendroclimatic approach can primarily be applied to all the climate-dependent tree-growth variables, specifically tree-ring width, but also wood density, isotopic composition and wood anatomical variables, such as vessel diameter etc. (e.g. Fonti et al. 2010). With temperate tree species, density variations are particularly valuable, as they do not change significantly with tree age, and the process of standardization (removal of growth related developments) can, therefore, be avoided. To the author's knowledge, this has not been exploited so far for tropical broad-leaved species. The use of isotopic measurements in dendroclimatology also avoids the need for a standardization process. Stable isotopes of tree-rings can be used for paleoclimate reconstructions with perfect annual resolution and statistically defined confidence limits. Stable carbon isotopes record the balance between stomatal conductance and photosynthetic rate, dominated at dry sites by relative humidity and soil water status and at moist sites by summer irradiance and temperature. Stable oxygen and hydrogen isotopic ratios partly record source water, which contains a temperature signal, as well as leaf transpiration, mainly controlled by vapor pressure deficit (Mccaroll and Loader 2004). An overview on isotope dendroclimatology with special emphasis on the tropics is given by Managave and Ramesh (2012).

Fig. 3: Various positions with wedging rings in an individual of the species *Anogeissus leiocarpus* from Benin; growth direction is from the bottom to the top.

3 Dendroclimatological studies in the tropics - recent achievements

3.1 South America

The scarcity of instrumental records in South America makes proxy-based climatic reconstructions highly valuable. From temperate tree species more than 300 tree-ring chronologies have been developed in the last 40 years, making tree-ring records the most abundant and widely distributed high resolution climate archive in South America (Boninsegna et al. 2009). However, only a few chronologies from subtropical and tropical environments exist.

In subtropical regions Villalba et al. (1992, 1998) developed chronologies from montane trees using *Juglans australis* and *Cedrela lilloi* species growing on the eastern slopes of the Andes (22–28°S). These chronologies (spanning from 1897-1994 for *Juglans australis* and from 1804–1994 for *Cedrela illioi*) revealed rainfall distributions and temperature variations on tree growth, which has enabled the reconstruction of annual and seasonal variations in precipitation. For the subtropical lowland forest in northwestern Argentina, Ferrero and Villalba (2009) were able to develop a chronology from *Schinopsis lerentzii* covering a period from 1829–2004 showing that tree growth was positively correlated with precipitation.

In 2012, Ramirez and Del Valle revealed local and global climate signals from tree- rings of *Parkinsonia praecox* from the Colombian Coast. Here, a chronology made up of 18 trees was developed that allowed for the reconstruction of local and global climate drivers spanning the previous 63 years. The chronology strongly correlated with rainfall and wind data as well as with an index of ENSO (El Niño Southern Oscillation).

Locoselli et al (2013) studied climate-growth relationships of two *Hymenaea* species in a mosaic of semi deciduous forest and cerrado (savannah) in Brazilian Minas Gerais State. They performed a multi-proxy analysis including ring widths, stable carbon isotopes, and vessel area chronologies covering periods of 68 to 80 years. Both species responded positively to rainfall and negatively to temperature in similar ways, but with different intensities and at different times of the year.

In the tropical regions of South America most tree-ring studies have focused on the presence and periodicity of growth rings rather than on the development of chronologies. Nevertheless Dünisch et al. (2003) were able to cross date a *Swietenia macrophylla* as well as a *Cedrela odorata* time series from a primary forest near Mato Grosso State (Brazil) and to develop chronologies from 33 and 51 tree individuals respectively. For the period 1890–2000 the authors found significant correlations between precipitation at the beginning and the end of the growing season and ring widths of *S. macrophylla*, while *C. odorata* growth correlated with precipitation of some months of the previous growing season. In a following study on *Cedrela fissilis* from Mato Grosso State (Brazil), Dünisch (2005) could develop a chronology with 63 tree individuals covering the period from 1890–2000 and revealed a direct correlation between tree growth and precipitation for the second half of the previous growing season.

At about the same time Schöngart et al. (2004) presented the first ENSO-sensitive chronology derived from *Piranhea trifoliata* from white-water floodplains consisting of 10 trees spanning the period 1800–2000, which permitted the dating of pre-instrumental El Niño events. In another dendroclimatological study Schöngart et al. (2005) developed chronologies for *Macrolobium acaciifolium* from two floodplain forests in the Central Amazon (nutrient rich white water and nutrient poor black-water). These chronologies revealed a significant correlation of tree growth with the length of the terrestrial phase (vegetation period).

In the Bolivian Amazon region, Brienen and Zuidema (2005) studied the climate-growth relationship between tree species and rainfall. They found three species showing a strong relationship with precipitation at the beginning of the rainy season and one species being more sensitive to rainfall of the previous season.

In a study on *Cedrela montana* from a humid mountain forest in Ecuador Bräuning et al. (2009) could develop a ring width chronology reaching back to 1910 with tree growth significantly negatively correlating with temperature.

Recently, Pucha-Cofrep et al. (2015) developed chronologies for *Bursera graveolens* and *Maclura tinctoria* from a semi-humid region in a premontane forest in Ecuador (Laipuna Nature Reserve). Ring-width chronologies covered 103 and 48 years, respectively, and showed a good positive relation to precipitation and a negative relation to temperature.

According to the review of ‚Dendroclimatology in South America‘ by Boninsegna et al (2009) the development of chronologies in humid subtropical or tropical climates remains a major challenge. Despite obvious advances in the last decades, the number of existing tree-ring chronologies is rather poor in those regions. Nevertheless the future of dendroclimatology in tropical regions is thought to be extremely promising and the attempts to identify annual growth rings in subtropical and tropical species from South America are steadily increasing (cf. Ferrero et al. 2014).

3.2 Africa

Of all continents, Africa's activities for promoting science in the realm of climate are currently the lowest in comparison with other areas globally (Gebrekirstos et al. 2014). The lack of observational climate data in Africa is recognized as a strong limitation to understand current and future climate variability. Instrumental rainfall records are sparse in time and space (Nicholson 2001) and currently do not show long-term decadal variability. Compared to other parts of the world, the scientific understanding of the African climatic system as a whole is low. Climate change will affect all sectors of society, therefore, the development of regional and subregional climate models is needed. Recent African dendroclimatological approaches have provided the setup of very valuable chronologies, which show a strong relationship between precipitation and other climatic factors. Nevertheless, it has to be pointed out that only a few African chronologies cover more than 150 years.

For Southern Africa, Stahle et al. (1999) developed the first chronologies of *Pterocarpus angolensis* from Zimbabwe. These chronologies were continuously developed further by Stahle's group and resulted in a tree-ring reconstructed rainfall variability in Zimbabwe (Therell et al. 2006). Fichtler et al. (2004) were able to develop chronologies for *Burkea africana* and *Pterocarpus angolensis* from northern Namibia spanning the 20th century (Fig. 4). These chronologies revealed a strong positive relation with precipitation and a negative one with temperature. In addition, they showed a correlation to Enso indices.

Trouet et al. (2006) could build a regional chronology for *Brachystegia spiciformis* from Zambia covering 57 years, which showed a significant positive influence of rainfall and relative humidity during the core rainy season on tree growth. Temperature showed a strong negative correlation with tree growth. As the species *B. spiciformis* is one of the dominant tree species in the Miombo woodlands, it has great potential for future dendroclimatological studies, as this vegetation type covers more than 2.8 million square km in southern Africa. Consequently, Trouet et al. (2010) added five additional chronologies for *B. spiciformis* from Zambia and Tanzania covering periods between 43 and 149 years (within the period of 1853–2002). Four out of five chronologies showed a positive influence of precipitation during the peak rainy season on tree growth. The results of correlation analyses with relative humidity and temperature were in line with the positive relations found with precipitation. In addition, all chronologies showed a consistent correlation with ENSO-indices.

For Central Africa, Gebrekirstos et al. (2008) could develop chronologies spanning up to 68 years for three deciduous *Acacia* species and for an evergreen species (*Balanites aegyptiaca*) from the rift valley in Ethiopia. Tree growth was strongly correlated with precipitation during the wet season.

De Ridder et al. (2013) developed chronologies for *Terminalia superba* from a plantation (covering the period of 1959 to 2007) and for natural stands in the Democratic Republic of Congo (DRC; 1973–2008) as well as for natural stands in the Ivory Coast (1895–2008). At a regional scale all chronologies were positively correlated with precipitation, significantly with rainfall at the beginning of the rainy season. In addition, the authors found weak synchronous behavior between the stands, despite being located 2400 km apart. In a following study De Ridder et al. (2014) developed the first tree-ring chronology for *Pericopsis elata* from the DRC consisting of 24 trees from 1852 to 2008. For this species, tree growth is only positively correlated with precipitation during the months of the peak rainy season.

For West Africa Schöngart et al. (2006) developed chronologies for six species varying in length from 118 to 288 years (288 for *Daniella oliveri*, 198 years for *Afzelia africana*, 173 years for *Diospyros abyssinica*, 140 years for *Pterocarpus erinaceus*, 133 years for *Isoberlinia doka* and 118 years for *Anogeissus leiocarpus*) originating from the central-western part of Benin and the north-eastern Ivory Coast, enabling a reconstruction of annual precipitation for the central-western part of Benin back to 1840.

In a study on the dendrochronological potential of 14 tropical species in Western Kenya, David et al. 2014 found a significant correlation with annual precipitation and moisture index for two species only (*Acacia mearnsii* and *Eucalyptus camaldulensis*). However, the authors state that the other species also showed a direct relationship with precipitation. Increasing the sample size and lengths would help to strengthen the dendroclimatic results for those species.

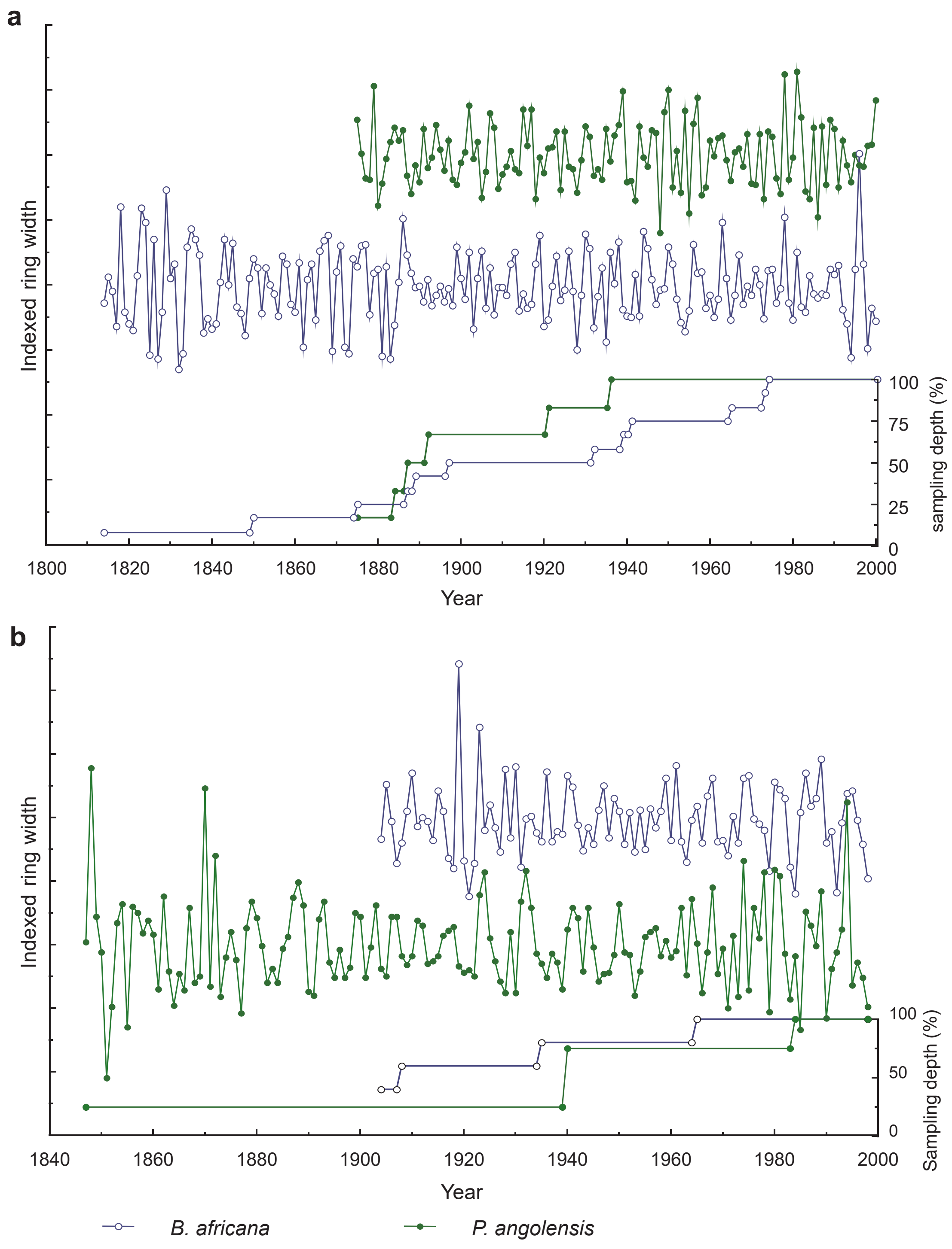

Fig. 4: Typical figure of indexed ring width chronologies and sampling depth for two species (*Burkea africana* and *Pterocarpus angolensis*) from two sites in Namibia, Ondangwa (a) and Katima Mulilo (b). Sampling depth 100% in Ondangwa for *B. africana* (12 trees), and for *P. angolensis* (5 trees); in Katima Mulilo for *B. africana* (5 trees), for *P. angolensis* (4 trees). Source: Fichtler et al. 2004.

In all of the broad-leaved species studied in Africa, precipitation (and relative humidity) had a positive influence on tree growth. There was often a negative correlation between growth and temperature. Some of these studies could prove the influence of ENSO on tree growth. Most studies were limited by sampling depths and chronology lengths. Nevertheless, they ended at revealing a climate-growth relationship and highlighted the great potential of several species. The next step requires the setup of tree-ring networks to extend the existing chronologies in time and space. This would allow climate reconstructions beyond instrumental records and could help to better understand the impact of global warming and extreme climatic events for the corresponding African regions.

3.3 Southeast Asia and Australia

For Southeast Asia teak (*Tectona grandis*) was one of the first tree species in tropical and subtropical regions used for dendroclimatological research (Fig. 5). Teak has a large natural geographical distribution, grown in countries such as India, Thailand, Myanmar and Laos. In addition, teak was brought to the Philippines and Indonesia. Berlage (1931) developed the first chronology and since then teak chronologies were continuously developed resulting in large compilations of teak tree-ring chronologies (e.g. Cook et al. 2010). In a recent review on dendrochronology in Southeast Asia, Pumijumnong (2013) gave a detailed overview on available teak chronologies and their response of tree growth to climate. Available teak chronologies are listed in the appendix cited after Pumijumnong (2013).

Besides teak studies, investigations on climate-growth relationships of broad-leaved trees from tropical and subtropical lowland forests are extremely rare. Only Vlam et al. (2014) developed chronologies for four species (*Afzelia xylocarpa, Chukrasia tabularis, Melia azedarach* and *Toona ciliata*) from western Thailand covering a time span of around 29 to 62 years. The authors found significant positive correlations between monthly precipitation and ring width for all species. In addition, all species showed strong negative correlations with wet season minimum temperatures.

For Australia, Heinrich et al. (2009) developed a chronology for *Toona ciliata*, with a length of 146 years, ranging from 1854 to 2000. The tree-ring widths showed significant positive correlations with precipitation and significant negative correlations with temperature over the period of 1900 to 2000, enabling rainfall reconstruction back to 1860. As *T. ciliata* has a wide natural distribution it would be a potential candidate for setting up a tree-ring network.

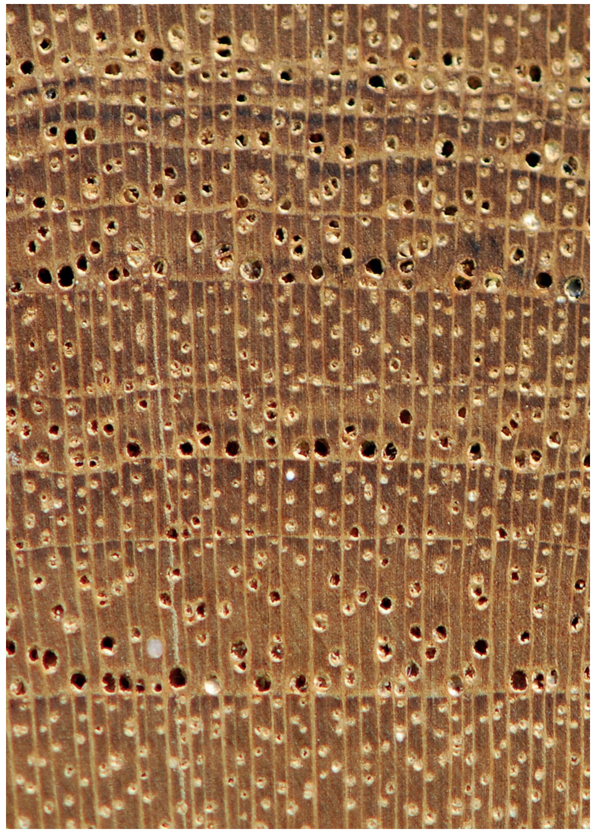

Fig. 5: Distinct tree ring structures in *Tectona grandis*; growth direction is from the bottom to the top.

4 Discussion

The large research gaps concerning the response of tropical trees and forests to climate change are mentioned continuously in various papers (e.g. Corlett 2011). However, the potential of tree-ring analyses to eliminate many of these research gaps does not seem to be adequately recognized (Zuidema et al. 2012). Despite the comparatively low scientific acceptance and attention in the past, tropical dendrochronologists continue to study the complexity of ring formation and anatomical plasticity to detect tree-ring boundaries in tropical broad-leaved species. The studies so far represent a considerable number of successful applications of dendroclimatological methods, originating from various continents with large climatic differences. Despite the heterogeneity of sample sites and species, tree growth was positively correlated with rainfall in all studies (except in montane habitats), often coupled with a negative correlation with temperature. In addition, diverse yet consistent relations to ENSO indices were found. This demonstrates the notion that tropical dendroclimatology is undergoing a promising development and can provide important information to better understand natural climate variability and the magnitude of human impact on tropical forests. Until now, tropical tree-ring studies mainly take place in the dry tropics, whereas studies in the wet tropical forests are still very much the exception - the spatial coverage of the chronologies in all tropical areas remains very limited.

Long-term monitoring studies indicate that forests in the tropics are rapidly changing. Directional changes have been reported for woody above-ground biomass, recruitment, growth and mortality rates of trees, the density of trees and especially woody vines or lianas. In addition, the species compositions of trees with respect to seed size, seed dispersal mode, wood density and maximum adult size (Wright, 2010) have also been reported. Taking into account the large share of tropical forests on a global scale (about 47%) in relation to the total global forested area, the understanding of tropical forest ecology and the evaluation of ongoing global climate change effects on tropical forests is of major importance. Yet no conclusive results exist on the effects of increasing CO_2 concentrations and elevated temperatures. Some studies have reported an increase in growth rate of tropical forest trees due to the physiological benefits of increasing levels of atmospheric CO_2 dominating potential negative temperature effects (Lewis et al. 2004). Others have reported a decrease in growth rate and declining productivity due to an increase in drought severity (Feeley et al. 2007). This lack of agreement is of great concern as the determination of growth rates of tropical trees is crucial to predict and define global carbon budgets (Houghton 2007; Caspersen et al. 2000).

Besides the insight into climate-growth relationships and the impact of climate change on tree growth, tree-ring chronologies serve as a vital source of reliable long-term data on increment and diameter-age relationships, which are urgently needed for sustainable forest management practices. In addition, long-term ring chronologies are a potentially powerful tool for analyzing demographic trends and ecological factors influencing tropical tree growth (Vetter and Botosso 1989). By looking back over the life time of a tree a better ecological understanding can be gained in relation to population dynamics or suppression and release effects. In particular, the increasing logging pressure on commercial timber species requires accurate information on growth rates and growth dynamics to implement effective management plans to ensure the survival of these species.

The successful set up of region wide tree-ring networks requires closer collaboration between researchers and the training of young scientists. This is crucial to make effective progress in tropical dendroclimatology. Future initiatives should focus on building up these networks to extend robust chronologies in time and space on the basis of widespread and locally dominant species. This is especially important for critical regions, where the environment is closely tied to its climate. The improvement of the predictive capacity of climate models concerning the impacts on tropical tree growth is highly necessary in terms of planning management strategies as well as for policy making.

References

Avissar, R. and Werth, D. (2005): Global hydroclimatological teleconnections resulting from tropical deforestation. In: Journal of Hydrometeorology 6, 134–145. https://doi.org/10.1175/jhm406.1

Berlage, H. P. (1931): Over het verband tusschen de dikte der jaarringen van djatiboomen (*Tectona grandis* L. F.) en den regenval op Java. In: Tectona 24, 939–953.

Bijaksana, S.; Ngkoimani, L. O.; D'Arrigo, R.; Krusic, P.; Palmer, J.; Sakulich, J. and Zulaikah, S. (2007): Status of tree-ring research from teak (*Tectona grandis*) for climate studies. In: Jurnal Geofisika 2, 1–7.

Bonan, G. B. (2008): Forests and climate change: forcings, feedbacks, and the climate benefits of forests. In: Science 320, 1444–1449. https://doi.org/10.1126/science.1155121

Boninsegna, J. A.; Argollo, J.; Aravena, J. C.; Barichivich, J.; Christie, D.; Ferrero, M. E.; Lara, A.; Le Quesne, C.; Luckman, B. H.; Masiokas, M.; Morales, M.; Oliveira, J. M.; Roig, F.; Srur, A. and Villalba, R. (2009): Dendroclimatological reconstructions in South America: A review. In: Palaeogeography, Palaeoclimatology, Palaeoecology 281, 210–228. https://doi.org/10.1016/j.palaeo.2009.07.020

Borgaonkar, H. P.; Sikder, A. B.; Ram, S.; Kumar, K. R. and Pant, G. B. (2007): Dendroclimatological investigations of high altitude Himalayan conifers and tropical teak in India. In: The Korean Journal of Quaternary Research 21, 15–25. https://doi.org/10.1007/s13196-012-0023-1

Borgaonkar, H. P.; Sikder, A. B.; Ram, S. and Pant, G. B. (2010): El Niño and related monsoon drought signals in 523-year-long ring width records of teak (*Tectona grandis* L.F.) trees from south India. In: Palaeogeography, Palaeoclimatology, Palaeoecology 285, 74–84. https://doi.org/10.1016/j.palaeo.2009.10.026

Buckley, B. M.; Palakit, K.; Duangsathaporn, K.; Sanguantham, P. and Prasomsin, P. (2007): Decadal scale droughts over northwestern Thailand over the past 448 years: links to the tropical Pacific and Indian Ocean sectors. In: Climate Dynamics 29, 63–71. https://doi.org/10.1007/s00382-007-0225-1

Bräuning, A. (2011): Editorial note for the special issue on 'Tropical Dendroecology'. In: Trees 25, 1–2. https://doi.org/10.1007/s00468-010-0530-x

Bräuning, A.; Volland-Voigt, F.; Burchardt, I., Ganzhi, O., Nauss, T. and Peters, T. (2009): Climatic control of radial growth of Cedrela montana in a humid mountain rainforest in southern Ecuador. In: Erdkunde 63, 337–345. https://doi.org/10.3112/erdkunde.2009.04.04

Brienen, R. J. W. and Zuidema, P. A. (2005): Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. In: Oecologia 146, 1–12. https://doi.org/10.1007/s00442-005-0160-y

– (2006a): Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. In: Journal of Ecology 94, 481–493. https://doi.org/10.1111/j.1365-2745.2005.01080.x

– (2006b): The use of tree rings in tropical forest management. Projecting timber yields of four Bolivian tree species. In: Forest Ecology and Management 226, 256–267. https://doi.org/10.1016/j.foreco.2006.01.038

Briffa, K. R. (1999): Interpreting high-resolution proxy climate data—the example of dendroclimatology. In: von Storch, H. and Navarra, A.: Analysis of climate variability. Berlin Heidelberg, 77–94. https://doi.org/10.1007/978-3-662-03167-4_5

Büntgen, U.; Tegel, W.; Nicolussi, K.; Mccormick, M.; Frank, D.; Trouet, V.; Et Al. (2011): 2500 years of European climate variability and human susceptibility. In: Science 331, 578–582. https://doi.org/10.1126/science.1197175

Callado, C.; Da Silva Neto, S.; Scarano, F. and Costa, C. (2001): Periodicity of growth rings in some flood-prone trees of the Atlantic Rain Forest in Rio de Janeiro, Brazil. In: Trees – Structure and Function 15, 492–497. https://doi.org/10.1007/s00468-001-0128-4

Caspersen, J. P.; Pacala, S. W.; Jenkins, J. C.; Hurtt, G. C.; Moorcroft, P. R. and Birdsey, R. A. (2000): Contributions of land-use history to carbon accumulation in Us forests. In: Science 290, 1148–1151. https://doi.org/10.1126/science.290.5494.1148

Clark, D. A. (2004): Tropical forests and global warming: slowing it down or speeding it up? In: Frontiers in Ecology and the Environment 2, 73–80. https://doi.org/0.1890/1540-9295(2004)002[0073:Tfagws]2.0.Co;2

Clark, D. A. and Clark, D. B. (2011): Assessing Tropical Forests' Climatic Sensitivities with Long-term Data. In: Biotropica 43, 31–40. https://doi.org/10.1111/j.1744-7429.2010.00654.x

Cook, E. R. and Kairiukstis, L. A. (eds.). (1990): Methods of dendrochronology: applications in the environmental sciences. Dordrecht. https://doi.org/10.1007/978-94-015-7879-0

Cook, E. R.; Anchukaitis, K. J.; Buckley, B. M.; D'Arrigo, R. D.; Jacoby, G. C. and Wright, W. E. (2010): Asian monsoon failure and megadrought during the last millennium. In: Science 328, 486–489. https://doi.org/10.1126/science.1185188

Corlett, R. T. (2011): Impacts of warming on tropical lowland rainforests. In: Trends in Ecology and Evolution 26, 606–613. https://doi.org/10.1016/j.tree.2011.06.015

Couralet, C.; Sterck, F. J.; Sass-Klaassen, U.; Van Acker, J. and Beeckman, H. (2010): Species-specific growth responses to climate variations in understory trees of a central African rain forest. In: Biotropica 42, 503–511. https://doi.org/10.1111/j.1744-7429.2009.00613.x

D'Arrigo, R.; Wilson, R.; Palmer, J.; Krusic, P.; Curtis, A.; Sakulich, J.; Bijaksana S.; Zulaikah, S. and Ngkoimani, L. O. (2006): Monsoon drought over Java, Indonesia, during the past two centuries. In: Geophysical Research Letters 33, L04709. https://doi.org/10.1029/2005GL025465

D'Arrigo, R.; Palmer, J.; Ummenhofer, C. C.; Kyaw, N. N. and Krusic, P. (2011): Three centuries of Myanmar monsoon climate variability inferred from teak tree rings. In: Geophysical Research Letters 38, L24705. https://doi.org/10.1029/2011gl049927

David, E. T.; Chhin, S. and Skole, D. (2014): Dendrochronological potential and productivity of tropical tree species in western Kenya. In: Tree–Ring Research 70, 119–135. https://doi.org/10.3959/1536-1098-70.2.119

De Boer, H. J. (1951): Tree ring measurements and weather fluctuations in Java from AD 1514. In: Royal Netherlands Academy of Arts and Sciences, Amsterdam B 54, 194.

De Ridder, M.; Trouet, V.; Van Den Bulcke, J.; Hubau, W.; Van Acker, J. and Beeckman, H. (2013): A tree-ring based comparison of *Terminalia superba* climate–growth relationships in West and Central Africa. In: Trees 27, 1225–1238. https://doi.org/10.1007/s00468-013-0871-3

De Ridder, M.; Toirambe, B.; Van Den Bulcke, J.; Bourland, N.; Van Acker, J. and Beeckman, H. (2014): Dendrochronological Potential in a Semi-Deciduous Rainforest: The Case of *Pericopsis elata* in Central Africa. In: Forests 5, 3087–3106. https://doi.org/10.3390/f5123087

Dixon, R. K.; Brown, S. R.; Houghton, A.; Solomon, A. M; Trexler, M. C. and Wisniewski, J. (1994): Carbon pools and flux of global forest ecosystems. In: Science 263, 185–190. https://doi.org/10.1126/science.263.5144.185

Dünisch, O. (2005): Influence of the El-niño southern oscillation on cambial growth of *Cedrela fissilis* Vell. in tropical and subtropical Brazil. In: Journal of applied botany and food quality 79, 5–11.

Dünisch, O.; Montóia, V. R. and Bauch, J. (2003): Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. In: Trees 17, 244–250. https://doi.org/10.1007/s00468-002-0230-2

Esper J.; Cook, E. R. and Schweingruber, F. H. (2002): Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. In: Science 295, 2250–2253. https://doi.org/10.1126/science.1066208

FAO (2014): State of the world's forests. enhancing the socioeconomic benefits from forests. Food and Agriculture Organization of the United Nations, Rome.

Feeley, K. J.; Wright, S. J.; Supardi, M. N. N.; Kassim, A. R. and Davies, S. J. (2007): Decelerating growth in tropical trees. In: Ecology Letters 10, 461–469. https://doi.org/10.1111/j.1461-0248.2007.01033.x

Ferrero, M. E. and Villalba, R. (2009): Potential of *Schinopsis lorentzii* for dendrochronological studies in subtropical dry Chaco forests of South America. In: Trees – Structure and Function 23, 1275–1284. https://doi.org/10.1007/s00468-009-0369-1

Ferrero, M. E.; Villalba, R. and Rivera, S. M. (2014): An assessment of growth ring identification in subtropical forests from northwestern Argentina. In: Dendrochronologia 32, 113–119. https://doi.org/10.1016/j.dendro.2014.01.003

Fichtler, E.; Clark, D.A. and Worbes, M. (2003): Age and long-term growth of trees in an oldgrowth tropical rain forest, based on analyses of tree rings and 14C. In: Biotropica 35, 306–317. https://doi.org/10.1111/j.1744-7429.2003.tb00585.x

Fichtler, E.; Trouet, V.; Beeckman, H.; Coppin P. and Worbes, M. (2004): Climate signals in tree rings of *Burkea africana* and *Pterocarpus angolensis* from semiarid forests in Namibia. In: Trees - Structure and Function 18, 442–451. https://doi.org/10.1007/s00468-004-0324-0

Field, C. B.; Behrenfeld, M. J.; Randerson, J. T. and Falkowski, P. (1998): Primary production of the biosphere: integrating terrestrial and oceanic components. In: Science 281, 237–240. https://doi.org/10.1126/science.281.5374.237

Fonti, P.; Von Arx, G.; García-González, I.; Eilmann, B.; Sass-Klaassen, U.; Gärtner, H. and Eckstein, D. (2010): Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. In: New Phytologist 185, 42–53. https://doi.org/10.1111/j.1469-8137.2009.03030.x

Fritts, H.C. (1976): Tree rings and climate. London, New York and San Francisco.

Gebrekirstos, A.; Mitlöhner, R.; Teketay, D. and Worbes, M. (2008): Climate-growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. In: Trees 22, 631–641. https://doi.org/10.1007/s00468-008-0221-z

Gebrekirstos, A.; Bräuning, A.; Sass-Klassen, U. and Mbow, C. (2014): Opportunities and applications of dendrochronology in Africa. Current Opinion in Environmental Sustainability 6, 48–53. https://doi.org/10.1016/j.cosust.2013.10.011

Gourlay, I.D. (1995): Growth ring characteristics of some African *Acacia* species. In: Journal of Tropical Ecology 11, 121–140. https://doi.org/10.1017/s0266467400008488

Groombridge, B. and Jenkins, M. D. (2003): World atlas of biodiversity. Earth's living resources in the 21st century. Berkeley, Los Angeles, London.

Heinrich, I.; Weidner, K.; Helle, G.; Vos, H.; Lindesay, J. and Banks, J. C. (2009): Interdecadal modulation of the relationship between Enso, Ipo and precipitation: insights from tree rings in Australia. In: Climate dynamics 33, 63–73. https://doi.org/10.1007/s00382-009-0544-5

Houghton, J. T.; Ding, Y.; Griggs, D. J.; Noguer, M.; van der Linden P. J. and Xiaosu, D. (eds.; 2001): Climate change 2001: the scientific basis - contribution of working group I to the IPCC Third Assessment Report, Cambridge

Hughes, M. K. (2002): Dendrochronology in climatology – the state of the art. In: Dendrochronologia 20, 95–116. https://doi.org/10.1078/1125-7865-00011

IPCC (2014): Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva.

Kyaw, N. N. (2003): Site influence on growth and phenotype of teak (*Tectona grandis* Linn. f.) in natural forests of Myanmar. PhD thesis. Göttingen.

Lewis, S. L.; Phillips, O. L.; Baker, T. R.; Lloyd, J.; Malhi, Y.; Almeida, S.; Higuchi, N.; Laurance, W. F.; Neill, D. A.; Silva, J. N. M.; Terborgh, J.; Lezama, A. T.; Martinez, R. V.; Brown, S.; Chave, J.; Kuebler, C.; Vargas. P. N. and Vinceti, B. (2004): Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. In: Philosophical Transactions of the Royal Society B 359, 421–436. https://doi.org/10.1098/rstb.2003.1431

Locosselli, G. M.; Buckeridge, M. S.; Moreira, M. Z. and Ceccantini, G. (2013): A multi-proxy dendroecological analysis of two tropical species (*Hymenaea spp.*, Leguminosae) growing in a vegetation mosaic. In: Trees 27, 25–36. https://doi.org/10.1007/s00468-012-0764-x

Managave, S. R. and Ramesh, R. (2012): Isotope dendroclimatology: A review with a special emphasis on tropics. In: Baskaran, M. (ed.): Handbook of environmental isotope geochemistry. Berlin, Heidelberg, 811–833. https://doi.org/10.1007/978-3-642-10637-8_38

Mann, M. E.; Ammann, C. M.; Bradley, R. S.; Briffa, K. R.; Crowley, T. J.; Hughes, M. K.; Jones, P. D.; Oppenheimer, M.; Osborn, T. J.; Overpeck, J. T.; Rutherford, S.; Trenberth, K. E. and Wigley, T. M. L. (2003): On past temperatures and anomalous late 20th century warmth. In: Eos 84, 256–258. https://doi.org/10.1029/2003eo270003

Mccarroll, D. and Loader, N. J. (2004): Stable isotopes in tree rings. In: Quaternary Science Reviews 23, 771–801. https://doi.org/10.1016/j.quascirev.2003.06.017

Menezes, M., U. Berger and Worbes, M. (2003): Annual growth rings and long-term growth patterns of mangrove trees from the Braganca Peninsula, Northern Brazil. In: Wetlands Ecology and Management 11, 233–242. https://doi.org/10.1023/A:1025059315146

Montagini, J. and Jordan, C. F. (2005): Tropical forest ecology. The basis for conservation and management. Berlin, Heidelberg.

Nicholson, S. E. (2001): A semi-quantitative, regional precipitation data set for studying African climates of the nineteenth century, part I. Overview of the data set. In: Climatic change 50, 317–353. https://doi.org/10.1023/A:1010674724320

Olson, D. M.; Dinerstein, E.; Wikramanayake, E. D.; Burgess, N. D.; Powell, G. V. N.; Underwood, E. C.; D'Amico, J. A.; Itoua, I.; Strand, H. E.; Morrison, J. C.; Loucks, C. J.; Allnutt, T. F.; Ricketts, T.H.; Taylor, H.; Kura, Y.;Lamoreux, J. F.; Wettengel, W. W.; Hedao, P. and Kassem, K. R. (2001): Terrestrial ecoregions of the world: a new map of life on earth. In: BioScience 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:Teotwa]2.0.Co;2

Palakit, K. (2004): Dendroclimatological studies of Teak (*Tectona grandis* L.F.): a case study in Mae Hong Son province, Thailand. PhD thesis. Salaya, Thailand.

Pucha-Cofrep, D.; Peters, T. and Bräunig, A. (2015): Wet season precipitation during the past century reconstructed from tree-rings of a tropical dry forest in Southern Ecuador. In: Global and Planetary Change 133, 65–78. https://doi.org/10.1016/j.gloplacha.2015.08.003

Pumijumnong, N. (2013): Dendrochronology in Southeast Asia. In: Trees – Structure and Function 27(2), 343–358. https://doi.org/10.1007/s00468-012-0775-7

Pumijumnong, N. and Eckstein, D. (2011): Reconstruction of pre-monsoon weather conditions in northwestern Thailand from the tree-ring widths of *Pinus merkusii* and *Pinus kesiya*. In: Trees – Structure and Function 25, 125–132. https://doi.org/10.1007/s00468-010-0528-4

Pumijumnong, N.; Eckstein, D. and Sass, U. (1995): Tree-ring research on *Tectona grandis* in northern Thailand. In: IAWA Journal 16, 385–392. https://doi.org/10.1163/22941932-90001428

Pumijumnong, N.; Eckstein, D. and Park, W. K. (2001): Teak tree-ring chronologies in Myanmar - a first attempt. In: Palaeobotanist 50, 35–40.

Ram, S.; Borgaonkar, H. P. and Sikder, A. B. (2008): Tree-ring analysis of teak (*Tectona grandis* L.F.) in central India and its relationship with rainfall and moisture index. In: Journal of earth system science 117, 637–645. https://doi.org/10.1007/s12040-008-0058-2

Ramírez, J. A. and Del Valle, J. I. (2012): Local and global climate signals from tree rings of *Parkinsonia praecox* in La Guajira, Colombia. In: International Journal of Climatology 32, 1077–1088. https://doi.org/10.1002/joc.2335

Rozendaal, D. M. A. and Zuidema, P.A. (2011): Dendroecology in the tropics: a review. In: Trees – Structure and Function 25, 3–16. https://doi.org/10.1007/s00468-010-0480-3

Schöngart J.; Piedade, M. T. F.; Ludwigshausen, S.; Horna V. and Worbes, M. (2002): Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. In: Journal of Tropical Ecology 18, 581–597. https://doi.org/10.1017/s0266467402002389

Schöngart, J.; Junk, W. J.; Piedade, M. T. F.; Hüttermann, A. and Worbes, M. (2004): Teleconnection between forest growth in the Amazonian floodplains and El Niño-Southern Oscillation effect. In: Global Change Biology 10, 683–693. https://doi.org/10.1111/j.1529-8817.2003.00754.x

Schöngart, J.; Piedade, M. T. F.; Wittmann, F.; Junk, W. J. and Worbes, M. (2005): Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. In: Oecologia 145, 454–461. https://doi.org/10.1007/s00442-005-0147-8

Schöngart, J.; Orthmann, B.; Hennenberg, K. J.; Porembski, S. and Worbes, M. (2006): Climate growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. In: Global Change Biology 12, 1139–1150. https://doi.org/10.1111/j.1365-2486.2006.01154.x

Schöngart, J. (2008): Growth-oriented logging (GOL): A new concept towards sustainable forest management in Central Amazonian varzea floodplains. In: Forest Ecology and Management 256, 46–58. https://doi.org/10.1016/j.foreco.2008.03.037

Schöngart, J.; Wittmann, F. and Worbes, M. (2010): Biomass and NPP of Central Amazonian floodplain forests. In: Junk, W. J.; Piedade, M. T. F.; Wittmann, F.; Schöngart, J. and Parolin, P. (eds.) (2010): Central Amazonian floodplain forests: ecophysiology, biodiversity, and sustainable management. Berlin. Heidelberg. New York.

Schweingruber, F. H. (1996): Tree rings and environment. Dendroecology. Birmensdorf.

Shah, S. K.; Bhattacharyya, A. and Chaudhary, V. (2007): Reconstruction of June–September precipitation based on tree-ring data of teak (*Tectona grandis* L.) from Hoshangabad, Madhya Pradesh, India. In: Dendrochronologia 25, 57–64. https://doi.org/10.1016/j.dendro.2007.02.001

Smith, K. T. (2008): An organismal view of dendrochronology. In: Dendrochronologia 26, 185–193. https://doi.org/10.1016/j.dendro.2008.06.002

Stahle, D. W.; Mushove, P. T.; Cleaveland, M. K.; Roig, F. and Haynes, G.A. (1999): Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. In: Forest Ecology and Management 124, 17–229. https://doi.org/10.1016/s0378-1127(99)00075-4

Therrell, M. D.; Stahle, D. W.; Ries, L. P. and Shugart, H. H. (2006): Tree-ring reconstructed rainfall variability in Zimbabwe. In: Climate Dynamics 26, 677–685. https://doi.org/10.1007/s00382-005-0108-2

Trouet, V.; Coppin, P. and Beeckman, H. (2006): Annual growth ring patterns in *Brachystegia spiciformis* reveal influence of precipitation on tree growth. In: Biotropica 38, 375–382. https://doi.org/10.1111/j.1744-7429.2006.00155.x

Trouet, V.; Esper, J.; Graham, N. E.; Baker, A.; Scourse, J. D. and Frank, D. C. (2009): Persistent positive North Atlantic Oscillation mode dominated the medieval climate anomaly. In: Science 324, 78–80. https://doi.org/10.1126/science.1166349

Trouet, V.; Esper, J., and Beeckman, H. (2010): Climate/growth relationships of *Brachystegia spiciformis* from the Miombo woodland in south central Africa. In: Dendrochronologia 28, 161–171. https://doi.org/10.1016/j.dendro.2009.10.002

Vaganov, E. A.; Hughes, M. K. and Shashkin, A. V. (2006): Growth dynamics of conifer tree rings - images of past and future environments. Berlin. Heidelberg. https://doi.org/10.1007/3-540-31298-6

Verheyden, A.; Kairo, J. G.; Beeckman, H. and Koedam, N. (2004): Growth rings, growth ring formation and age determination in the mangrove *Rhizophora mucronata*. In: Annals of Botany 94, 59–66. https://doi.org/10.1093/aob/mch115

Vetter, R. E. and Botosso, R. C. (1989): Remarks on age and growth rate determination of Amazonian trees. In: Iawa Journal 10, 133–146. https://doi.org/10.1163/22941932-90000481

Villalba, R.; Holmes, R. L. and Boninsegna, J. A. (1992): Spatial patterns of climate and tree growth variations in subtropical northwestern Argentina. In: Journal of Biogeography 19, 631–649. https://doi.org/10.2307/2845706

Villalba, R.; Grau, H. R.; Boninsegna, J. A.; Jacoby, G. C. and Ripalta, A. (1998): Tree-ring evidence for long-term precipitation changes in subtropical South America. In: International Journal of Climatology 18, 1463–1478. https://doi.org/10.1002/(Sici)1097-88(19981115)18:13<1463::Aid-Joc324>3.0.Co;2-A

Vlam, M.; Baker, P. J.; Bunyavejchewin, S. and Zuidema, P. A. (2014): Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. In: Oecologia, 174, 1449–1461. https://doi.org/10.1007/s00442-013-2846-x

Worbes, M. (1985): Structural and other adaptations to long-term flooding by trees in Central Amazonia. In: Amazoniana 9, 459–484.

– (1995): How to measure growth dynamics in tropical trees. A review. In: IAWA Journal 16, 337–351. https://doi.org/10.1163/22941932-90001424

– (1999): Annual growth rings, rainfall dependent growth and long-term growth patterns of tropical trees from the Forest Reserve Caparo in Venezuela. In: Journal of Ecology 87, 391–403. https://doi.org/10.1046/j.1365-2745.1999.00361.x

– (2002): One hundred years of tree ring research in the tropics - a brief history and an outlook to future challenges. In: Dendrochronologia 20, 217–231. https://doi.org/10.1078/1125-7865-00018

Worbes, M. and Junk, W. J. (1999): How old are tropical trees? The persistence of a myth. In: IAWA Journal 20, 255–260. https://doi.org/10.1163/22941932-90000689

Worbes, M. and Fichtler, E. (2010): Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. In: Junk, W. J.; Piedade, M. T. F.; Wittmann, F.; Schöngart, J. and Parolin, P. (eds.) Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Dordrecht., 329–346. https://doi.org/10.1007/978-90-481-8725-6_17

Worbes, M. Klinge, H.; Revilla, J. D. and Martius, C. (1992): On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. Journal of Vegetation Science 3, 553–564. https://doi.org/10.2307/3235812

Worbes, M.; Staschel, R.; Roloff, A. and Junk, W. J. (2003): Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. In: Forest Ecology and Management 173, 105–123. https://doi.org/10.1016/s0378-1127(01)00814-3

Wright, S. J. (2010): The future of tropical forests. In: Annals of the New York Academy of Sciences 1195, 1–27. https://doi.org/10.1111/j.1749-6632.2010.05455.x

Zuidema, P.A.; Vlam, M. and Chien, P. D. (2011): Ages and long-term growth patterns of four threatened Vietnamese tree species. In: Trees - Structure and Function 25, 29–38. https://doi.org/10.1007/s00468-010-0473-2

Zuidema, P. A.; Brienen, R. J. and Schöngart, J. (2012): Tropical forest warming: looking backwards for more insights. In: Trends in ecology and evolution 27, 193–194. https://doi.org/10.1016/j.tree.2011.12.007

Author

Esther Fichtler
Department of Crop Sciences
Crop Production Systems in the Tropics
Georg-August-Universität Göttingen,
Grisebachstraße 6
37077 Göttingen
Germany
efichtl@gwdg.de

Appendix

Summary of available tree-ring width chronologies from tropical broad-leaved tree species from moist broadleaf and dry broadleaf forests

Tree species	Location	Time span	Response	References
South America				
Juglans australis	Andes, subtropical montane forest	1814–1994, 1689–1981, 1783–1982	precipitation & temperature	Villalba et al. 1998
Cedrela lilloi	Andes, subtropical montane forest	1752–1994, 1810–1981, 1729–1982	precipitation & temperature	Villalba et al. 1998
Schinopsis lerentzii	Argentina, subtropical lowlands	1829–2004	precipitation	Ferrero and Villalba 2007
Parkinsonia praecox	Columbia, coast	1940–2003	precipitation, wind, ENSO	Ramirez and del Valle 2012
Hymenaea coubaril	Brazil, semideciduous forest & savannah	~1935–2010	precipitation & temperature	Locoselli et al. 2013
Hymenaea stigonocarpa	Brazil, semideciduous forest & savannah	~1935–2010	precipitation & temperature	Locoselli et al. 2013
Swietenia macrophylla	Brazil, tropical primary forest	1890–2000	precipitation	Dünisch et al. 2003
Cedrela odorata	Brazil, tropical primary forest	1890–2000	precipitation	Dünisch et al. 2003
Cedrela fissilis	Brazil, tropical primary forest	1890–2000	precipitation	Dünisch et al. 2005
Macrolobium acaciifolium	Brazil, Central Amazon Floodplain Forest	1857–2003, ~1605–2003	length of vegetation period	Schöngart et al. 2004a
Piranhea trifoliata	Brazil, Central Amazon Floodplain Forest	1800–2000	ENSO	Schöngart et al. 2004b
Cedrela montana	Ecuador, tropical mountain forest	1910–2007	temperature	Bräuning et al. 2009
Bursera graveolens	Ecuador, premontane dry forest	1908–2011	precipitation & temperature	Pucha–Cofrep et al. 2015
Maclura tinctoria	Ecuador, premontane dry forest	1964–2012	precipitation & temperature	Pucha–Cofrep et al. 2015
Amburana cearensis	Bolivia, tropical lowland forest	*not specified*	precipitation	Brienen and Zuidema 2005
Cedrela odorata	Bolivia, tropical lowland forest	*not specified*	precipitation	Brienen and Zuidema 2005
Cedralinga catenaeformis	Bolivia, tropical lowland forest	*not specified*	precipitation	Brienen and Zuidema 2005
Tachigali vasquezii	Bolivia, tropical lowland forest	*not specified*	precipitation	Brienen and Zuidema 2005
cariniana pyriformis	Colombia, Chocó	1828–2009	precipitation & ENSO	Moreno and del Valle 2015
Africa				
Pterocarpus angolensis	Zimbabwe	1876–1996, 1873–1997	precipitation	Stahle et al. 1999
Burkea afrikana	Namibia, Caprivi strip	1933–1998	precipitation & temperature	Fichtler et al. 2004
Pterocarpus angolensis	Namibia, Caprivi strip	1938–1998	precipitation & temperature	Fichtler et al. 2004
Burkea afrikana	Namibia, Oshikoto	1890–2000	precipitation & temperature	Fichtler et al. 2004
Pterocarpus angolensis	Namibia, Oshikoto	1920–2000	precipitation & temperature	Fichtler et al. 2004

Tree species	Location	Time span	Response	References
Brachystegia spiciformis	Zambia, Mongu, Miombo woodlands	1940–2002, 1953–2000, 1970–2000	precipitation & temperature	Trouet et al. 2006
Brachystegia spiciformis	Tanzania, Miombo woodlands	1955–1998	precipiation, temperature & ENSO	Trouet et al. 2010
Brachystegia spiciformis	Zambia, Livingstone, Miombo woodlands	1925–2002	precipiation, temperature & ENSO	Trouet et al. 2010
Brachystegia spiciformis	Zambia, Choma, Miombo woodlands	1901–2000	precipiation, temperature & ENSO	Trouet et al. 2010
Brachystegia spiciformis	Zambia, Mumbwa, Miombo woodlands	1853–2002	precipiation, temperature & ENSO	Trouet et al. 2010
Brachystegia spiciformis	Zambia, Mpika, Miombo woodlands	1871–2002	precipiation, temperature & ENSO	Trouet et al. 2010
Acacia senegal	Ethiopia, rift valley	1937–2003	precipitation	Gebrekirstos et al. 2008
Acacia seyal	Ethiopia, rift valley	1939–2003	precipitation	Gebrekirstos et al. 2008
Acacia tortilis	Ethiopia, rift valley	1927–2003	precipitation	Gebrekirstos et al. 2008
Balanites aegyptiaca	Ethiopia, rift valley	1936–2003	precipitation	Gebrekirstos et al. 2008
Terminalia superba	Democratic Republic of Congo	1973–2008	precipitation	De Ridder et al. 2013
Terminalia superba	Ivory Coast	1895–2008	precipitation	De Ridder et al. 2013
Pericopsis elata	Democratic Republic of Congo	1852–2008	precipitation	De Ridder et al. 2014
Daniella oliveri	Ivory Coast	1713–2001	precipitation	Schöngart et al. 2006
Diospyros abyssinica	Ivory Coast	1828–2001	precipitation	Schöngart et al. 2006
Anogeissus leiocarpus	Ivory Coast	1887–2001	precipitation	Schöngart et al. 2006
Daniella oliveri	Central–Western Benin	1760–2001	precipitation	Schöngart et al. 2006
Afzelia africana	Central–Western Benin	1803–2001	precipitation	Schöngart et al. 2006
Pterocarpus erinaceus	Central–Western Benin	1868–2001	precipitation	Schöngart et al. 2006
Isoberlinia doka	Central–Western Benin	1861–2001	precipitation	Schöngart et al. 2006
Anogeissus leiocarpus	Central–Western Benin	1883–2001	precipitation	Schöngart et al. 2006
Acacia mearnsii	Western Kenya	1991–2010	precipitation & moisture index	David et al. 2014
Eucalyptus camaldulensis	Western Kenya	1994–2010	precipitation & moisture index	David et al. 2014
Southeast Asia & Australia				
Tectona grandis	Indonesia, Central Java	1514–1929	precipitation, Sea level pressure	De Boer (1951)*
Tectona grandis	Indonesia, Java, Muna	1564–1995, 1673–2005	PDSI, ENSO, stream flow	D'Arrigo et al. (2006, 2011)*, Bijaksana et al. (2007)*
Tectona grandis	Thailand, Maehongson	1558–2005	precipitation, PDSI	Palakit (2004)*, Buckley et al. (2007)*
Tectona grandis	Thailand, Phrae	1880–1990	precipitation	Pumijunong et al. (1995)*
Tectona grandis	Central India, South India	1654–2001, 1481–2003	precipitation	Boraonkar et al. (2007, 2010)*

Tree species	Location	Time span	Response	References
Tectona grandis	Central India	1835–1997	precipitation	Shah et al. (2007)
Tectona grandis	Central India	1827–2001	precipitation & moisture index	Ram et al. (2008)*
Tectona grandis	Myanmar, Mandalay	1834–1998	precipitation	Pumijunong (2001)*
Tectona grandis	Myanmar, Taungoo	1880–2000	precipiation	Kyaw (2003)*
Tectona grandis	Myanmar, Mabein	1875–2000	precipitation	Kyaw (2003)*
Tectona grandis	Myanmar, Kanbalu	1865–2000	precipitation	Kyaw (2003)*
Tectona grandis	Myanmar, Maingtha Forest Reserve	1613–2009	precipitation & PDSI	D'Arrigo et al. (2011)*
Afzelia xylocarpa	Western Thailand	1976–2011	precipiation & temperature	Vlam et al. 2014
Chukrasia tabularis	Western Thailand	1982–2010	precipiation & temperature	Vlam et al. 2014
Melia azedarach	Western Thailand	1970–2011	precipiation & temperature	Vlam et al. 2014
Toona ciliata	Western Thailand	1950–2011	precipiation & temperature	Vlam et al. 2014
Toona ciliata	subtropical Australia, Queensland	1854–2000	precipiation & temperature	Henrich et al. 2009

PDSI = Palmer Drought Severity Index; ~ approx. readout dates, as dates were only available from graphs; * cited after Pumijunong (2013)