

## CLIMATIC CONTROL OF RADIAL GROWTH OF CEDRELA MONTANA IN A HUMID MOUNTAIN RAINFOREST IN SOUTHERN ECUADOR

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With 5 figures and 1 table

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**Summary:** *Cedrela montana* is a deciduous broad-leaved tree species growing in the humid mountain rainforests of southern Ecuador. High-resolution dendrometer data indicate a regular seasonal growth rhythm with cambial activity during January to April. Amplitudes of daily radial stem diameter variations are correlated with the amount of the maximum daily vapour pressure deficit. During humid periods, daily stem diameter variations are considerably smaller than during drier periods. This indicates that cambial activity is limited by available moisture even in such a very humid mountain climate. Wood anatomical studies on microcores show the formation of a marginal parenchyma band at the beginning of the growth period. This parenchyma band can be used to delineate annual growth rings. We were able to establish the first ring-width chronology from *Cedrela montana* which covers the time until 1840. However, the chronology is presently statistically robust back to 1910 only. Correlation functions calculated with NCEP/NCAR data indicate a significantly positive relationship of tree growth with temperatures during the growth period during January to April. However, only 8% of the growth variance is explained by this climatic factor. In the future, this relationship may be useful to reconstruct past temperature conditions of the study area.

**Zusammenfassung:** *Cedrela montana* ist eine laubwerfende Baumart mit Vorkommen in den humiden Bergwäldern Südecuadors. Zeitlich hoch aufgelöste Dendrometermessungen belegen eine regelmäßige jährliche Zuwachsrhythmik mit einer kambialen Aktivitätsphase von Januar bis April. Die Amplituden täglicher Schwankungen der Stammdurchmesser sind mit der Höhe des maximalen täglichen Wasserdampf-sättigungsdefizits korreliert. Während feuchter Witterungsphasen fallen diese Schwankungen deutlich geringer aus als während trockener Witterungsperioden. Dies deutet auf eine Limitierung der kambialen Aktivität durch die verfügbare Feuchtigkeit selbst in diesem sehr feuchten Bergwaldklima hin. Holzanatomische Studien an Mikroborkernen belegen die Bildung eines marginalen Parenchymbandes zu Beginn einer Zuwachperiode. Dieses Parenchymband wird zur Abgrenzung der jährlichen Wachstumsringe genutzt. Es konnte die erste Jahrringbreiten-Chronologie von *Cedrela montana* erstellt werden, die maximal bis 1840 zurückreicht, jedoch derzeit erst ab 1910 statistisch ausreichend belegt ist. Korrelationsberechnungen mit NCEP/NCAR Daten ergeben eine signifikant positive Korrelation zwischen Jahrringbreitenwachstum und der Temperatur während der Wachstumsmonate Januar bis April, die jedoch nur 8% der Wachstumsvarianz erklären. Bei Verbesserung des Kalibrationsmodells könnte die Jahrringchronologie künftig zur Rekonstruktion der Temperaturverhältnisse im Untersuchungsgebiet genutzt werden.

**Keywords:** Tree rings, dendrometer, wood anatomy, dendrochronology, tropical mountain rain forest, Ecuador, *Cedrela montana*

### 1 Introduction

Dendroclimatology is a widely applied technique for deriving high-resolution palaeoclimate reconstructions in temperate and boreal climate zones and in subtropical mountain environments (e. g. BRIFFA et al. 2002). In comparison, very little tree-ring information is available from tropical mountain regions, despite the general lack of high-resolution palaeoclimate information from the tropics. Available data on tree rings in tropical regions cover South America (e. g. DETIENNE 1989; JACOBY 1989; VETTER and BOTOSSO 1989; BONINSEGNA et al.

1989; STAHL 1999; WORBES 2002; BRIENEN 2005; SCHÖNGART et al. 2004, 2005), Africa (e.g. GOURLAY 1995; VERHEYDEN et al. 2004; GEBREKIRSTOS et al. 2008), Indonesia and Thailand (e.g. JACOBY and D'ARRIGO 1990; POUSSART et al. 2004). In fact, a considerable number of climate-sensitive tree-ring chronologies used for the reconstruction of tropical climate variations were developed from subtropical regions with pronounced rainfall seasonality or from semiarid temperate zones. Therefore, many tree-ring based reconstructions of inner-tropical climate history are mainly based on climatic teleconnections between the inner tropics and adjacent re-

gions. For example, drought sensitive conifers from Mexico and southwestern North America were used to reconstruct the temporal variability of sea surface temperatures, El Niño events, the Southern Oscillation Index (SOI) or the Pacific Decadal Oscillation (PDO) (VILLALBA 1994; STAHLÉ et al. 1998; BIONDI 2001; DÍAZ et al. 2001; CLEAVELAND et al. 2003; GEDALOF et al. 2002; D'ARRIGO et al. 2005). However, climatic teleconnections between subtropical regions and the inner tropics may vary during different climatic episodes (D'ARRIGO et al. 2005). Therefore, climate reconstructions from the tropics are urgently needed. A serious constraint for tropical dendroclimatology is the fact that the majority of tropical tree species do not form distinct anatomical growth boundaries, due to the lack of climatic seasonality. In the inner tropics, temperature variations along altitudinal gradients are usually greater than within the annual cycle. In contrast, rainfall patterns often show distinctive seasonal or sub-annual variations that may trigger the formation of detectable growth boundaries in tropical trees. Growth boundaries allowing the detection of annual tree rings may be initiated by cambial dormancy due to lack of water supply, or by phenological phases like fruiting, flowering or leaf shedding in deciduous species (BRÄUNING et al. 2008a). Hence, before tree-ring series can be measured and interpreted, the relationship between tree growth, seasonal formation of different wood tissues and climate must be minutely analysed.

During recent years, considerable methodological progress was achieved in detecting and analysing annual growth increments in tropical tree species (WORBES 2002). More and more tropical tree species are discovered to form annual or subannual growth boundaries that can be used for dendroecological analysis. E.g., in the lowlands of northern Peru, El Niño events are coupled with abundant rainfall which leads to drastic increases of growth rates in the deciduous tree species *Bursera graveolens* and *Prosopis pallida* (RODRIGUEZ et al. 2005). Nevertheless, tree-ring chronologies from the tropical Andes are still extremely rare or cover less than one century. Here, we introduce a new tree-ring chronology derived from *Cedrela montana* growing in a humid tropical mountain rainforest in the Reserva Biológica San Francisco in southern Ecuador. *C. montana* (Meliaceae) is a slow-growing deciduous tree species with a height of up to 30 m (NIETO and RODRIGUEZ 2003). The wood is characterized by hardness and high durability which makes *C. montana* a tree species of high economic value.

The study site is located in a tropical mountain rainforest at the northern slope of the Podocarpus National Park in southern Ecuador (3°58'S, 79°04'W) at ca. 2000 m a.s.l. (BENDIX and Beck 2009). The slope descends to the valley of Río San Francisco which facilitates the inflow of humid air masses from the Amazon lowland into the eastern part of the research area. At the study site, the mean annual temperature is 15.5 °C (cf. FRIES et al. 2009) and average annual rainfall adds to 2176 mm with an additional input of ca. 120 mm water intake by fog (EMCK 2007; BENDIX et al. 2008). The region is characterized by a slight seasonality of rainfall with a wetter season during April to June and a drier season during October to December, when the generally very cloudy area receives higher amounts of solar irradiance which might lead to atmospheric water stress of the vegetation due to high vapour pressure deficit (BENDIX et al. 2008). During this season, a relatively dry period ('veranillo del Niño') may occur in some years. The soils in the study area show a strong heterogeneity, but humic cambisols with pH values between 3.9–5.8 in the A horizon dominate on the strait slopes between crests and valley floors (WILCKE et al. 2008). The forests of the study area are a hotspot of biodiversity, hosting more than 180 tree species belonging to 53 plant families forming a canopy with a mean height of 20–25 m at the study site (HOMEIER 2004).

## 2 Seasonal growth dynamics of *Cedrela montana*

To specify seasonal growth dynamics of *Cedrela montana*, radial stem diameter variations were measured every 30 min with electronic point dendrometers (Type DR, Ecomatic, Germany) that register radial changes of the trunk. For this purpose parts of the outer bark were removed without wounding the cambial zone to reduce the influence of swelling processes occurring in the bark. During daytime, while the trees transpire more water than they take up by the roots and transport through the trunk, stem diameters usually shrink, except during very wet periods. During nighttimes, when transpiration ceases, the trunk resaturates with water taken up by the roots and tree diameters increase. Thus, maximum tree diameters occur during the early morning hours before the onset of leaf transpiration whereas tree diameter minima are usually found during the late afternoon. The difference between the daily maximum and the preceding minimum diameter is the amplitude of daily radial change (dA), whereas the difference between two consecutive daily maxima is the net rate of

daily radial change (dR) (HAUSER 2003; BRÄUNING et al. 2009). In case of active growth the latter indicates the formation of new cells in the xylem. In case of

cambial dormancy and net water loss of the trunk, however, stem diameters can also decrease and dR becomes negative.

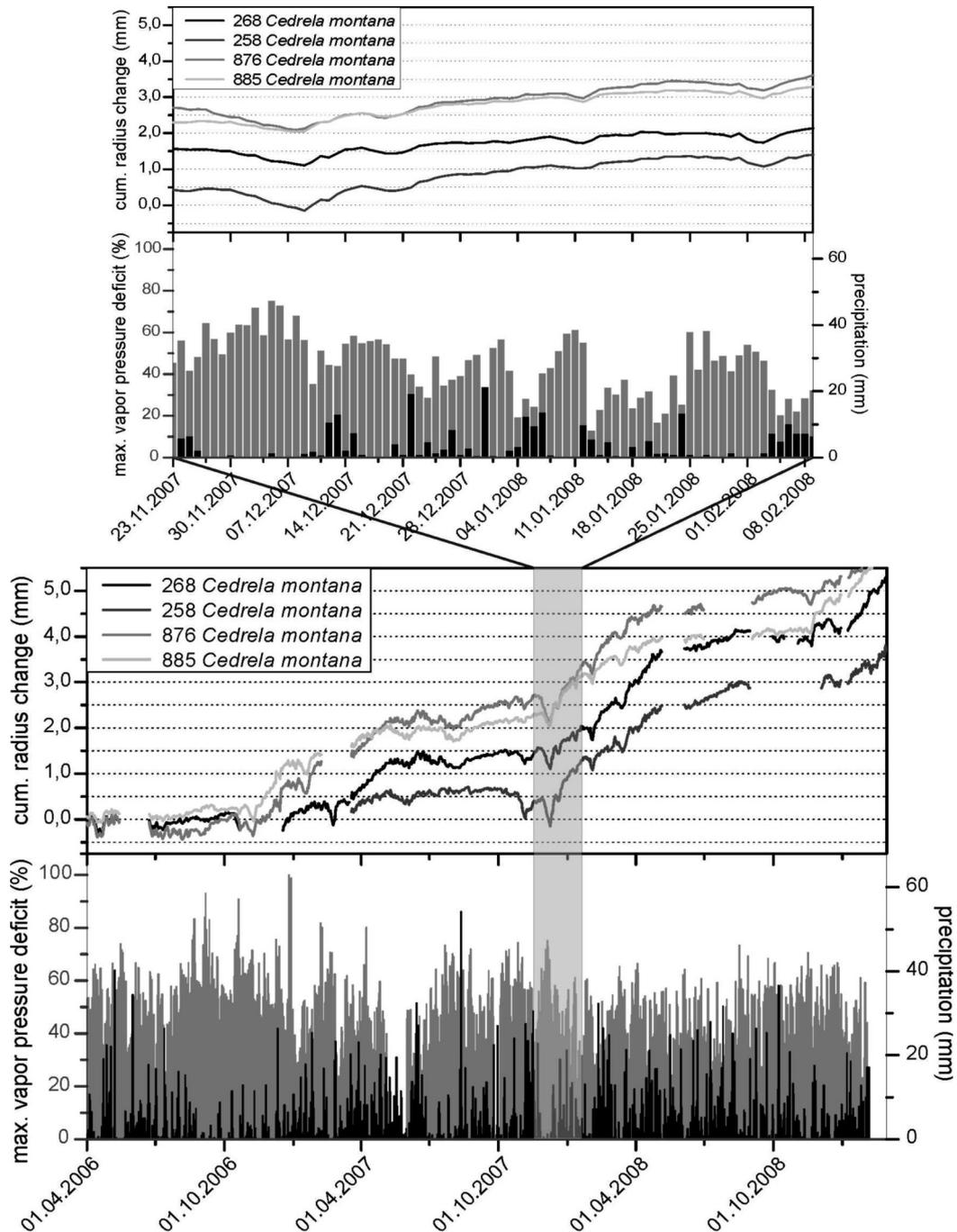


Fig. 1: Cumulated daily radial stem variations of four *Cedrela montana* individuals during April 2006 to January 2009 (lower graph, upper panel). Periods with interruptions of the individual curve are caused by data gaps due to failure of data registration by the data logger. Daily sums of precipitation (black bars) and maximum vapour pressure deficit (grey bars; lower panel). Inlet shows the period 23.11.07–08.02.08 which represents the beginning of the growing season. Note the close correspondence between phases of active stem growth and humid periods and phases of synchronous stem shrinkage during periods of four or more days without or with very little rainfall.

The cumulated daily maximum stem diameters for four studied *Cedrela* trees during the almost three-year long period April 2006 to January 2009 are shown in figure 1. It is obvious that the major stem diameter variations are quite homogenous between all studied trees. The long-term trend of the dendrometer curves indicates a pronounced seasonality of cambial activity. Cambial growth is initiated around January, as indicated by a drastic increase in radial diameter. Around late April or beginning of May, growth rates decrease and stem diameters show only minor variations. These 'plateaus' correspond to the more or less leafless period of *Cedrela* (BRÄUNING et al. 2008a) and mark periods when stem diameter variations are determined by changes in the hydrological status of the trunks, but not by cambial activity. Absolute growth rates vary considerably between the individuals: during the study period, tree no. 258 showed a radial diameter increase of ca. 3.8 mm while tree no. 876 grew more than 5.5 mm.

Beside this general growth trend, the dendrometer curves shown in figure 1 also reveal highly synchronised short-term stem diameter variations that are characterised by stem shrinkage of up to more than 0.5 mm. Such periods may occur during the ac-

tive growing phase as well as during cambial dormancy and are caused by consecutive shrinking of the stem in short rainless periods as indicated by climate data measured at the same altitude in a short distance (< 1 km) to the trees (Fig. 1). It is surprising that in such a humid tropical mountain climate several days without precipitation are enough to induce stem shrinkage in trees (BRÄUNING et al. 2008b, 2009). Figure 2 examines the relationship between the daily amplitude  $dA$  of stem diameter variations and climatic conditions. During a relatively wet period (03.–14.08.2007, 12 days),  $dA$  is rather small (below 0.07 mm) and significantly correlated with the daily maximum vapour pressure deficit (VOLLAND-VOIGT et al. 2009), except for tree 258. During the rainless period from 26.11.–08.12.2007 (13 days),  $dA$  is much bigger (up to 0.29 mm), but correlations with climate are quite low (Fig. 2). It has to be kept in mind that *Cedrela* sheds its leaves during the dry period which can be seen as an adaptation to the generally drier conditions with less rainfall and increased maximum vapour pressure deficits during October to December (Fig. 1).

For the evaluation of cambial activity and wood formation, microcores were collected with an increment puncher (FORSTER et al. 2000) in monthly in-

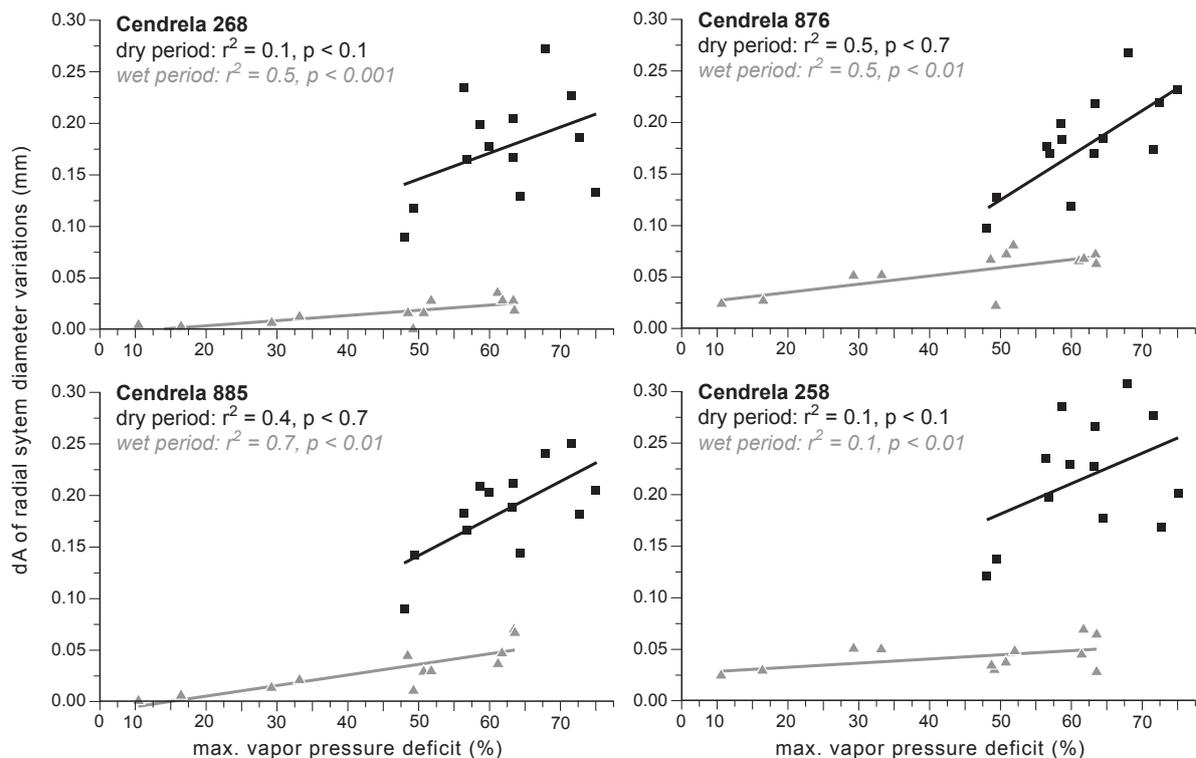


Fig. 2: Amplitudes of daily radial stem variations ( $dA$ ) in *Cedrela montana* during the wet period 3.8.–14.8.2007 (12 days, grey symbols) and during the dry period 26.11.–8.12.2007 (13 days, black symbols).

tervals from all studied trees. From these cores, thin sections of ca. 20  $\mu\text{m}$  thickness were cut with a microtome. These thin sections were stained with solutions of safranin red and astra blue to indicate the distribution of ligneous and living wood anatomical tissues. The combination between dendrometer data and wood anatomical evidence indicates that *C. montana* shows intensive cambial activity and the formation of new xylem (wood) cells during beginning of January and middle of April (Figure 3). Growth boundaries consist of marginal parenchyma bands including slightly tangentially arranged vessels and seem to be formed at the beginning of the growing period. However, in some of the microsections the parenchyma bands are difficult to detect, which might lead to the occurrence of missing or partly missing rings (see below). To summarize, the seasonal cyclicality of wood formation and cambial dormancy in *Cedrela montana* and the seasonality of the formation of characteristic wood tissues could be detected by a combination of high-resolution dendrometer measurements and wood anatomical studies.

### 3 The development of a *Cedrela montana* tree-ring chronology

Wood samples from 37 *Cedrela* trees were collected with an increment borer. Most of the trees collected were younger than 50 years, however, some trees older than 160 years were found, reaching back to 1840 (Fig. 4). In total, 89 radii were collected and cross-dated successfully, which means that the indi-

vidual tree-ring showed characteristic growth patterns that could be synchronized between samples and assigned to a distinct year of formation (STOKES and SMILEY 1968). However, some wood samples included missing rings and false rings, making synchronisation between ring-width curves of different trees challenging and time consuming. This leads to an overall relatively weak correlation of the individual tree-ring series (Tab. 1). The consequence is that a statistically reliable quality of the *Cedrela* chronology is only reached after 1910, when the chronology includes more than 13 individual tree-ring series and passes the recommended threshold of the ‘expressed population signal’ (EPS) statistic, a measure of the reliability of a tree-ring chronology (WIGLEY et al. 1984). During 1930–1949, EPS temporarily drops to 0.83, which does not have a strong impact on the reliability of the chronology. The low common signal among the trees implies that the individual ring-width curves of different trees show strong individual variations (possibly partly due to stand dynamics) and a rather weak common climate signal. This requires a high number of samples before deriving climate-tree growth relationships is possible.

To remove the biological growth trend inherent in tree-ring series, the measured raw ring-width values had to be detrended and transformed to dimensionless tree-ring index series (COOK and KAIRIUKSTIS 1990). As a trend function we chose a cubic smoothing spline with a cutoff of 50% of the variance at a frequency of two thirds of the individual series length. This procedure was carried out

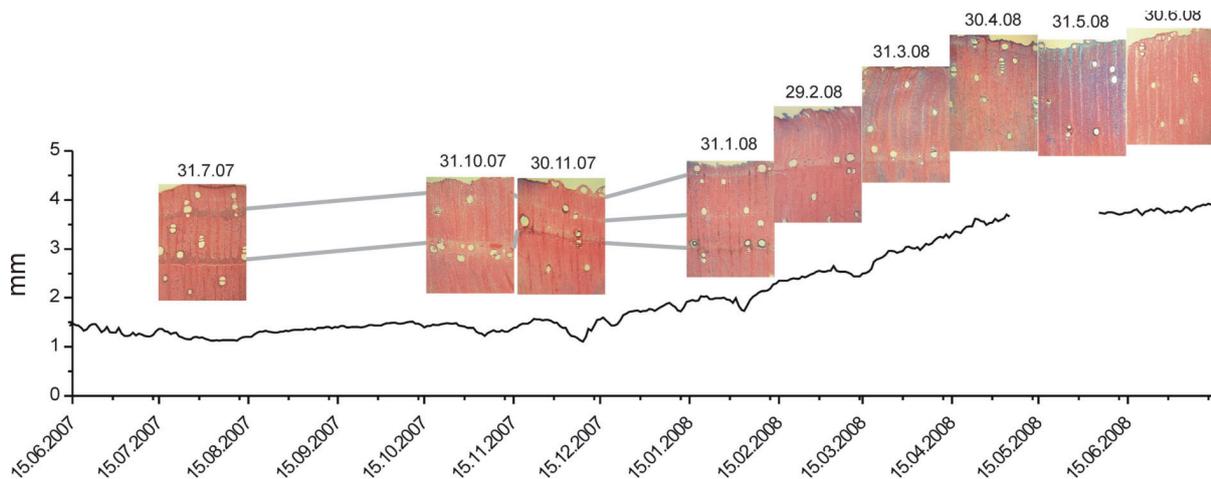


Fig.3: Wood anatomical microsections and cumulative daily radial stem variations of one *C. montana* tree. Marginal parenchyma bands consist of cells of larger diameter and indicate annual growth boundaries. Grey bars between microsections link identical parenchyma bands in wood samples collected at different dates. Some microsections (e.g. August–September 2007, December 2007) were not processed due to disturbed wood tissue during sampling.

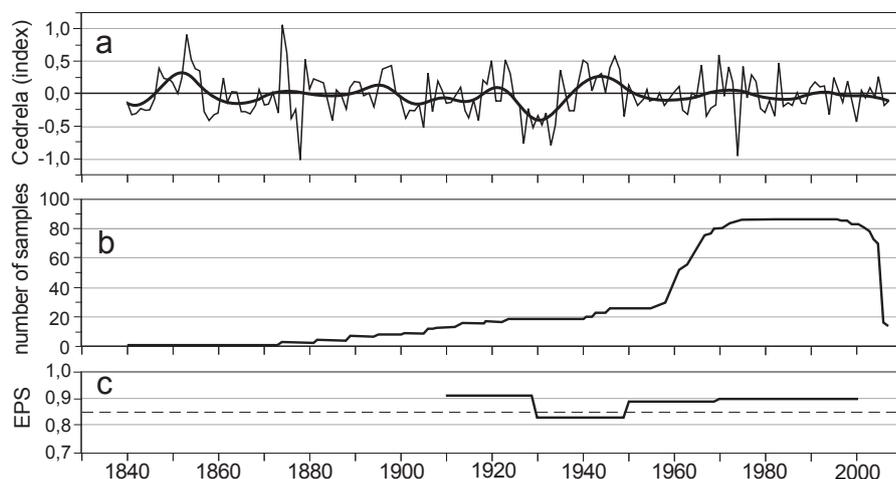


Fig. 4: a. Ring width chronology of *Cedrela montana* (thin line) and long-term growth variations smoothed with a 5-year Fast Fourier Filter (bold line); b. Number of tree-ring samples (radii) included in the chronology; c. Expressed Population Signal (EPS) of the chronology. The horizontal line indicates the recommended threshold of 0.85.

with the software ARSTAN (COOK 1985). Before applying the trend function, a so-called power transformation was carried out to reduce the influence of outliers (missing rings) on the chronology (COOK and PETERS 1997). The resulting tree-ring index chronology (Fig. 4) mirrors inter-annual tree-ring variations as well as pronounced decadal variations like the tree-ring minimum period during 1925–1934. It is worth mentioning that well-known El Niño events like 1982/83 or 1997/98 did not affect ring width at the study site. This is in line with local climate data that also do not indicate a big influence of El Niño in the study area (BENDIX et al. 2008).

#### 4 Climate-growth relationships

Due to very short available local instrumental climate data series (only 10 years), correlation functions between annual tree growth and climate data were carried out with various climate variables derived from NCEP/NCAR data (KALNAY et al. 1996) for the grid point in southern Ecuador next to the study site. Bootstrapped correlation functions, in

which correlation coefficients of two data sets are repeatedly (normally 1000 times) computed from randomly selected subsets of the complete data set were calculated between climate variables and the *Cedrela* chronology with the software DENDROCLIM 2002 (BIONDI and WAIKUL 2004). Since wood anatomical and dendrometer evidence indicated an active growing period between January to April (Figs. 1 and 2), a time window of the calendar year prior to growth until September of the growth year was regarded as having potential influence on growth of *Cedrela*. The climatic variables tested included monthly means of convective precipitation, precipitation rate, shortwave radiation flux, solar radiation, specific humidity and air temperature. None of the correlations found were statistically significant, except for temperature during the active growing period from January to April (Fig. 5). This is unexpected, since it was shown that continuous warm and dry conditions during the growing period can limit the cambial activity and reduce the time available for cell formation. However, from figure 1 it is also evident that the speed of wood formation varies between different years as can be deduced from

Table 1: Statistical characteristics of the ARSTAN standard tree-ring chronology of *Cedrela montana* from southern Ecuador

No. of trees/ cores	rbar <sup>1)</sup>	% missing rings	AC1 <sup>2)</sup>	MS <sup>3)</sup>	period with EPS>0.85
37/89	0.30	1.02	0.23	0.30	1908-2007

<sup>1)</sup> mean correlation between all tree-ring series included in the chronology

<sup>2)</sup> first-order autocorrelation of the chronology

<sup>3)</sup> mean sensitivity

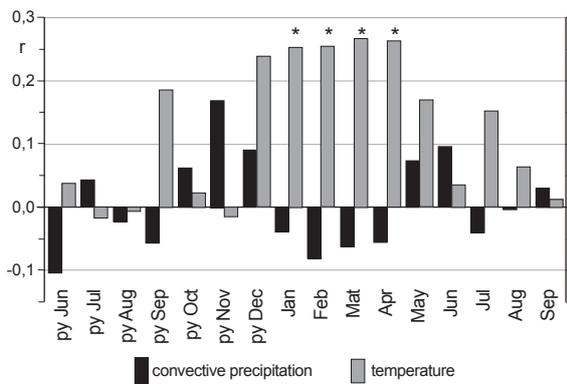


Figure 5: Growth-climate response of *Cedrela montana*. Correlations significant at  $p < 0.05$  are marked by asterisks.

the steeper increase of stem diameter in the growing season 2008 in comparison with 2007 (Fig. 1). It has yet to be tested if this difference can be related to different temperature conditions or if other environmental factors control the rate of cell division during the growing season.

Beside monthly climate data, we calculated a seasonal mean of temperature during January to April and found a correlation coefficient with the *Cedrela* chronology of  $r = 0.286$  ( $p < 0.05$ ; 1949–2007,  $n = 59$ ). Although this correlation is statistically significant, it only explains ca. 8% of the common variance between the climate data and the chronology, which is not enough to derive a temperature reconstruction based on the tree-ring data. A correlation of climate data registered from the local weather station in the study area and the NCEP/NCAR data did not yield a significant relationship ( $r = -0.23$ ; 1999–2008;  $n = 9$ ). This raises the question if the NCEP/NCAR data are representative for the study area, which is characterized by a strong differentiation of local climate due to the complex topography (RICHTER 2003). On the other hand, the trees might also respond to some regional climate factor that is not reflected in the short local climate data series. Clearly, this problem needs further research as soon as longer local climate data series will be available.

## 5 Concluding remarks and outlook

The presented chronology of *Cedrela montana* is the first tree-ring series from southern Ecuador and to our knowledge the longest from humid tropical mountain areas in central South America. The fact that ring-width patterns of different individuals can be crossdated and merged to a chronology indicates that the growth patterns are caused by a common

environmental forcing, although the correlation analyses with existing climate data did not yet lead to satisfying results about the nature of the climatic control of tree growth in this humid area and needs further investigation. The length of more than 160 years for some individual trees indicates the potential to extend the chronology which at the moment reliably covers the past 100 years, further back into the past. Radiocarbon dates collected from the conifer *Prumnopitys montana* (Podocarpaceae) growing in the same area revealed tree ages of  $418 \pm 35$  years BP (sample no. Erl-12870, SCHARF 2009, oral communication), demonstrating the potential for developing even much longer tree-ring series from the region. Ring width might not be the optimal wood parameter to detect the influence of climate on the trees and to reconstruct former environmental conditions. High-frequency densitometry analyses of *Prumnopitys* show promising results to detect growth boundaries and interannual wood density variations that may be related to interannual differences in climatic conditions (BRÄUNING et al. 2009). The application of stable isotope analyses of  $^{13}\text{C}$ ,  $^{18}\text{O}$  and  $^2\text{H}$  of tree rings or growth zones (e.g. SCHLESER et al. 1999; POUSSART et al. 2004; SCHNAKENBURG et al. 2008) may help to clearly identify annual growth boundaries and to develop high-resolution climate-sensitive data series. For example, variations in stable oxygen isotopes in *Prosopis* growing in the western Andean foreland indicate the influence of El Niño (EVANS and SCHRAG 2004; RODRIGUEZ et al. 2005). The presented properly dated *Cedrela* chronology provides a sound basis to perform further analyses including stable isotope analyses and wood density measurements that may reveal a higher climatic sensitivity than the ring width series or may be indicative for other climatic variables than temperature.

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