



# The frankincense tree *Boswellia neglecta* reveals high potential for restoration of woodlands in the Horn of Africa



Mulugeta Mokria<sup>a,b,e,\*</sup>, Motuma Tolera<sup>c</sup>, Frank J. Sterck<sup>b</sup>, Aster Gebrekirstos<sup>a,e</sup>, Frans Bongers<sup>b</sup>, Mathieu Decuyper<sup>b,d</sup>, Ute Sass-Klaassen<sup>b</sup>

<sup>a</sup> World Agroforestry Centre (ICRAF), United Nations Avenue, Gigiri, P.O. Box 30677, 00100 Nairobi, Kenya

<sup>b</sup> Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

<sup>c</sup> Hawassa University, Wondo Genet College of Forestry and Natural Resources, P.O. Box 128, Shashemene, Ethiopia

<sup>d</sup> Laboratory of Geo-Information Science and Remote Sensing, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

<sup>e</sup> Institute of Geography, Friedrich-Alexander-University Erlangen-Nuremberg, Wetterkreuz 15, 7, 91058 Erlangen, Germany

## ARTICLE INFO

### Article history:

Received 17 July 2016

Received in revised form 8 October 2016

Accepted 16 November 2016

### Keywords:

*Boswellia neglecta*

Dendrochronology

Remote-sensing

Leaf-phenology

Growth dynamics

Restoration

## ABSTRACT

*Boswellia neglecta* S. Moore is a frankincense-producing tree species dominantly found in the dry woodlands of southeastern Ethiopia. Currently, the population of this socio-economically and ecologically important species is threatened by complex anthropogenic and climate change related factors. Evaluation of tree age and its radial growth dynamics in relation to climate variables helps to understand the response of the species to climate change. It is also crucial for sustainable forest resource management and utilization. Dendrochronological and remote-sensing techniques were used to study periodicity of wood formation and leaf phenology and to assess the growth dynamics of *B. neglecta*. The results show that *B. neglecta* forms two growth rings per year in the study area. The growth ring structure is characterized by larger vessels at the beginning of each growing season and smaller vessels formed later in the growing season, suggesting adaptation to decreasing soil moisture deficits at the end of the growing season. Seasonality in cambial activity matches with a bimodal leaf phenological pattern. The mean annual radial growth rate of *B. neglecta* trees is 2.5 mm. Tree age varied between 16 and 28 years, with an average age of 22 years. The young age of these trees indicates recent colonization of *B. neglecta* in the study region. The growth rate and seasonal canopy greenness (expressed by Normalized Difference Vegetation Index – NDVI) were positively correlated with rainfall, suggesting that rainfall is the main climatic factor controlling growth of *B. neglecta*. The observed temporal changes in leaf phenology and vessel size across the growth rings indicate that the species is drought tolerant. Therefore, it can be regarded as a key tree species for restoration of moisture-related limited areas across the Horn of Africa.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

Dry tropical forests and woodlands are playing a significant role in climate change mitigation (Canadell and Raupach, 2008; Miura et al., 2015). They have a far-reaching impact on rainfall. For instance, rainfall in the Congo basin is the outcome of moisture evaporated over East Africa (Van Der Ent et al., 2010). In addition, these forests are a major source of income for millions of people (Blackie et al., 2014; Miura et al., 2015). Despite their ecological, hydrological and economic importance, tropical dry forests are caught in a spiral of deforestation, due to complex interactions

between people and their environments and overall vulnerability of these ecosystems (Flintan et al., 2013; Sunderland et al., 2015). Climate change-induced reduction in rainfall and increasing temperature and heat waves is another growing concern in the dry tropics (IPCC, 2007), threatening the tropical forest carbon sink potential, thereby aggravating climate change impacts (Allen et al., 2015; Corlett, 2016; Hiltner et al., 2015; IPCC, 2007; Mokria et al., 2015). Under changing climate, dryland forests provide substantial resilience by buffering households against the direct effects of drought which typically affect crop production (Lawry et al., 2015; Wagner et al., 2013). Thus, dryland forests and drought-tolerant tree species are crucial to combat desertification and to expand options for adapting to the present, as well as projected climate change impacts (De Leeuw et al., 2014; van Noordwijk et al., 2015).

\* Corresponding author at: World Agroforestry Centre (ICRAF), United Nations Avenue, Gigiri, P.O. Box 30677, 00100 Nairobi, Kenya.

E-mail addresses: [m.mokria@cgiar.org](mailto:m.mokria@cgiar.org), [mulugeta.mokria@fau.de](mailto:mulugeta.mokria@fau.de) (M. Mokria).

In Ethiopia, dryland forests comprise the largest proportion of forest resources accounting for about 48% of the total land mass (WBISPP, 2004) and 45.7% of the total carbon stock (Moges et al., 2010). These forests are endowed with the major gum and resin producing genera of *Acacia*, *Boswellia*, and *Commiphora* and are of high cultural, economic and ecological importance (Lemenih et al., 2003; Worku et al., 2012). *B. neglecta* (Burseraceae) is one of these frankincense-producing tree species dominantly found in the dry woodlands of southeastern Ethiopia (Tadesse et al., 2007). In the study area, frankincense contributes 30% to the total household income, ranked second after livestock production (Lemenih et al., 2003; Woldeamanuel, 2011). Sustaining or even extending the income from *B. neglecta* is a primary issue in the region, notably because frankincense production from another species, *B. papyrifera*, is hampered by lack of successful recruitment (Tolera et al., 2013) and high rates of adult tree mortality (Groenendijk et al., 2012). Hence, there is an urgent need to develop sustainable management options for these forests and their resources to better benefit the local, national and international communities.

Developing restoration and sustainable management options for dryland forests in general and *B. neglecta* in particular requires knowledge on growth dynamics, age of the population and response to changing climate conditions. Dendrochronology and remote-sensing are powerful tools to collect that information (Gebrekirstos et al., 2014; Qu et al., 2015). Although, the dendrochronological potential of tropical tree species has been demonstrated for different tropical regions, it is still challenging in areas characterized with high off-season rainfall and multiple rainy seasons (Wils et al., 2009, 2011a, 2011b; Worbes, 2002). In Ethiopia, there are a few successful dendrochronological studies conducted on selected tree species growing in semi-arid climate conditions (Gebrekirstos et al., 2008; Krepkowski et al., 2011; Sass-Klaassen et al., 2008; Wils et al., 2011a, 2011b). The growth ring formation, the time of establishment and population development can be detected using tree ring analysis (Gebrekirstos et al., 2014; Tolera et al., 2013). Tree responses to temporal water deficits can be further specified by using wood anatomical characteristics as interannual indicators (De Micco and Aronne, 2012; Worbes et al., 2013). The remote-sensing technique is robust to assess periodicity of leaf phenology (Decuyper et al., 2016; Zhang et al., 2006). The combination of dendrochronology and remote-sensing techniques enables the study of the main physiological and anatomical changes, as well as integrated responses to changing climate conditions at the whole plant level (Battipaglia et al., 2015; Chaves et al., 2002; Decuyper et al., 2016). In this study, a combination of leaf phenology, wood anatomy and climate-growth relationships was used to assess the potential of *B. neglecta* for restoration in water-limited area. We propose knowledge-based management of dryland forests to improve future frankincense production in the Horn of Africa.

## 2. Materials and methods

### 2.1. Ecological range and socio-economic significance of *Boswellia neglecta*

*B. neglecta* occurs in Ethiopia, Kenya, Somalia, Tanzania, and Uganda (PROTA4U: <https://www.prota4u.org/protaindex.asp>; 2016). This species grows in well-drained soil with limited access to water. The adult tree can reach heights of 5 m and a maximum stem diameter of 30 cm (Moore, 1877). In Ethiopia, *B. neglecta* is dominantly found in the dry *Acacia-Commiphora* woodlands of the south and southeastern parts of the country. Frankincense produced from *B. neglecta* is known as “Borena type”. Frankincense is

widely used for domestic consumption and contributes about one-third of the annual household income, making the species an economic priority for Ethiopia (Lemenih and Kassa, 2011; Woldeamanuel, 2011).

### 2.2. Study area and climate

The study was conducted in the semi-arid woodland in the Borena zone, “Arero” district, located (4°5′–5°8′N and 38°23′–39°45′E) in southern Ethiopia. The altitude of the study area ranges from 750 to 1700 m a.s.l. (Fig. 1a). The semi-arid zone of Ethiopia is characterized by an altitude range of 400–2200 m; mean annual rainfall of 300–800 mm. The potential evapotranspiration ranges from 1900 to 2100 mm, and the growing period spans between 46 and 60 days (FAO, 2006). The dominant woody species in this agroecological zone are *Boswellia neglecta*, *Boswellia papyrifera*, *Acacia seyal*, *Acacia senegal*, *Commiphora africana* and *Acacia nilotica*, (FAO, 2006; Worku et al., 2012). Soils in the study area are largely sandy (71.1%) and have only minor amounts of clay, with low levels of organic carbon and nitrogen (Tefera et al., 2007).

The rainfall is bimodal and the main rainy season occurs from March to May (hereafter referred to as MAM), while a shorter rainy season occurs from October to November (hereafter referred to as ON). Meteorological data from 1989 to 2012 was obtained from the nearby weather station in “Chew-Bet”, 20 km from the study site. The mean annual rainfall is 385 ( $\pm 148$  SD) mm. The rainfall in the long rainy season (MAM) contributes 53% (range = 22–80%), while the rainfall in the short rainy season (ON) contributes 35% (range = 4–65%) to the annual rainfall. The remaining 12.6% (range = 2–29%) come from occasional rains during the dry seasons. The mean minimum and maximum temperature for the period from 1962 to 2008 is 14 ( $\pm 0.9$  °C) and 26 ( $\pm 1.9$  °C), respectively (Fig. 1b).

### 2.3. Growth periodicity, leaf phenology, and wood anatomical characteristics

The periodicity of growth ring formation was assessed via a cambial marking experiment, conducted on five randomly selected *B. neglecta* trees for two consecutive years (2010–2012); however, we were able to sample only two trees because the other three trees were found damaged. At the beginning of the longer dry season in June 2010 the cambium was injured with a nail at 1 m stem height. After harvesting the stem disks in September 2012 the number of rings formed since cambial marking was assessed. This was done by preparing transversal micro-thin sections (thickness of 20–30  $\mu$ m) from the wood tissue formed after cambial marking. The sections were stained with a mixture of Astra-blue and Safranin for about 3–5 min and then rinsed with demineralized water and dehydrated with a graded series of ethanol (50%, 96%, and 100%) (Schweingruber et al., 2006) to improve the visibility of wood anatomical features. The detailed wood anatomical features were evaluated from photographs taken using a digital camera (Leica DFC 320, Cambridge, UK), mounted on a microscope (Leica DM2500, Cambridge, UK).

The wood anatomical characteristic of *B. neglecta*, notably the vessel arrangement, and temporal changes in vessel size, were investigated from transversal micro-thin sections prepared from four microcore samples and two stem disks, collected randomly from the population of *B. neglecta*. The micro-thin sections were prepared according to the method described in Schweingruber et al. (2006). To perform this analysis, the digital photographs taken across the full length of the thin-sections were transformed to grayscale to distinguish vessel lumen area from the background tissue based on gray-level thresholds ranging from 0 to 255 using ImageJ (Image processing and analysis software) (Abràmoff et al.,

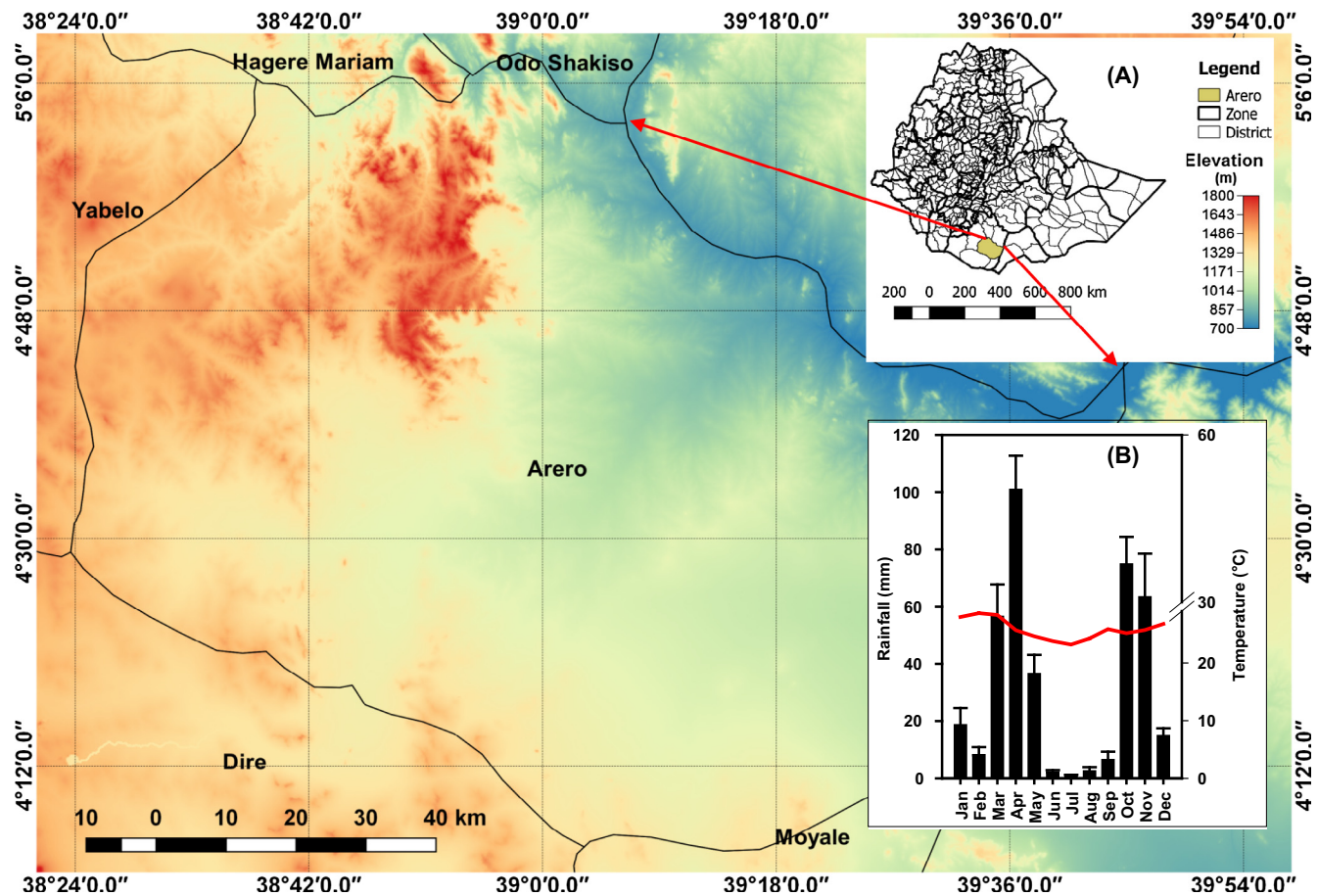


Fig. 1. Location of the study area in the Borena zone, Arero district (a) and climate diagram for the data from the "Chew-Bet" meteorological station (b) showing mean monthly rainfall and mean maximum monthly temperature. The SE is shown as an error bar.

2005). In total, 46 growth ring were randomly selected and measuring frames were created in the earlywood and latewood, where vessel lumen areas then were measured using ImageJ. Frequently, features other than vessels were automatically identified by the system as vessels. In these cases, size and shape filtering techniques were applied during the measurement to reduce measurement errors (Abràmoff et al., 2005; González and Eckstein, 2003). For size filtering, minimum and maximum vessel sizes were defined to be  $1500 \mu\text{m}^2$  and  $65,000 \mu\text{m}^2$ , respectively. Shape filtering (i.e., circularity) was used to exclude non-vessel objects of irregular shape but having the same size as vessels (Abràmoff et al., 2005; González and Eckstein, 2003).

The intra- and inter-annual dynamics in leaf phenology were assessed using the Normalized Difference Vegetation Index (NDVI) (Qu et al., 2015). NDVI values for the period 2000–2012 (13 years) were extracted from the moderate resolution imaging spectroradiometer (MODIS13Q1) product from NASA (USGS). The spatial resolution of MODIS data is 250 m, with a temporal resolution of two days merged to 16 days composites. Homogeneous forest patches were identified and only MODIS pixels with a full coverage of the identified forest patches were taken into account for analysis. To avoid distortions such as the bare soil scattering effect on surface reflectance, a nearby area with bare soil was selected as control (Kokaly and Clark, 1999). To verify the dynamics in NDVI, we used photographs of parts of the same forest taken during dry and wet seasons to assess changes in leaf phenology.

#### 2.4. Growth ring measurement, crossdating and long-term growth trajectories

Growth ring analysis was based on 10 stem disks and 15 increment cores, collected from a total 25 *B. neglecta* trees with no obvious stem and crown damage. Trees with thicker stems sized trees were however favoured to capture the maximum age of the study species. After the samples were air-dried, the transverse sections of cores and stem disks were sanded and polished progressively using sandpaper with an increasing grit size between 60 and 1200 to ensure the visibility of growth ring and wood anatomical features. The anatomical features of the growth ring boundaries were carefully studied first on the stem disks and then all growth rings were marked on both stem disks and increment cores. Ring-width measurements were done with 0.001 mm precision, under a stereo microscope (Leica MS 5, Cambridge, UK) connected to the semi-automatic device (LINTAB, RinnTech, Heidelberg, Germany), supported by TSAP-win (Time Series Analysis and Prediction) software (Rinn, 2011).

Growth ring series were crossdated visually and statistically using TSAP-Win software (Rinn, 2011; Wils et al., 2011a, 2011b) and dated to their exact year of formation using standard dendrochronological techniques (Cook and Kairiukstis, 1990). The COFECHA software was used to check the accuracy of crossdating (Holmes, 1983). Before calculating a chronology reflecting the site specific growth variation of the studied *B. neglecta* trees, the individual growth ring series were detrended applying a cubic spline function to remove age-related growth trends and possible effects of other non-climatic signals (Cook and Kairiukstis, 1990). The



detrended tree ring series were then combined into a single chronology by computing a biweight robust mean value, which minimizes the impacts of outliers on the computation of average index values. Both the detrending and chronology development were computed simultaneously using the computer program ARSTAN (Cook, 1985).

From the dated series, the year of establishment can be estimated for each sample tree. The cumulative growth trajectories and mean annual radial increment can be derived from tree ring series, to evaluate growth rates and growth variation in the entire life span. The mean radial growth rate differences among the sampled trees were tested applying a one-way ANOVA, using SPSS software. The general diameter/age relationship is represented by the cumulative growth curve (CGC) which is sigmoidal for biological systems (Devaranavadi et al., 2013). Thus, a predictive relationship between tree age obtained from tree-ring analysis and stem diameter at sampling height was conducted using a sigmoidal regression function, using SigmaPlot software.

### 2.5. Climate-growth analyses

The Pearson correlation test was used to assess the relationship between climate variables, growth ring, and NDVI values. Monthly rainfall and monthly temperature from 2000 to 2012 were used to assess NDVI-rainfall and NDVI-temperature correlations. Seasonally averaged NDVI from 2000 to 2012 and seasonal rainfall from 1989 to 2012 was used to assess growth ring-NDVI and growth ring-rainfall correlations.

## 3. Results

### 3.1. Growth periodicity, leaf phenology, and wood anatomical characteristics

*B. neglecta* forms distinct growth rings (Fig. 2a and b). The occurrence of tangentially arranged smaller solitary vessels and thicker cell-wall thickness are wood anatomical features depicting

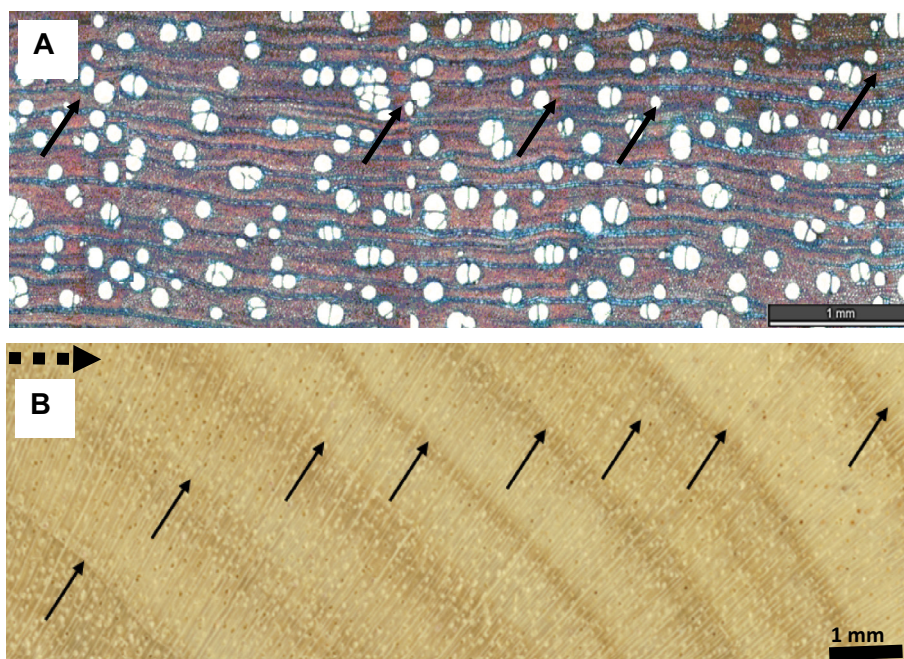
growth rings boundaries. The vessel patterns across growth ring indicate that *B. neglecta* is a diffuse-porous tree, with larger vessels in the beginning of the growth ring (earlywood) and successively smaller vessels toward the end of the growth ring (latewood). Vessels are mostly solitary and only sporadically occur in clusters. The size of the earlywood and latewood vessels range from 4 to  $62 \times 10^3 \mu\text{m}^2$  (mean =  $20 \pm 11$  SD  $\times 10^3 \mu\text{m}^2$ ) and 1.6 to  $30 \times 10^3 \mu\text{m}^2$  (mean =  $7 \pm 4$  SD  $\times 10^3 \mu\text{m}^2$ ), respectively. The average vessel size of the earlywood and latewood is significantly different ( $t_{(1633)} = 25.8$ ,  $p < 0.0001$ ).

*B. neglecta* formed four growth rings between cambial marking (June 2010) and harvesting time (September 2012), indicating the formation of two growth rings per year. The presence of four growth rings are closely corresponds to four distinct wet periods from October to November 2010 (ring #1); March to May 2011 (ring #2), October to November 2011 (ring #3) and March to May 2012 (ring #4) (Fig. 3a–c).

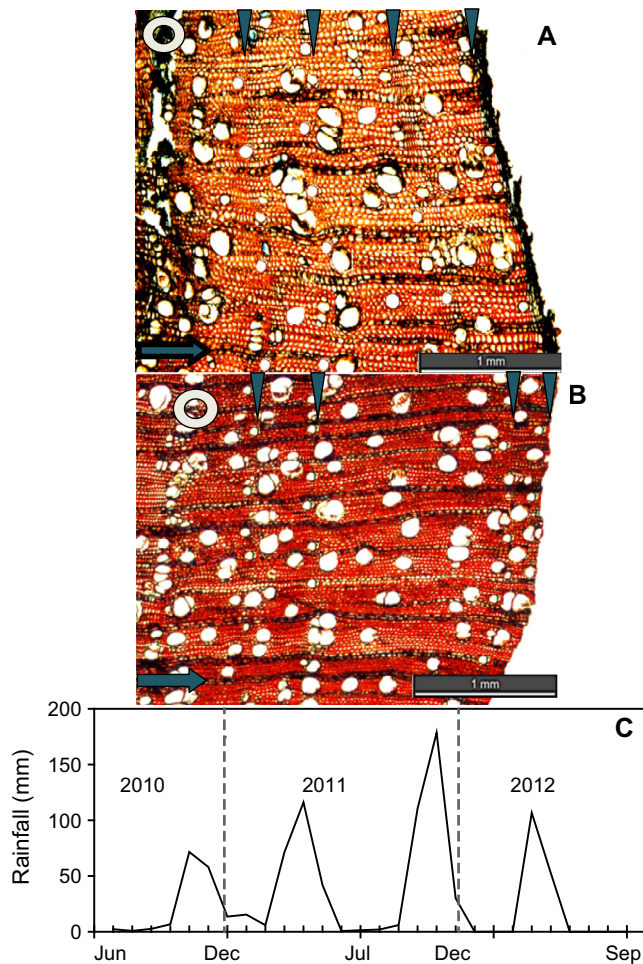
*B. neglecta* showed a bimodal periodicity in leaf phenology corresponding to rainfall seasonality (Appendix A). The first rapid increasing trend of NDVI values was observed in March and reached its maximum in April. From mid-September onwards, a second increase in NDVI values was observed, reaching its maximum in October (Appendix B). The result from the NDVI values is in line with our successive observations and photographic documentation of the seasonal dynamics in leaf phenology during field campaigns (Fig. 4a–d).

### 3.2. Growth dynamics, age of the population and long-term growth trajectory

After careful ring detection of all tree-ring series, 13 trees samples were successfully crossdated (Fig. 5). The number of growth ring per sample ranged from 32 to 56. Taking into account the fact of formation of two rings per year leads to tree ages ranging from 16 to 28 years (Table 1). The site chronology was constructed using the 13 crossdated time series and contains 60 seasonal growth ring spanning the period from 1982 to 2012 (Fig. 5). The mean annual radial increment was 2.5 mm and ranges from 2.1 to 3.6 mm. The



**Fig. 2.** A microscopic picture of thin-section (a) and sanded stem disk (b) of *B. neglecta*. The solid arrows indicate growth ring boundaries. The horizontal broken arrow indicates growth direction.



**Fig. 3.** Periodicity of growth-ring formation of *B. neglecta* trees (a and b), with the contemporary rainfall data (c): The micro-thin sections showing cambial marking position indicated by circles and the number of growth rings formed between cambial marking (June 2010) and harvesting (September 2012) indicated by triangular shape. The horizontal arrow shows growth direction.

interannual growth variation was high as indicated by the standard deviation (0.47) and mean sensitivity (0.40) (Table 1). There is a significant difference in average radial growth rate among the sample trees (one-way ANOVA,  $F_{12,548} = 7.36$ ,  $P < 0.001$ ). The long-term mean annual diameter increment showed an increasing trend (Fig. 6a). The relationship between tree age and stem diameter at sampling height is significant ( $P < 0.05$ ) (Fig. 6b).

### 3.3. Influence of climate factors on growth and leaf phenology

The correlation between growth-ring-width and rainfall of the contemporary rainy season is positive ( $r = 0.18$ ,  $n = 47$ ,  $p = 0.2$ ) (Fig. 7) as well as the relationship between radial growth rate and seasonally averaged NDVI ( $r = 0.34$ ,  $n = 26$ ,  $p = 0.1$ ) (Fig. 7). The correlation between monthly rainfall and monthly NDVI values was positive and significant ( $r = 0.7$ ,  $n = 156$ ,  $p = 0.001$ ).

## 4. Discussion

### 4.1. Seasonality in rainfall as triggering factor for vegetation dynamics

This study shows that *B. neglecta* trees growing in southern Ethiopia produce two growth rings per year, corresponding to the yearly number of wet seasons in the study area, suggesting that

the lengths of wet and dry periods were strong enough to control the cambial periodicity of this species. This result is in agreement with other studies reporting double growth ring formation in bimodal rainfall areas in eastern Africa (e.g., Gourlay, 1995). The positive relationship between rainfall and radial growth confirms that rainfall seasonality is a growth-limiting factor in the study region, as was found for several other dendrochronological studies conducted in the dry tropics (Die et al., 2012; Gebrekirstos et al., 2008; Sass-Klaassen et al., 2008; Trouet et al., 2010). Moreover, the leaf phenological periodicity of *B. neglecta* is biannual (Appendix A), in line with the cambium periodicity. It significantly corresponds with rainfall seasonality, suggesting that the amount of rainfall and seasonality is impacting the vegetative dynamics of the study woodland. The changing vegetation conditions within two to three months also indicate that *B. neglecta* rapidly responds to moisture deficits. This indicates that the tree is able to avoiding drought-induced damage through dropping its leaves and reducing its vessel size. Plant strategies to cope with drought usually involves a mixture of stress avoidance and tolerance strategies that vary between species (Chaves et al., 2002; Gebrekirstos et al., 2006; Locosselli et al., 2013). Studies have shown that plants in arid areas quickly respond to drought, indicating rapid vegetation reaction to periodic water deficits (Decuyper et al., 2016; Locosselli et al., 2013; Zhang et al., 2006; Vicente-Serrano et al., 2013). Species adapted to grow in dry environments tend to survive and grow better under extreme drought conditions than mesic-adapted species (McDowell et al., 2008; Vicente-Serrano et al., 2013). Additionally, *B. neglecta* showed distinct temporal changes in vessel area across its growth ring again reflecting the potential to adapt and/or acclimate to low moisture conditions (Lovisolo and Schubert, 1998; Worbes et al., 2013). The tangentially arranged smaller size solitary vessels in the late growth zone indicate that *B. neglecta* is not very susceptible to drought-induced cavitation, as has been shown for other species (e.g., Scholz et al., 2013). Trees in arid and semi-arid areas may avoid drought impacts either by shedding their leaves, reducing the size of their water conducting system, or by both mechanisms concurrently (Gebrekirstos et al., 2006; Gizińska et al., 2015; Kondoh et al., 2006; Sass-Klaassen et al., 2011; Scholz et al., 2013). Generally, succulent stem species like *B. neglecta* have an effective strategy against drought stress, making them successful as a pioneer species in tropical dry forests (Borchert and Pockman, 2005; Worbes et al., 2013). *B. neglecta* survived and even expanded across the (sometimes extremely) water-limited dryland conditions of south-eastern Ethiopia. These characteristics make *B. neglecta* one of the key tree species for this environment and useful for dryland restoration interventions under changing climate.

### 4.2. Stem growth dynamics and history of population

The crossdating among sample trees also indicates that common climate signals were captured in each of the radial growth rings. This implies that the radial growth rates of *B. neglecta* were influenced by the same climate factors, mainly rainfall which was also found in Battipaglia et al., 2015; Sheffer et al., 2011; Worbes et al., 2013. However, nearly 50% of sample trees failed to crossdate, indicating that ring identification, dating to the correct calendar years and crossdating was complex in the study region. Additional stress factors such as herbivory may make crossdating more complex. *B. neglecta* has palatable leaves and no thorns and heavy browsing may have impacted the growth dynamics. This, in turn, may have led to the formation of partially indistinct or totally missing growth rings around the stem circumference (Giantomasi et al., 2015; Goiran et al., 2012; Maron and Crone, 2006). Another plausible theory is that under conditions with two, often irregular, rainy seasons, the cambium of some or



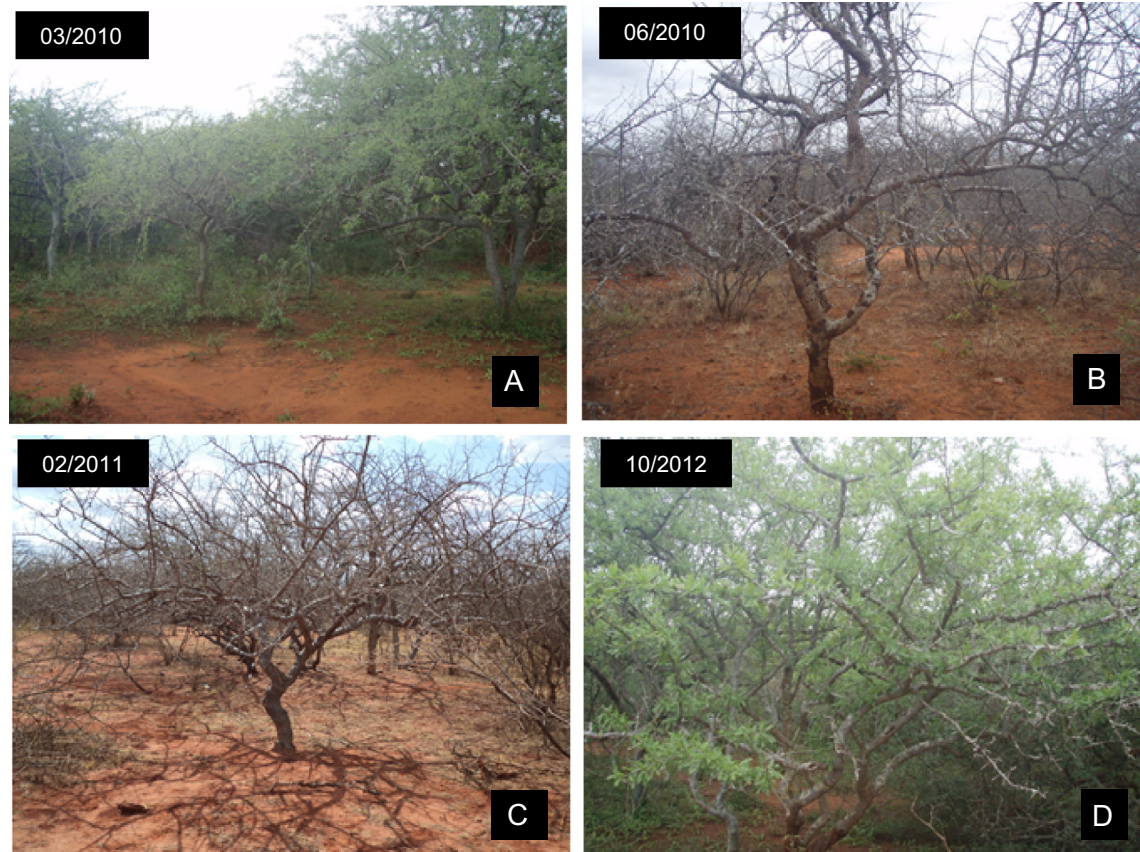


Fig. 4. Documentation of leaf phenological patterns at *B. neglecta* dominated dry woodland, southern Ethiopia.

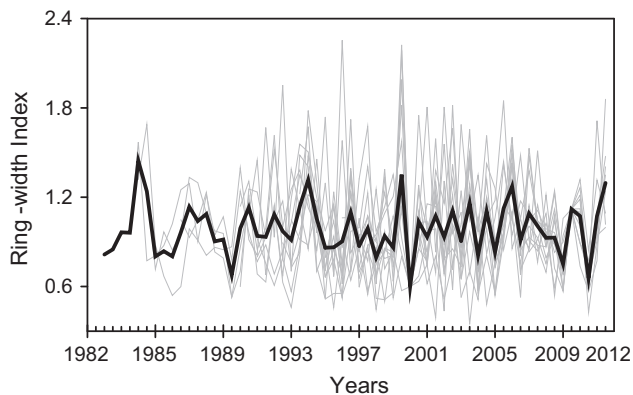


Fig. 5. The site specific chronology (bold dark) and individual ring width index of well-crossdated tree-ring series (gray), from *B. neglecta*, southern Ethiopia.

all trees remain inactive after a prolonged dry season, or when the rainy season is too short or not intense enough (Krepkowski et al., 2011; Wils et al., 2009; Worbes, 2002). This would lead to a missing growth ring in some or even all trees and can obscure exact dating of growth rings. This might partially explain the low climate-growth relationships. Generally, in open-access woodland several growth stress factors affect tree growth and complicate tree ring analysis, as has been shown for both lowland and highland areas in Ethiopia (Gebrekirstos et al., 2008; Wils et al., 2011a, 2011b) and in Mali, West Africa (Sanogo et al., 2016).

The sampled trees were on average 22 years old (range 16–28), indicating that colonization of the study site by this species is a recent phenomenon. Individual trees differed significantly in aver-

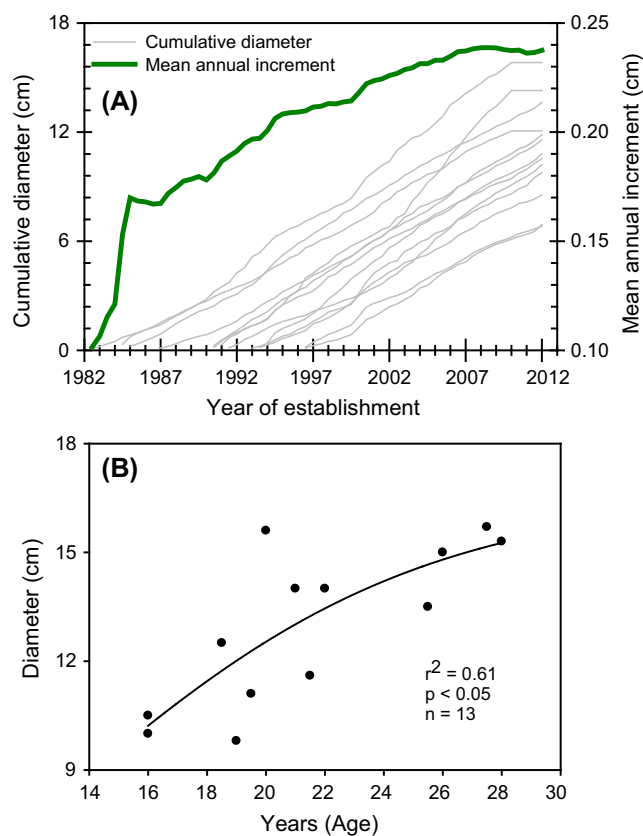
age radial growth rate which is possibly associated with age differences (e.g., Johnson and Abrams, 2009). The radial growth rate of *B. neglecta* showed a long-term increasing pattern and a close relationship between age and diameter. The study area has been used as rangeland and the pastoralists use fire to control bush encroachment (Angassa and Oba, 2008; Dalle et al., 2006). However, between 1968 and 1976 an official ban on traditional rangeland burning practice was implemented in the study area and other parts of southeastern Ethiopia (Angassa and Oba, 2008), indicating that banning of fire led to woody species encroachment in the region (Angassa and Oba, 2008; Dalle et al., 2006). The fire ban policy has possibly created favourable environmental conditions for *B. neglecta* to successfully establish and survive in the study area, further supporting our argument that the population is young and reflects recent colonization. The establishment period of the study species reported in this study is in agreement with the increasing trends of woody species encroachment in sub-Saharan Africa (Mitchard and Flintrop, 2013).

#### 4.3. Implications for forest management and extending the economic benefits from frankincense

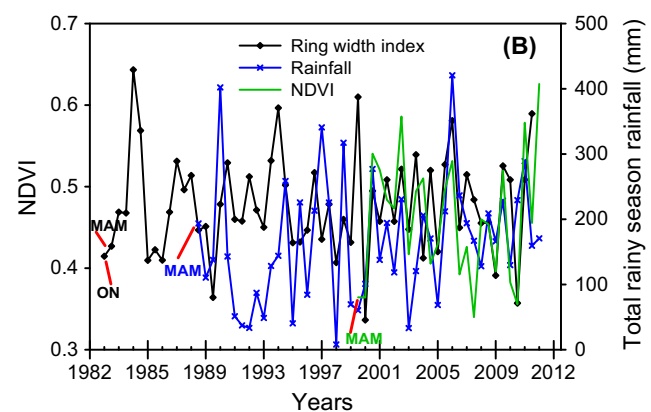
Dryland forests are playing crucial ecological, social and economic roles (Blackie et al., 2014; Miura et al., 2015) and have a potential to buffer livelihoods against drought-induced failures in agricultural production (Lawry et al., 2015; Wagner et al., 2013). In many regions, however, dryland forests continue to degrade due to complex anthropogenic factors, including lack of investment in their sustainable management and restoration (Flintan et al., 2013; IPCC, 2007). Climate change is another growing concern in the tropics and expected to exacerbate dryland forest

**Table 1**Summary of seasonal mean radial growth increment of *B. neglecta* trees. Tree-age (year) equals to [number of rings/2]. Standard deviation represented as [ $\pm$ SD].

Tree code	Number of growth-rings	Seasonal growth ring width ( $SD \pm$ mm)	Correlation ( $r$ ) with master series	Auto corr.	Mean sens.
ST1	38	1.10 [ $\pm 0.39$ ]	0.55	0.14	0.39
ST2	39	1.21 [ $\pm 0.60$ ]	0.66	0.01	0.53
ST3	55	1.24 [ $\pm 0.38$ ]	0.61	0.21	0.35
ST4	32	1.06 [ $\pm 0.48$ ]	0.48	0.06	0.44
ST5	44	1.35 [ $\pm 0.34$ ]	0.66	0.28	0.35
ST6	42	1.22 [ $\pm 0.51$ ]	0.55	0.46	0.35
ST7	51	1.13 [ $\pm 0.39$ ]	0.58	0.10	0.36
ST8	37	1.47 [ $\pm 0.51$ ]	0.61	0.14	0.34
ST9	43	1.23 [ $\pm 0.40$ ]	0.48	0.08	0.44
ST10	32	1.03 [ $\pm 0.37$ ]	0.63	0.11	0.32
ST11	52	1.49 [ $\pm 0.63$ ]	0.46	0.12	0.42
ST12	56	1.08 [ $\pm 0.39$ ]	0.48	0.08	0.35
ST13	40	1.79 [ $\pm 0.79$ ]	0.53	0.17	0.42
Average	43	1.25 [ $\pm 0.47$ ]	0.56	0.15	0.39

**Fig. 6.** Life-time growth trajectory (a) and age-diameter relationship (b) of *B. neglecta* trees, southern Ethiopia.

degradation, in particular in those regions that are already exposed to limited water resources (Allen et al., 2015; IPCC, 2007). On the other hand, millions of hectares of dryland forest landscapes need to be restored to help tackle global challenges such as poverty, climate change, soil erosion and desertification in order to safeguard biodiversity (Reynolds et al., 2007). This study presents useful information that can help to understand growth dynamics, establishment and other responses of *B. neglecta* trees to changing climate. This information is crucial for planning sustainable forest management and guide restoration interventions. The age and growth rate data of the study species indicates a high potential for increasing populations for future frankincense production. Thus, investment in the management of this forest would help to improve the livelihoods of the local community depending on this

**Fig. 7.** Comparison between the ring width-rainfall (1989–2012) and ring width-Normalized Difference Vegetation Index (NDVI), spanning from (2000–2012). ON and MAM indicate October–November, and March–May growth on the black line. Total rainfall over March–May (from 1989) and NDVI (from 2000) are represented by a blue and by a green line, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forest product as source of their income. Based on the leaf-phenological patterns and wood anatomical characteristics of *B. neglecta*, we characterize this species as drought adaptive, a key factor for the establishment and survival of trees in drought-prone areas (Worbes et al., 2013). Therefore, we recommend *B. neglecta* as a key tree species in drylands with potential for restoration schemes in water-limited areas across similar environments in eastern Africa. With proper management, the multifunctional species *B. neglecta* can help the community to adapt to the existing as well as projected impacts of climate change in the drylands by boosting the economic benefits through frankincense and fodder production. Since frankincense production from *B. neglecta* is conducted in the dry season in a non-destructive way, it plays a pivotal role in climate change adaption and mitigation.

## 5. Conclusions

Evidence from dendrochronological and remote-sensing techniques showed that the population of *B. neglecta* in southeastern Ethiopia is young and characterized by a bi-annual leaf phenological and stem growth pattern which is strongly corresponding to rainfall seasonality in the study region. This indicates that moisture availability is the main driver of vegetation dynamics in the study region. The current *Boswellia* population being young also indicate a strong potential for future frankincense production if this dryland forest is properly managed and well valued. The seasonal physio-



logical and anatomical responses of *B. neglecta* to periodic changes in water availability indicate that this species is drought adaptive. We conclude that *B. neglecta* is a key tree species in drylands and can be used for restoration of drylands and create a drought-resilient landscape.

## Acknowledgments

We are grateful to Wageningen University for laboratory facilities and financial support. We also thank Hawassa University, Wondo Genet College of Forestry and Natural Resources for their laboratory and logistical support. We are grateful to Borana zone Agricultural Office for their permission to collect samples and carry out this study. We acknowledge financial support from CGIAR Research Program on Forests, Trees and Agroforestry (FTA) during the preparation of this manuscript. This research is also supported by the Dutch-Ethiopian FRAME programme 'FRAnkincense, Myrrh and arabic gum: sustainable use of dry woodland resources in Ethiopia', funded by the Netherlands Foundation for the Advancement of Scientific Research in the Tropics (NWO-WOTRO, grant W01.65.220.00). We thank funding from Wageningen University, the British Ecological Society (BES grant number 2732/3420) and the Swedish International Development Agency (Sida). We also thank all who have supported us during field and laboratory activities and members of the COST Action FP1106 STReSS for the discussion of the results.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.11.020>.

## References

- Abbramoff, M.D., Magalhães, P.J., Ram, S.J., 2005. Image processing with ImageJ. *Biophoton. Int.* 11, 36–43. <http://dx.doi.org/10.1117/1.3589100>.
- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 1–55.
- Angassa, A., Oba, G., 2008. Herder perceptions on impacts of range enclosures, crop farming, fire ban and bush encroachment on the rangelands of Borana, Southern Ethiopia. *Hum. Ecol.* 36, 201–215. <http://dx.doi.org/10.1007/s10745-007-9156-z>.
- Battipaglia, G., Zalloni, E., Castaldi, S., Marzaioli, F., Cazzolla-Gatti, R., Lasserre, B., Tognetti, R., Marchetti, M., Valentini, R., 2015. Long tree-ring chronologies provide evidence of recent tree growth decrease in a central African tropical forest. *PLoS ONE* 10, 1–21. <http://dx.doi.org/10.1371/journal.pone.0120962>.
- Blackie, R., Baldauf, C., Gautier, D., Gumbo, D., Kassa, H., Parthasarathy, N., Paumgarten, F., Sola, P., Waeber, S., Sunderland, P., Sunderland, T., 2014. Tropical Dry Forests. The State of Global Knowledge and Recommendations for Future Research. Discussion Paper. CIFOR, Bogor, Indonesia. p. 38.
- Borchert, R., Pockman, W.T., 2005. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiol.* 25, 457–466. <http://dx.doi.org/10.1093/treephys/25.4.457>.
- Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. *Science* 320, 1456–1457. <http://dx.doi.org/10.1126/science.1155458>.
- Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osório, M.L., Carvalho, I., Faria, T., Pinheiro, C., 2002. How plants cope with water stress in the field. Photosynthesis and growth. *Ann. Bot.* 89, 907–916. <http://dx.doi.org/10.1093/aob/mcf105>.
- Cook, E., Kairiukstis, L., 1990. *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Boston, MA.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree-ring Standardization.
- Corlett, R.T., 2016. The impacts of droughts in tropical forests. *Trends Plant Sci.* 21. <http://dx.doi.org/10.1016/j.tplants.2016.02.003>.
- Dalle, G., Maass, B., Isselstein, J., 2006. Rangeland condition and trend in the semi-arid Borana lowlands, southern Oromia, Ethiopia. *Afr. J. Range Forage Sci.* 23, 49–58. <http://dx.doi.org/10.2989/10220110609485886>.
- De Micco, V., Aronne, G., 2012. Morpho-anatomical traits for plant adaptation to drought. In: *Plant Responses to Drought Stress*. Springer, Berlin, Heidelberg, pp. 37–61. <http://dx.doi.org/10.1007/978-3-642-32653-0>.
- Decuyper, M., Chavez, R.O., Copini, P., Sass-Klaassen, U., 2016. A multi-scale approach to assess the effect of groundwater extraction on *Prosopis tamarugo* in the Atacama Desert. *J. Arid Environ.* 131, 25–34. <http://dx.doi.org/10.1016/j.jaridenv.2016.03.014>.
- De Leeuw, J., Njenga, M., Wagner, B., Iiyama, M. (Eds.), 2014. *Treesilience: An Assessment of the Resilience Provided by Trees in the Drylands of Eastern Africa*. The World Agroforestry Centre (ICRAF), Nairobi, Kenya.
- Devaranavadi, S.B., Bassappa, S., Wali, S.Y., 2013. Height-age growth curve modelling for different tree species in drylands of North Karnataka. *Glob. J. Sci. Front. Res. Agric. Vet. Sci.* 13, 13.
- Die, A., Kitin, P., Kouame, F.N.G., Van Den Bulcke, J., Van Acker, J., Beeckman, H., 2012. Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (*Tectona grandis*) in Ivory Coast. *Ann. Bot.* 110, 861–873. <http://dx.doi.org/10.1093/aob/mcs145>.
- FAO, 2006. Country Pasture/Forage Resource Profiles: Ethiopia. Viale delle Terme di Caracalla, 00153 Rome, Italy.
- Flintan, F., Behnke, R., Neely, C., 2013. Natural Resource Management in the Drylands in the Horn of Africa. Brief Prepared by a Technical Consortium Hosted by CGIAR in Partnership with the FAO Investment Centre. Technical Consortium Brief 1. International Livestock Research Institute, Nairobi.
- Gebrekirstos, A., Bräuning, A., Sass-Klassen, U., Mbow, C., 2014. Opportunities and applications of dendrochronology in Africa. *Curr. Opin. Environ. Sustain.* 6, 48–53. <http://dx.doi.org/10.1016/j.cosust.2013.10.011>.
- Gebrekirstos, A., Mitlöhner, R., Teketay, D., Worbes, M., 2008. Climate-growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. *Trees* 22, 631–641. <http://dx.doi.org/10.1007/s00468-008-0221-z>.
- Gebrekirstos, A., Teketay, D., Fetene, M., Mitlöhner, R., 2006. Adaptation of five co-occurring tree and shrub species to water stress and its implication in restoration of degraded lands. *For. Ecol. Manage.* 229, 259–267. <http://dx.doi.org/10.1016/j.foreco.2006.04.029>.
- Giantomasi, M.A., Alvarez, J.A., Villagra, P.E., Debandi, G., Roig-Junent, F.A., 2015. Pruning effects on ring width and wood hydrosystem of *Prosopis flexuosa* DC from arid woodlands. *Dendrochronologia* 35, 71–79. <http://dx.doi.org/10.1016/j.dendro.2015.07.002>.
- Gizińska, A., Miodek, A., Wilczek, A., Włoch, W., Iqbal, M., 2015. Wood porosity as an adaptation to environmental conditions. *Nat. J.*
- Goiran, S.B., Aranibar, J.N., Gomez, M.L., 2012. Heterogeneous spatial distribution of traditional livestock settlements and their effects on vegetation cover in arid groundwater coupled ecosystems in the Monte Desert (Argentina). *J. Arid Environ.* 87, 188–197. <http://dx.doi.org/10.1016/j.jaridenv.2012.07.011>.
- González, I.G., Eckstein, D., 2003. Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiol.* 23, 497–504. <http://dx.doi.org/10.1093/treephys/23.7.497>.
- Gourlay, I.D., 1995. The definition of seasonal growth zones in some African acacia species – a review. *IAWA* 16, 353–359.
- Groenendijk, P., Eshete, A., Sterck, F.J., Zuidema, P.A., Bongers, F., 2012. Limitations to sustainable frankincense production: blocked regeneration, high adult mortality, and declining populations. *J. Appl. Ecol.* 49, 164–173. <http://dx.doi.org/10.1111/j.1365-2664.2011.02078.x>.
- Hiltner, U., Bräuning, A., Gebrekirstos, A., Huth, A., 2015. Impacts of precipitation variability on the dynamics of a dry tropical montane forest. *Ecol. Modell.* 320, 92–101.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78. <http://dx.doi.org/10.1016/j.ecoleng.2008.01.004>.
- IPCC, 2007. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*.
- Johnson, S.E., Abrams, M.D., 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. *Tree Physiol.* <http://dx.doi.org/10.1093/treephys/tp008>.
- Kokaly, R.F., Clark, R.N., 1999. Spectroscopic determination of leaf biochemistry using band-depth analysis of absorption features and stepwise multiple linear regression. *Rem. Sens. Environ.* 67, 267–287. [http://dx.doi.org/10.1016/S0034-4257\(98\)00084-4](http://dx.doi.org/10.1016/S0034-4257(98)00084-4).
- Kondoh, S., Yahata, H., Nakashizuka, T., Kondoh, M., 2006. Interspecific variation in vessel size, growth and drought tolerance of broad-leaved trees in semi-arid regions of Kenya. *Tree Physiol.* 26, 899–904. <http://dx.doi.org/10.1093/treephys/26.7.899>.
- Krepkowski, J., Bräuning, A., Gebrekirstos, A., Stroh, S., 2011. Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. *Trees* 25, 59–70. <http://dx.doi.org/10.1007/s00468-010-0460-7>.
- Lawry, S., McLain, R., Kassa, H., 2015. Strengthening the Resiliency of Dryland Forest-based Livelihoods in Ethiopia and South Sudan: A Review of Literature on the Interaction between Dryland Forests, Livelihoods and Forest Governance. Working Paper 182. CIFOR, Bogor, Indonesia.
- Lemenih, M., Abebe, T., Olsson, M., 2003. Gum and resin resources from some *Acacia*, *Boswellia* and *Commiphora* species and their economic contributions in Liban, south-east Ethiopia. *J. Arid Environ.* 55, 465–482. [http://dx.doi.org/10.1016/S0140-1963\(03\)00053-3](http://dx.doi.org/10.1016/S0140-1963(03)00053-3).
- Lemenih, M., Kassa, H., 2011. Opportunities and Challenges for Sustainable Production and Marketing of Gums and Resins in Ethiopia. CIFOR, Bogor, Indonesia.
- Locosselli, G.M., Buckeridge, M.S., Moreira, M.Z., Ceccantini, G., 2013. A multi-proxy dendroecological analysis of two tropical species (*Hymenaea* spp., Leguminosae)



- growing in a vegetation mosaic. *Trees-Struct. Funct.* 27, 25–36. <http://dx.doi.org/10.1007/s00468-012-0764-x>.
- Lovisolo, C., Schubert, A., 1998. Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L. *J. Exp. Bot.* 49, 693–700. <http://dx.doi.org/10.1093/jxb/49.321.693>.
- Maron, J.L., Crone, E., 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proc. R. Soc. B: Biol. Sci.* 273, 2575–2584. <http://dx.doi.org/10.1098/rspb.2006.3587>.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739. <http://dx.doi.org/10.1111/j.1469-8137.2008.02436.x>.
- Mitchard, E.T.A., Flintrop, C.M., 2013. Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982–2006. *Philos. Trans. R. Soc. B: Biol. Sci.* 368, 20120406. <http://dx.doi.org/10.1098/rstb.2012.0406>.
- Miura, S., Amacher, M., Hofer, T., San-Miguel-Ayanz, J., Thackway, R., 2015. Protective functions and ecosystem services of global forests in the past quarter-century. *For. Ecol. Manage.* 352, 35–46. <http://dx.doi.org/10.1016/j.foreco.2015.03.039>.
- Moges, Y., Eshetu, Z., Nune, S., 2010. Ethiopian Forest Resources: Current Status and Future Management Options in View of Access to Carbon Finances. Addis Ababa.
- Mokria, M.G., Gebrekirstos, A., Aynekulu, B.E., Bräuning, A., 2015. Tree dieback affects climate change mitigation potential of a dry Afromontane forest in northern Ethiopia. *For. Ecol. Manage.* 20–25. <http://dx.doi.org/10.1016/j.foreco.2014.02.008>.
- Moore, S.L.M., 1877. *Taxon: Boswellia neglecta* S. Moore. *J. Bot.* 15, 185.
- Qu, B., Zhu, W., Jia, S., Lv, A., 2015. Spatio-temporal changes in vegetation activity and its driving factors during the growing season in China from 1982 to 2011. *Rem. Sens.* 7, 13729–13752. <http://dx.doi.org/10.3390/rs71013729>.
- Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S. P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. *Science* (80-) 316, 847–851. <http://dx.doi.org/10.1126/science.1131634>.
- Rinn, F., 2011. TSAP-Win. Time Series Analysis and Presentation for Dendrochronology and Related Applications 110.
- Sanogo, K., Gebrekirstos, A., Bayala, J., Villamor, G.B., Kalinganire, A., Dodiomon, S., 2016. Potential of dendrochronology in assessing carbon sequestration rates of *Vitellaria paradoxa* in southern Mali, West Africa. *Dendrochronologia* 40, 26–35. <http://dx.doi.org/10.1016/j.dendro.2016.05.004>.
- Sass-Klaassen, U., Couralet, C., Sahle, Y., Sterck, F.J., 2008. Juniper from Ethiopia contains a large-scale precipitation signal. *Int. J. Plant Sci.* 169, 1057–1065. <http://dx.doi.org/10.1086/590473>.
- Sass-Klaassen, U., Sabajo, C.R., den Ouden, J., 2011. Vessel formation in relation to leaf phenology in pedunculate oak and European ash. *Dendrochronologia* 29, 171–175. <http://dx.doi.org/10.1016/j.dendro.2011.01.002>.
- Scholz, A., Rabaey, D., Stein, A., Cochard, H., Smets, E., Jansen, S., 2013. The evolution and function of vessel and pit characters with respect to cavitation resistance across 10 *Prunus* species. *Tree Physiol.* 33, 684–694. <http://dx.doi.org/10.1093/treephys/tpt050>.
- Schweingruber, F., Börner, A., Schulze, E.-D., 2006. Atlas of woody plant stems. Evolution, structure, and environmental modifications. *J. Veg. Sci.* <http://dx.doi.org/10.3170/2008-8-18577>.
- Sheffer, E., Yizhaq, H., Shachak, M., Meron, E., 2011. Mechanisms of vegetation-ring formation in water-limited systems. *J. Theor. Biol.* 273, 138–146. <http://dx.doi.org/10.1016/j.jtbi.2010.12.028>.
- Sunderland, T., Apgaua, D., Baldauf, C., Blackie, R., Colfer, C., Cunningham, A.B., Dexter, K., Djoudi, H., Gautier, D., Gumbo, D., Ickowitz, A., Kassa, H., Parthasarathy, N., Pennington, R., Paumgarten, F., Pulla, F., Sola, P., Tng, D., Waebery, Wilmé, L., 2007. Global dry forests: a prologue. *Int. For. Rev.* 17, 1–9.
- Tadesse, W., Desalegn, G., Alia, R., 2007. Natural gum and resin bearing species of Ethiopia and their potential applications. *Invest. Agrar. Sist. Recur. For.* 16, 211–221.
- Tefera, S., Snyman, H.A., Smit, G.N., 2007. Rangeland dynamics in southern Ethiopia: (1) botanical composition of grasses and soil characteristics in relation to land-use and distance from water in semi-arid Borana rangelands. *J. Environ. Manage.* 85, 429–442. <http://dx.doi.org/10.1016/j.jenvman.2006.10.007>.
- Tolera, M., Sass-Klaassen, U., Eshete, A., Bongers, F., Sterck, F.J., 2013. Frankincense tree recruitment failed over the past half century. *For. Ecol. Manage.* 304, 65–72. <http://dx.doi.org/10.1016/j.foreco.2013.04.036>.
- Trouet, V., Esper, J., Beeckman, H., 2010. Climate/growth relationships of *Brachystegia spiciformis* from the Miombo woodland in southcentral Africa. *Dendrochronologia* 28, 161–171. <http://dx.doi.org/10.1016/j.dendro.2009.10.002>.
- Van Der Ent, R.J., Savenije, H.H.G., Schaeffli, B., Steele-Dunne, S.C., 2010. Origin and fate of atmospheric moisture over continents. *Water Resour. Res.* 46, 1–12. <http://dx.doi.org/10.1029/2010WR009127>.
- van Noordwijk, M., Bruijnzeel, S., Ellison, D., Sheil, D., Morris, C., Gutierrez, V., Cohen, J., Sullivan, C., Verbist, B., Muys, B., 2015. Ecological Rainfall Infrastructure: Investment in Trees for Sustainable Development. ASB Policy Brief 47. ASB Partnership for the Tropical Forest Margins, Nairobi.
- Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.L., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Morán-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. *Proc. Natl. Acad. Sci. U.S.A.* 110, 52–57. <http://dx.doi.org/10.1073/pnas.1207068110>.
- Wagner, B., de Leeuw, J., Njenga, M., Jamnadass, R., 2013. Towards Greater Resilience in the Drylands: Trees Are the Key. Nairobi, Kenya.
- WBISPP, 2004. Forest Resources of Ethiopia (Addis Ababa, Ethiopia).
- Wils, T.H.G., Robertson, I., Eshetu, Z., Touchan, R., Sass-Klaassen, U., Koprowski, M., 2011a. Crossdating *Juniperus procera* from North Gondar, Ethiopia. *Trees-Struct. Funct.* 25, 71–82. <http://dx.doi.org/10.1007/s00468-010-0475-0>.
- Wils, T.H.G., Robertson, I., Eshetu, Z., Sass-klaassen, U.G.W., Koprowski, M., 2009. Periodicity of growth ring in *Juniperus procera* from Ethiopia inferred from crossdating and radiocarbon dating. *Dendrochronologia* 1–14. <http://dx.doi.org/10.1016/j.dendro.2008.08.002>.
- Wils, T.H.G., Sass-Klaassen, U.G.W., Eshetu, Z., Brauning, A., Gebrekirstos, A., Couralet, C., Robertson, I., Touchan, R., Koprowski, M., Conway, D., Briffa, K.R., Beeckman, H., 2011b. Dendrochronology in the dry tropics: the Ethiopian case. *Trees-Struct. Funct.* 25, 345–354. <http://dx.doi.org/10.1007/s00468-010-0521-y>.
- Woldeamanuel, T., 2011. Dryland Resources, Livelihoods and Governance: Diversity and Dynamics in Use and Management of Gum/Resin Trees in Ethiopia, pp. 1–152.
- Worbes, M., 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. *Dendrochronologia* 2, 217–231.
- Worbes, M., Blanchart, S., Fichtler, E., 2013. Relations between water balance, wood traits and phenological behavior of tree species from a tropical dry forest in Costa Rica – a multifactorial study. *Tree Physiol.* 33, 527–536. <http://dx.doi.org/10.1093/treephys/tpt028>.
- Worku, A., Teketay, D., Lemenih, M., Fetene, M., 2012. Diversity, regeneration status, and population structures of gum and resin producing woody species in Borana, Southern Ethiopia. *For. Trees Livelihoods* 21, 85–96. <http://dx.doi.org/10.1080/14728028.2012.716993>.
- Zhang, X., Friedl, M.A., Schaaf, C.B., 2006. Global vegetation phenology from Moderate Resolution Imaging Spectroradiometer (MODIS): evaluation of global patterns and comparison with in situ measurements. *J. Geophys. Res.: Biogeosci.* 111, 1–14. <http://dx.doi.org/10.1029/2006JG000217>.