JUNIPER FROM ETHIOPIA CONTAINS A LARGE-SCALE PRECIPITATION SIGNAL

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Most semiarid regions are facing an increasing scarcity of woody vegetation due mainly to anthropogenic deforestation aggravated by climate changes. However, there is insufficient information to reconstruct past changes in climate and to evaluate the implications of future climate changes on the vegetation. Tree-ring analysis is a powerful tool for studying tree age, population dynamics, growth behavior, and climate-growth relationships among tropical tree species and for gaining information about the environmental forces driving growth change as well as for developing proxies for climate reconstruction. Wood anatomical and dendrochronological methods were used on *Juniperus procera* trees from two Ethiopian highland forests to check (i) whether tree-ring series of juniper are cross-datable and hence suitable for building tree-ring chronologies, and if so, (ii) which climate factors mainly drive wood formation in juniper from this region. Visible growth layers of the juniper wood were shown to be annual rings. Tree-ring sequences could be cross-dated between trees growing at the same site and between trees growing at sites 350 km apart. Evidence was found that annual growth of junipers is mainly controlled by one climatic factor, precipitation. This strong precipitation influence proves the potential of African juniper chronologies for accurate climate reconstruction and points out the relevance of building a network of juniper chronologies across East Africa.

Keywords: dendroclimatology, *Juniperus procera*, Ethiopia, dry highland forest.

Introduction

In tropical regions characterized by one pronounced dry season, many tree species form annual growth rings (Worbes 1995). Here, tree-ring analysis offers the opportunity to obtain information about age, growth rates, and yield of trees and to study the relation between tree growth and environmental factors such as climate. The latter enables the development of proxies for climate reconstruction as well as predictions of the effect of climate changes on tree vegetation in the future. However, dendrochronology is still a challenge in tropical regions, because tree rings are often irregular and/or narrow and may be missing or exhibit unclear boundaries (Sass et al. 1995; Brienen and Zuidema 2005; Schöngart et al. 2006; Wils and Eshetu 2007).

Juniperus procera Hochst. ex Endl., native to the mountains of eastern Africa, is a characteristic coniferous species of the Afromontane flora (White 1978). This tall (up to 50 m high) evergreen forest tree is the only tropical African juniper and grows in the dry forests of the Ethiopian highlands, preferably between 2300 and 3200 m asl, where the mean annual rainfall ranges from 500 to 1100 mm (Gardner 1926). Those juniper-dominated woodlands once covered a large part of the country (Bekele 2000), but since the beginning of the 20th century, they have been increasingly under pressure from expanding agriculture and bush-meat markets; they are now reduced to some isolated patches (Negussie 1995; Darbyshire et al. 2003; Nyssen et al. 2004).

In the context of increasing concern about global climate change, this study is an opportunity to assess the potential of *J. procera* for dendroclimatic investigations in this poorly documented tropical region (Fichtler et al. 2004; Verheyden et al. 2005; Schöngart et al. 2006; Therrell et al. 2006; Trouet et al. 2006). Moreover, to support conservation, restoration, and sustainable use of the remaining woodlands, more information is needed about the growth pattern and population dynamics of *J. procera* (Couralet et al. 2005).
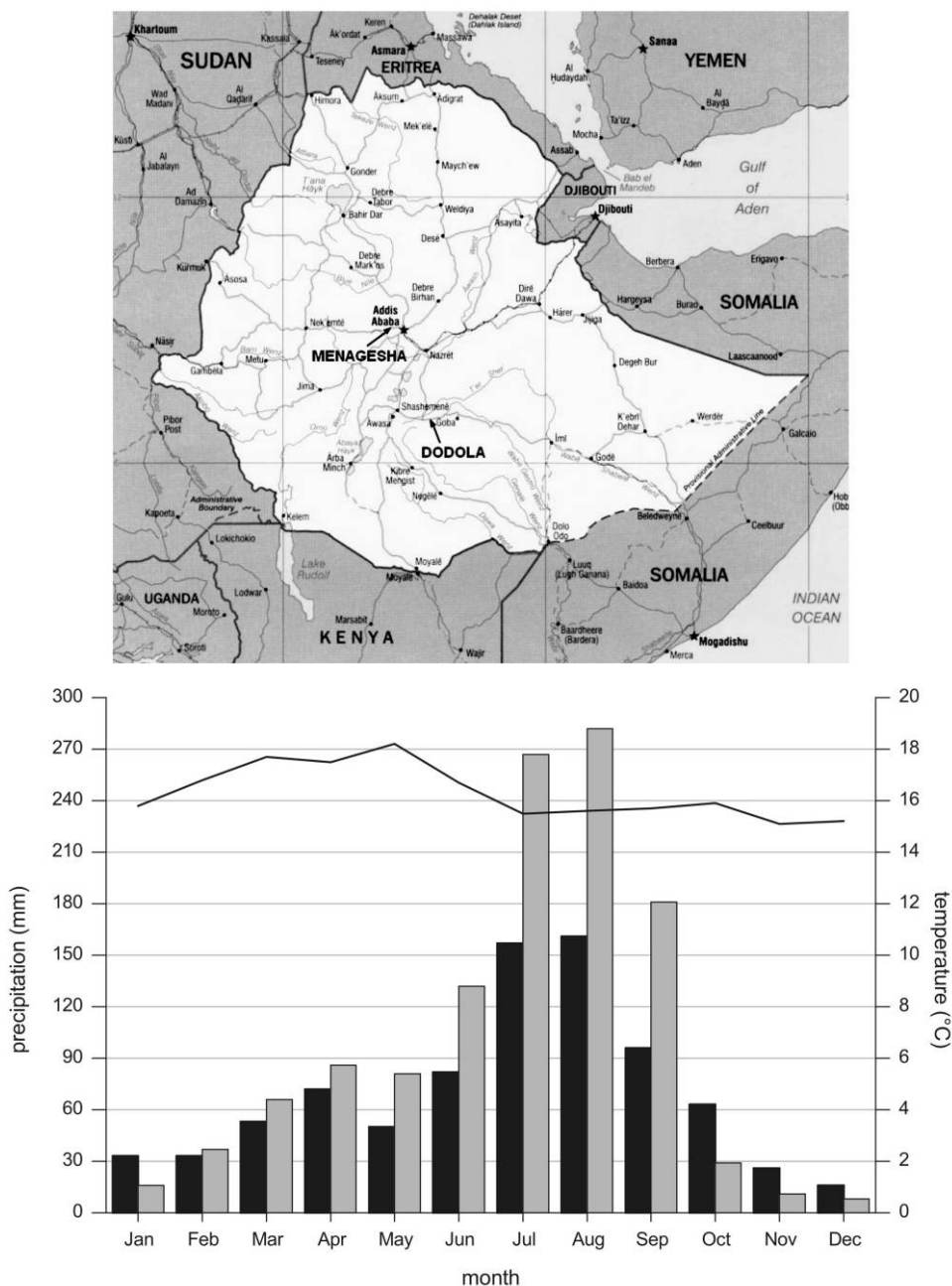
Study Sites

The two sites investigated are located 300 km apart in the Ethiopian highlands (fig. 1). The Menagesha-Suba Forest stretches on the southwest-facing slopes of Mount Wechecha (8°97′N–9°00′N, 38°35′E–38°38′E; 2300–2900 m asl), an extinct volcano 45 km southwest of the capital city Addis Ababa. The Adaba-Dodola Forest is located on the northern side of the Bale Mountains (6°50′N–7°00′N, 30°07′E–39°22′E, 2400–3100 m asl).

Both woodlands are remnants of dry evergreen mountain forests dominated by *Juniperus procera*. Despite their conservation status as National Forest Priority Areas, repeated human interference has led to heavy degradation, and now closed forest is restricted to remote areas difficult to access.

The climate is tropical alpine, with an average temperature of 10°–16°C and a mean annual precipitation of ∼1200 mm at both sites. The climate records are derived from the Dodola

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Fig. 1   Top, map of Ethiopia showing the two study sites. Bottom, climate diagram for Addis Ababa (gray bars; 09°03′N, 38°42′E, 2400 m asl) and Adaba-Dodola (black bars; 06°58′N, 39°11′E; 2490 m asl). For temperature, the line represents the average for the common years.

and Addis Ababa stations, located in the vicinity of the two study sites and at similar altitudes. They show a slight difference in the total amount of rainfall, but the annual distribution patterns are very similar (fig. 1). The longest climate records available are from Addis Ababa and cover the period 1900–2002 for precipitation and 1955–1990 for temperature. All records reflect a bimodal distribution in rainfall, with a main rainy season from June/July to September/October and a minor one from January/February to April/May.

Material and Methods

Because juniper species are known to be problematic for dendrochronological studies (Conway et al. 1997; Esper 2000; Bräuning 2001; Sigl et al. 2006), we mainly worked with whole-stem sections from fallen trees or remains of recently cut trees. In Adaba-Dodola, 11 stem disks were collected; two originated from trees planted at a known date and were not used for chronology building. In Menagesha-Suba, 26 increment cores from

13 living trees and 11 stem disks were collected. The stem disks were taken from stumps, between 30 and 50 cm above the ground; two increment cores per tree were collected at breast height. The diameters of the sampled trees ranged from 16 to 46 cm.

All samples were air-dried. The stem disks were gradually sanded (120–800 grit), and the 26 increment cores were mounted on wooden holders and hand-trimmed with a Stanley knife. From a first macroscopic inspection, distinct concentric growth bands were visible (fig. 2).

Tree-ring widths were measured with a precision of 0.01 mm along four radii of the stem sections using a LINTAB measuring table (RinnTech, Heidelberg) associated with the program TSAP (Rinn 1996). The time series were visually and statistically cross-dated to obtain mean tree-ring series for each juniper tree (Cook and Kairiukstis 1990). TSAP also provides a statistical description of the cross-dated time series consisting of information on mean tree-ring width, SD, and mean sensitivity. Tree-ring chronologies for the two sites, Adaba-Dodola and Menagesha-Suba, were constructed following a standard den-

drochronological protocol: a 30-yr spline was fitted to the single tree-ring records to remove any age-related trend in the series. Tree-ring indices were then calculated by dividing each of the original tree-ring widths by the value of the fitted spline (ARSTAN; http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html). Subsequently, the nine (Dodola) and 24 (Menagesha-Suba) index series were averaged into two single-site chronologies for *Juniperus procera* from Adaba-Dodola and Menagesha-Suba, respectively.

To evaluate the signal strength in the site chronologies, we calculated the running correlation (RBar) and the expressed population signal (EPS), which are measures of the average correlation between the tree-ring series of each site (Wigley et al. 1984; Verheyden et al. 2005). Climate-growth analyses were carried out (DendroClim2002; Biondi and Waikul 2004) to assess the effect of changes in monthly mean temperature and the monthly sum of precipitation on the annual variation of tree-ring width during the period (covered by long precipitation records from Addis Ababa) from 1900 to 2002 (maximum period) and from 1950 to 2002 (recent period). We studied the
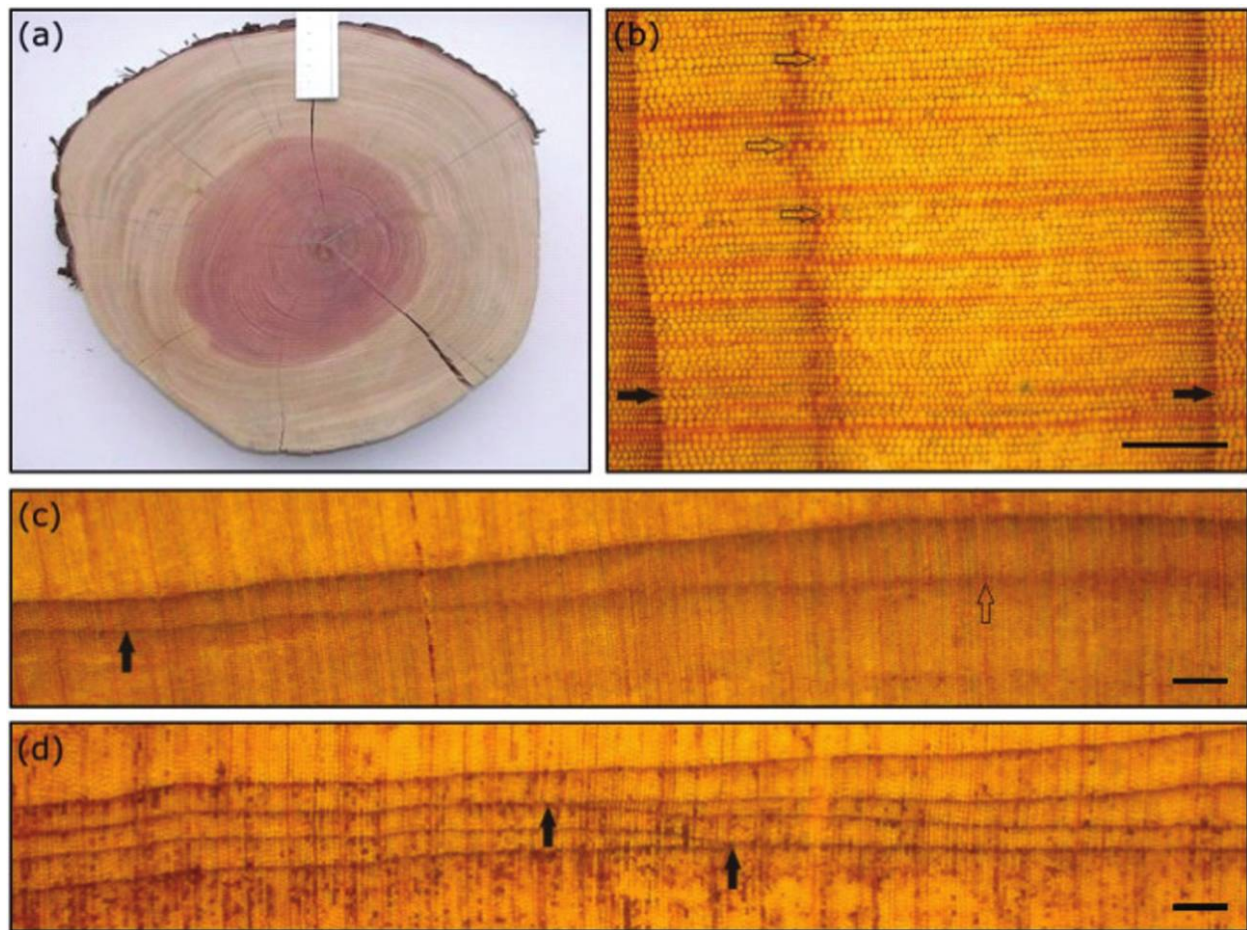
Fig. 2 *a*, Stem disk of *Juniperus procera* with distinct growth layers. *b*, Two distinct ring boundaries (filled arrows) and tangentially lined-up axial parenchyma cells (open arrows). *c*, Distinct (filled arrow) and unclear (open arrow) boundaries in the same ring. *d*, Two growth rings wedging in. All scale bars are 1 cm.
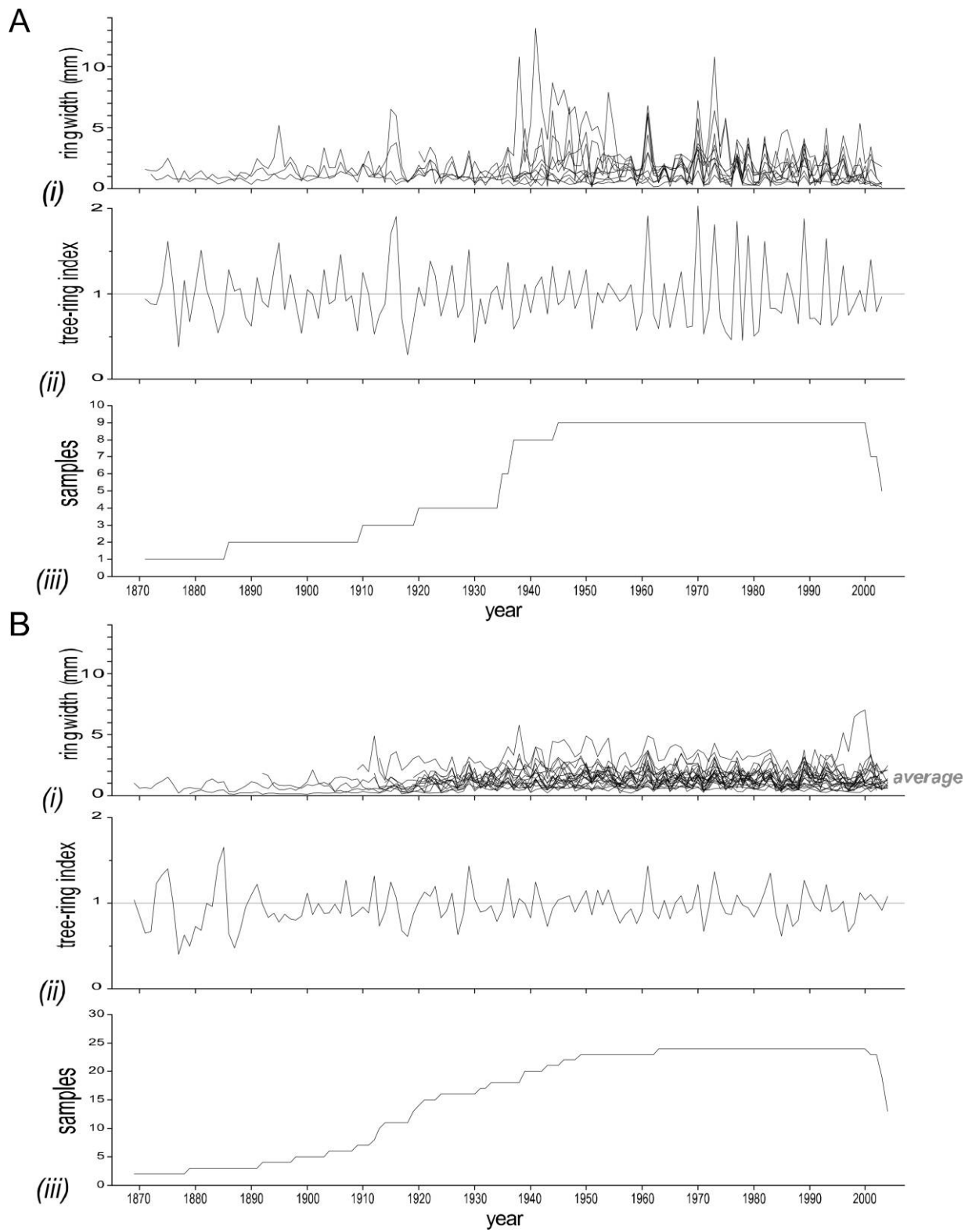
Fig. 3 Tree-ring records from Adaba-Dodola (*A*) and Menagesha (*B*) showing the raw tree-ring series (*i*), the standard chronology (*ii*), and the replication of trees (*iii*).

effect of precipitation and temperature from June of the previous year (end of the previous rainy season) until October of the observed year.

Results and Discussion

Wood Anatomy and Tree Rings

The wood of *Juniperus procera* is light brown or golden in appearance, with clearly distinguishable more reddish heartwood (fig. 2*a*). Concentric tree rings are macroscopically visible: the late wood consisting of small, thick-walled tracheids is darker in appearance than the early wood consisting of wider, thin-walled tracheids. The boundaries between rings are quite sharply marked by flattened, almost rectangular tracheids with thicker cell walls (fig. 2*b*). Even so, measurement was hampered by the occurrence of wedging or partly missing rings, mostly associated with phases of low growth rates (fig. 2*c*, 2*d*) or eccentric growth. Another distracting but common feature is the presence of tangential bands of axial parenchyma cells filled with what are probably phenolic substances (fig. 2*b*). These darker bands occur almost exclusively in the widest tree rings (but not necessarily in the younger parts of the stems) and might be the result of less favorable periods in the growing season (e.g., unusual climatic conditions, but also browsing or wounding). We could not favor one or another hypothesis because these bands sometimes appear simultaneously in several trees but can also be found in single trees in different years. Eventually, false ring boundaries could be identified: the tracheids are flattened, often with thicker cell walls, and are sometimes associated with axial parenchyma cells (fig. 2*b*). False rings show less abrupt changes in tracheid size and cell-wall thickness in comparison with real tree rings. However, it is sometimes impossible to distinguish between real and false ring boundaries, and both structures can even appear along the same boundary (fig. 2*c*). In this case, cross-dating between tree-ring series of different trees is the only possible way to discriminate between real and false rings. False rings were most frequently observed in wider tree rings in both younger and older parts of the stem. False and double rings frequently occur in several, but not all, trees for years that show a clear bimodal pattern in rainfall distribution, with a short dry period between the minor and major rainy seasons. Wood anatomical studies and pointer-year analysis focusing more specifically on intra-annual changes in cell size or cell-wall contents might clarify the relationship between wood formation and environmental conditions at a high temporal resolution (Wimmer et al. 2000; Rigling et al. 2002; Cherubini et al. 2003; Masiokasa and Villalba 2004; Verheyden et al. 2005; Heinrich and Banks 2006*a*, 2006*b*; Liang and Eckstein 2006; Schmitz et al. 2006; De Micco et al. 2007).

Cross-Dating of Tree-Ring Series

Nine out of the 11 trees from Dodola and all 24 trees from Menagesha-Suba could be visually and statistically cross-dated. The resulting site chronologies run from 1871 until 2003 for Dodola and from 1855 until 2004 for Menagesha-Suba (fig. 3). This is a strong indication of the annual nature of growth rings (Worbes 1995; Stahle 1999).

Mean ring widths, expressing the growth rates of the trees, showed a huge variability (table 1; fig. 3). In Dodola, the mean annual growth rate amounts to 1.71 mm/yr, which is considerably higher than that in Menagesha, where it reaches only 1.38 mm/yr. We might speculate that such intersite differences resulted from a more equal rain distribution (fig. 1), better soil conditions, or higher water-holding capacity in Dodola. The year-to-year variability, expressed as mean sensitivity, is high (Fritts 1976), which, together with low values of autocorrelation (fig. 1), indicates strong responses to annually changing environmental conditions, especially in the junipers growing at Dodola. The RBar and EPS indicated rather low values for Dodola, which were expected because of the limited number of sampled trees and the difficulties in cross-dating the tree-ring series (see fig. 4). The junipers from Menagesha, however, yielded fairly high values that reach the commonly accepted EPS threshold of 0.85 (Wigley et al. 1984) from ∼1900 on. The high correlation between the two site chronologies ($r = 0.63$) indicates that growth of the junipers in both areas is influenced by the same external factor (fig. 6). Response-function analysis revealed no significant influence of temperature. Instead, we found that the annual growth of the junipers in both sites was correlated to the amount of precipitation, especially during the major rainy season from June/July to September (JJAS; fig. 5). Figure 6 illustrates this relationship, yielding correlations of $r = 0.49$ for Dodola and $r = 0.33$ for Menagesha (1950–2002). The distribution of the significant correlations suggests that junipers at Dodola might start growing earlier (June) and hence grow longer than junipers from Menagesha, which could be the reason for their higher growth level. Our results point to a large-scale JJAS precipitation signal in the growth pattern of *J. procera* in the Ethiopian dry Afromontane forests. This result was not unforeseen because in dry Afromontane forests, even at higher elevations, as in our study sites, precipitation is expected to be the most growth-limiting factor. The amount of the JJAS precipitation in Ethiopia was found to be governed primarily by ENSO (El Niño–Southern Oscillation; Korecha and Barnson 2007), which explains the large-scale character of the precipitation signal.

It is, however, interesting to see that strong climate-growth relationships are observed for poorly replicated juniper chronologies, where the trees lack statistical evidence of intercorrelation, as in Dodola (fig. 4*a*). Well-replicated chronologies (Menagesha) contained a weaker climate signal. This can be the consequence of differences in site-specific factors determining water availability as well as the fact that for only one site, far away and at low elevation, was a recorded precipitation data set available that was long enough for calculation of climate-growth relationships. However, to confirm this assumption, more material has to be

Table 1

Statistical Characteristics of Tree-Ring Series from Dodola and Menagesha, Ethiopia

Site	Period	No. trees	MRW (mm)	SD (mm)	MS	AC1
Dodola	1871–2003	9	1.71	1.23	.66	.17
Menagesha	1855–2004	24	1.38	.69	.38	.45

Note.   MRW = mean ring width, SD = mean standard deviation, MS = mean sensitivity, AC1 = first-order autocorrelation.
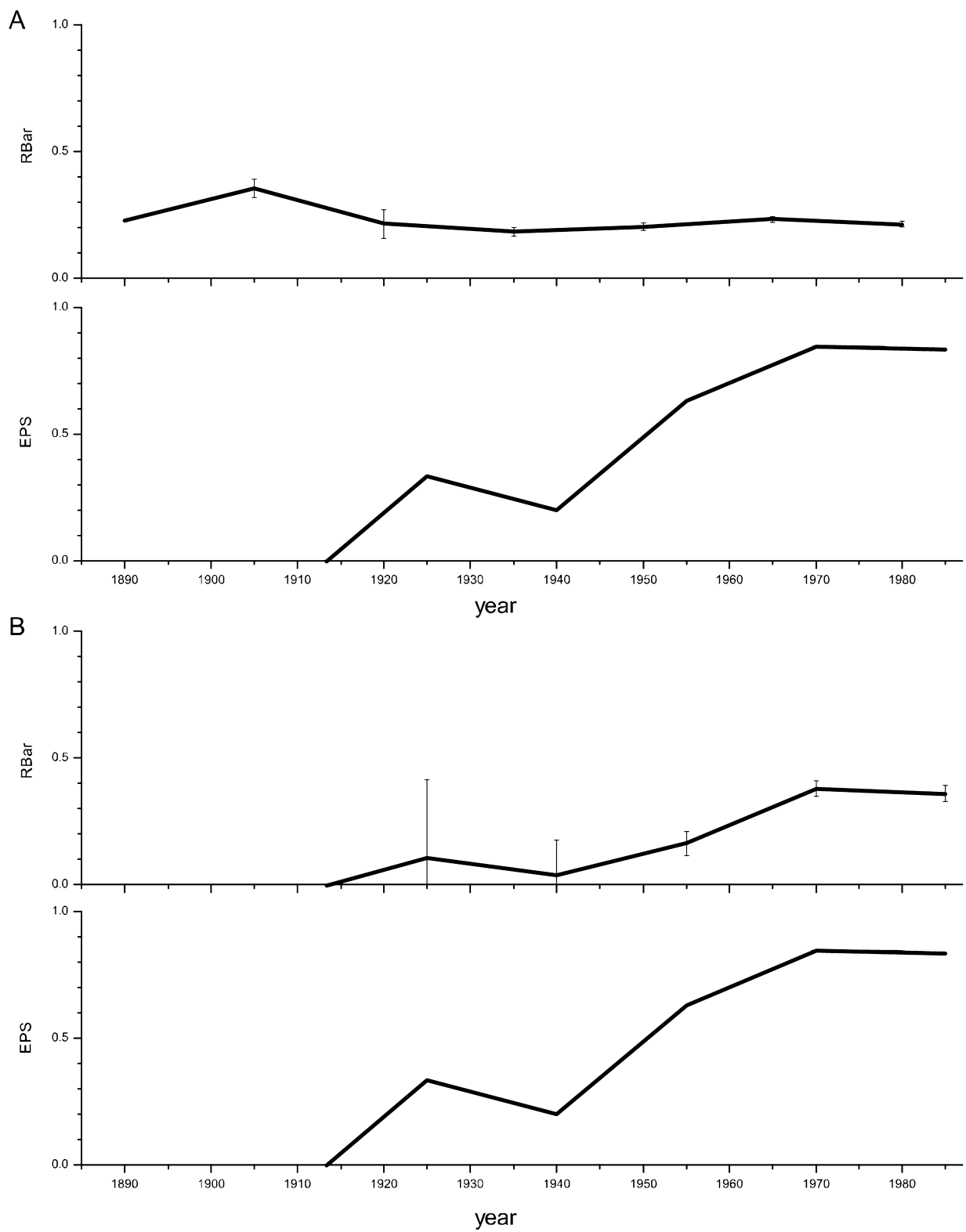
Fig. 4 Running correlation statistics between trees of the same site for Dodola (*A*) and Menagesha (*B*). Interval length = 30 yr, 15-yr overlap; running correlation (RBar; upper plot) and running expressed population signal (EPS; lower plot).
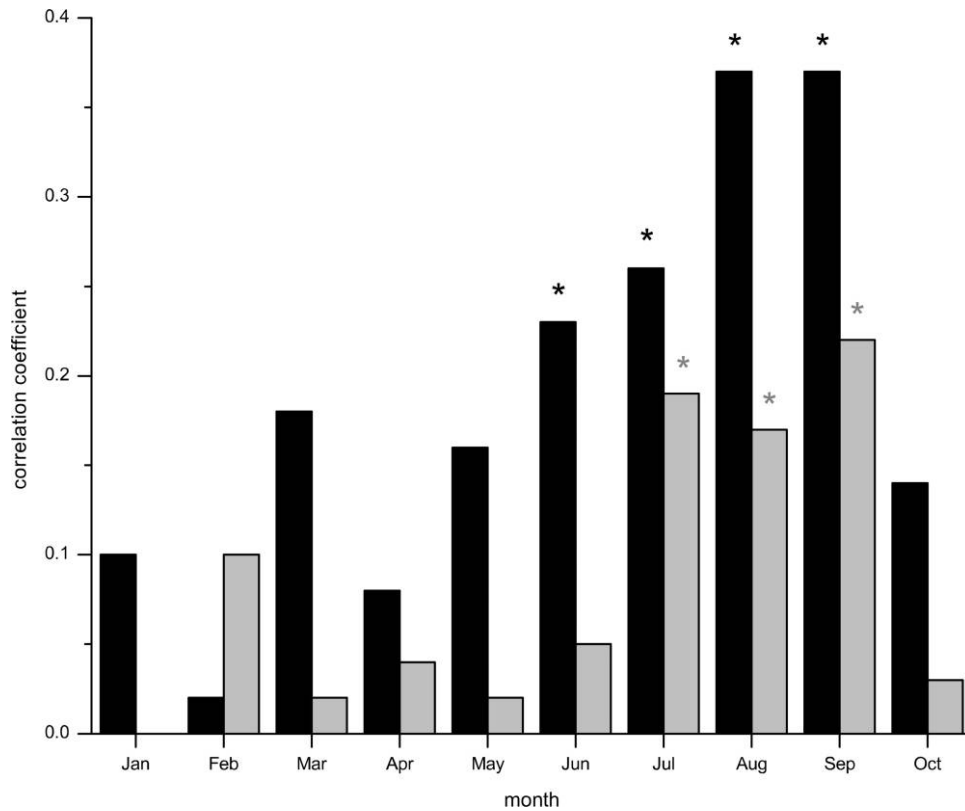
Fig. 5 Results of correlation analysis. Asterisk indicates 95% significance (black bars for Dodola, gray bars for Menagesha).

gathered systematically and investigated, if possible in combination with cambial-marking studies (Verheyden et al. 2004) or dendrometer observations and growth experiments (Heinrich and Banks 2006a). It would be useful to investigate how long

and when precisely the junipers are actually growing. This information is extremely helpful for (1) cross-dating, by providing information on the chance of missing or double rings (density variations); (2) identification of external triggers that cause
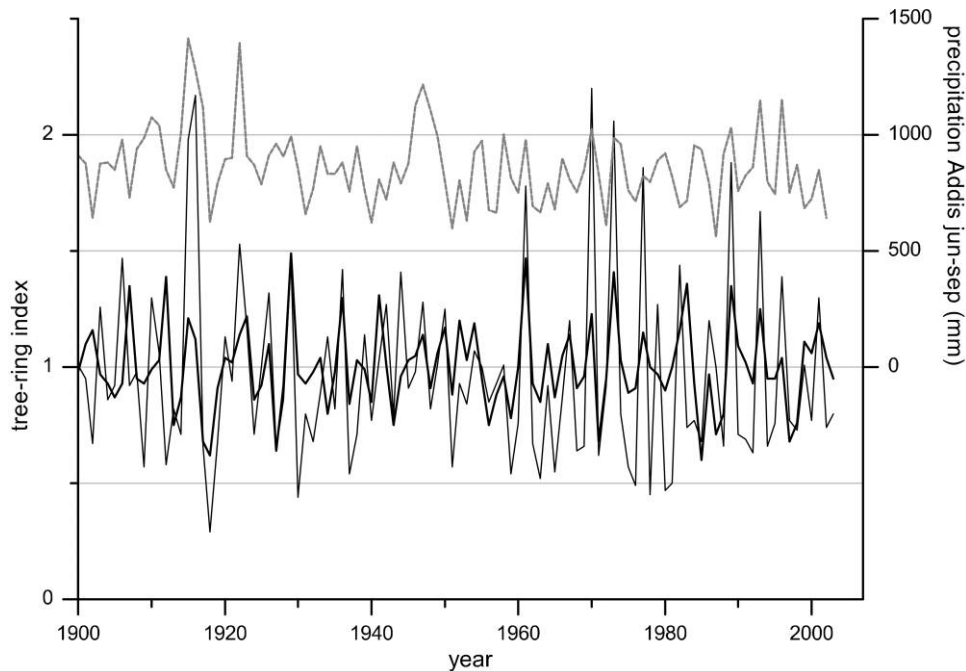

Fig. 6 Master chronology of the sampled trees in both sites (two bottom lines) and sum of precipitation (June–September) from Addis Ababa (top line).

intra-annual density variations, with the possibility of using them as additional high-resolution variables (Wimmer et al. 2000); and (3) coming up with biological (tree-level) and ecological (site hydrology) interpretations of statistical climate-growth relationships. Ultimately, this study suggests that tree-ring formation in juniper can be used to predict the production of juniper-dominated woodlands under different scenarios of climate change.

Conclusions

This study proves that the growth of *Juniperus procera* growing in the Ethiopian highlands is strongly influenced by the amount of precipitation during the major growing season from June/July to September (JJAS). Because the JJAS precipitation is mainly governed by ENSO, juniper can be considered as an important proxy of past changes in ENSO activity. Hence, our chronologies can be taken as a starting point to build up a network of juniper chronologies for this region that can be integrated with juniper tree-ring networks, for example in Asia (Bilham et al. 1984; Bräuning 1999, 2001; Esper 2000; Esper et al. 2002; Zhang et al. 2003; Treydte et al. 2006; Touchan

et al. 2007). Moreover, we expect that *Juniperus* chronologies and collections of the species in various climatic areas of Africa will enable us to predict juniper productivity under different scenarios of global climate change. This is highly relevant for the Horn of Africa, which is expected to be exposed to more and more frequent droughts.

Acknowledgments

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