Original article

Growth ring formation of *Dichrostachys cinerea* and *Senegalia mellifera* in arid environments in Namibia

R. Shikangalah[a,*], B. Mapani[b], I. Mapaure[c], U. Herzschuh[d], A. Musimba[c], X. Tabares[d]

[a] *Department of Geography, Faculty of Humanities and Social Sciences, University of Namibia, Private Bag 13301, Windhoek, Namibia*
[b] *Department of Geology, Faculty of Science, University of Namibia, Private Bag 13301, Windhoek, Namibia*
[c] *Department of Biological Sciences, Faculty of Science, University of Namibia, Private Bag 13301, Windhoek, Namibia*
[d] *Alfred Wegner Institute for Polar Research, Telegrafenberg, Potsdam, Germany*

ARTICLE INFO

ABSTRACT

Dichrostachys cinerea and *Senegalia mellifera* trees are the most widespread invasive encroacher species in Namibia. Understanding their growth performance under arid conditions is key to understanding and managing the arid ecosystems of Namibia. To determine their utility in dendrochronology, we analyzed the formation of growth rings for two species from three sites in Namibia. We applied cross-dating techniques to 69 tree discs, the analysis of which confirmed the formation of annual growth rings. The rings are characterised by alternating layers of low and high vessel density and are separated by bands of marginal parenchyma. *D. cinerea* shows a well-defined pattern of growth rings, whereas the ring patterns of *S. mellifera* are more complex. Because aging trees tend to display narrower rings toward the outside of the stem, we applied both ring-width index and basal area increment methods in developing ring-width chronologies for the two species. Descriptive statistics for the chronologies indicate that the average ring chronologies are of good quality and that the trees are responding to common environmental signals. The basal area increment methodology produced better statistics than the ring-width index for these two species. Furthermore, statistical characteristics of the chronologies indicate that *D. cinerea* has a higher mean sensitivity (MS), expressed population signal (EPS), and signal-to-noise ratio (SNR) than *S. mellifera*. Thus, we find that both species are suitable for dendrochronological study, with *D. cinerea* being better than *S. mellifera*.

1. Introduction

Climate change impacts biodiversity at multiple scales, from genes and species to communities and ecosystems (Visser et al., 2004; Singer and Parmesan, 2010; Staudinger et al., 2012). Dendrochronology has become a particularly useful tool for understanding climate change because trees can record both environmental and site conditions over thousands of years (IPCC et al., 2001; Carrer and Urbinati, 2010; Stoffel and Bollschweiler, 2010), by adding a new ring layer to the stem each growing season (Sheppard, 2010; Chhetri and Shrestha, 2009). Local conditions influence the growth of each ring, resulting in wider or narrower rings depending on the favorability of conditions for growth. Thus, trees record past and present conditions, and provide clues about future environmental conditions (Fritts, 2012; Novak et al., 2013; Anchukaitis, 2017).

The information that trees record is important for understanding ecosystem dynamics and predicting changes in the ecological surroundings, because trees can provide information that extends well past the instrumental record. This information is especially valuable in arid and semi-arid environments, where sound land management is crucial due to the climate-related vulnerability of such environments and the frequent lack of observational data. This holds particularly true for Namibia as the country is the most arid in southern Africa and second only in aridity to the Sahara Desert in North Africa (Food and Agriculture Organization (FAO), 2005; Turpie et al., 2010). More than ninety percent of Namibia's landmass is classified as semi-arid, arid, or hyper-arid, and the country is characterized by sporadic rainfall and high evaporation rates (Mendelsohn et al., 2002; Shanyengana et al., 2004; Barnard, 2012).

A number of species in semi-arid parts of Africa have shown potential for dendrochronological studies (Gourlay, 1995; Wils et al., 2009; Gaspard et al., 2018; Rahman et al., 2018). In many arid African regions, the transition from wet season to dry season results in detectable anatomical changes as the trees lose or produce new leaves

(Gourlay, 1995; Worbes, 1999). Such changes include the development of growth rings in response to the wet-dry cycles. However, such growth rings might not be reliable for developing tree ring chronologies because the cambium is not always active. Severe drought stress might cause erratic growth in the cambium, leading to the formation of smaller growth rings in the same season (Gourlay, 1995; Wils et al., 2009; Nath et al., 2016). In tropical ecosystems such as those found in Namibia, growth rings may be evident as systematic transitions from large vessel zones to layers of smaller vessels that are defined by the wet-dry cycles (Worbes, 1999; Nath et al., 2016).

Despite extremely dry conditions, *Dichrostachys cinerea* and *Senegalia mellifera* thrive in Namibia and have become the most problematic encroacher species (Strohbach, 2000; de Klerk, 2004; Joubert et al., 2008). These two species have substantially reduced the carrying capacity of rangelands for livestock production in Namibia by about 8 million hectares, of which 5.3 million hectares are severely infested (Bester, 1999). Of the country's 71 million hectares of commercial rangelands, 34.89 million hectares (about 50 %) are under bush encroachment. These two species account for 40 % of the encroached area (Bester, 1999). We focus here on these two species because, unlike other encroachers such as *Terminalia prunioides*, *Terminalia sericea*, *Colophospermum mopane*, *Senegalia erubescens*, *Senegalia fleckii*, and *Vachellia reficiens*, which are considered to be local encroachers, *Dichrostachys cinerea* and *Senegalia mellifera* are aggressive encroachers (Bester, 1999; Curtis and Mannheimer, 2005; Marais et al., 2015; Hauwanga et al., 2018).

Although a number of studies have been carried out on *Dichrostachys cinerea* and *Senegalia mellifera* (e.g. Bester, 1999; Bhugeloo, 2014; Shorrocks and Bates, 2015; Zacharias et al., 2018), little is known about their dendrochronological aspects or growth patterns, or the processes involved in their establishment. Both species are deciduous, shedding their leaves at the end of each growing season. Such wet and dry spells result in tree ring formation as defined for tropical deciduous trees (Nath et al., 2016; Zacharias et al., 2018). This study examines the growth ring development of *D. cinerea* and *S. mellifera* and their potential for constructing chronologies. It also investigates whether the anatomical features responsible for growth rings differ significantly between the two species.

2. Study sites

The study was conducted at three sites, namely Lake Otjikoto (19° 11′ 41″ S; 17° 32′ 59″ E), situated 20 km northwest of Tsumeb; Onyoka Farm on the Waterberg National Park in central Namibia (20° 25′ 0″ S; 17° 13′ 0″ E), and Kuzikus Farm (23° 20′ 0″ S; 18° 21′ 59″ E) in the south-east of the country. These three sites cover a significant rainfall gradient as shown in Fig. 1. Lake Otjikoto has an annual rainfall range of 550 mm–600 mm and an average annual temperature of 25 °C (Mendelsohn et al., 2002). Waterberg is a moderately wet area, with an annual rainfall range of 450 mm–500 mm and an average annual temperature of 30 °C. Kuzikus is drier, receiving less than 300 mm of precipitation per year on average, and has a mean annual temperature of 31 °C (Mendelsohn et al., 2002). The Lake Otjikoto site consists of loamy to clayey vertisol soils, which have good water-holding capacities. Waterberg and Kuzikus have deep sandy dystrophic Kalahari soils, which are poor in nutrients (Mendelsohn et al., 2002; Rodgers et al., 2017; Ndunge, 2018).

3. Material and methods

Wood samples of *D. cinerea* and *S. mellifera* were collected from twenty-four randomly selected trees of each species at each of the three sites. All forty-eight specimen discs from each site (for a total of 144 discs) were allowed to air dry. However, out of the 144 discs, only those with visible rings (32 for *D. cinerea* and 37 for *S. mellifera*) were selected for analysis. The selection was such that for each site, at least one disc

each of *D. cinerea* and *S. mellifera* was used for comparative and cross-dating purposes.

For each tree, one sample disc was taken at a height of about 1.0 m, air dried, polished, and scanned at 2400 dpi resolution. According to Gourlay (1995), there is an increased risk of measuring missing or false rings that occurred during periods of drought stress when doing dendrochronological research drought-prone regions. To identify any missing rings and to remove false rings, we used a four-step cross-dating system. First, the rings were identified under binocular microscope. The scanned images were then uploaded and examined using WinDENDRO software, which automatically counts and dates each marginal parenchyma (Fig. 2). To make sure that all the rings were correctly detected and dated by WinDENDRO software, at least four different paths radiating from the pith were created and analyzed (Grudd, 2006; Heinrich et al., 2009). The rings were then checked again under the binocular microscope for correction and validation. Finally, cross-dated rings were verified with the COFECHA programme (Holmes, 1983), which is commonly used in dendrochronology to check the cross-dating and to ensure the quality and measurement accuracy in all the growth ring segments (Grissino-Mayer, 2001). COFECHA creates a master chronology of all the discs for one species and calculates the correlation coefficient to indicate how well the inter-annual variability in the ring width correlates with the other ring-widths of the same species (Holmes, 1983; Steenkamp et al., 2008). These steps of microscope to WinDENDRO to microscope to COFECHA and back, were repeated until the COFECHA results showed that rings were identified correctly.

For the purpose of examining the growth ring patterns, Ring Width Index (RWI) and Basal Area Increment (BAI) chronologies were created using the dplR package (Bunn, 2008) of R 3.4.4 (R Core Team, 2018). We used a spline with a 50 % frequency response to remove age- and size-related growth trends (Cook and Kairiukstis, 1990). Because growth rings naturally become narrower as the trees get older, the chronology was detrended to create an object containing standardized ring-width index values (Meko et al., 1995). Detrending involves the estimation and removal of the low-frequency variability that is due to biological trends from growth time-series caused by e.g., age and/or geometry (Fritts, 1976; Cook and Kairiukstis, 1990; R Core Team, 2018). Individual tree-ring width series were detrended in two steps, first by using a negative exponential curve for the BAI and then by fitting a cubic smoothing spline with a 50 % frequency response (Cook et al., 1990; Meko et al., 1995). To account for the geometric constraints of RWI, the ring-width measures were transformed to BAI (Biondi and Qeadan, 2008; Buras and Wilmking, 2014; Le Moullec et al., 2019). A detrended BAI mean growth curve was then constructed for each cross-section (Le Moullec et al., 2019).

A mean value chronology was developed to study the source of growth variation and was calculated from all individual residual series for successive 10-year periods lagged by intervals of one year (Bunn, 2008, 2010). Tree-ring indices were then combined to develop a residual chronology using a Tukey's bi-weight robust mean, which reduces the effect of outliers. Interseries correlations between the individual tree-ring series of each species and the master chronology for that species were calculated. The mean sensitivity (MS) was also calculated in order to study the year-to-year variability of growth rings. The Expressed Population Signal (EPS) and Signal-to-Noise Ratio (SNR) were analysed for climate signals and for the strength of the common signals in the tree-ring dataset, after the method of Wigley et al. (1984) and Hollesen et al. (2015).

Series were analysed to show the variability differences of growth ring between the species across the rainfall gradient from Lake Otjikoto to Kuzikus. Then the species were evaluated using the BAI master chronology due to the absence of biological effects and geometric constraints. The hypothesis is that all species at all sites can act as proxies for climate change under varying ecological boundaries. Climate information was obtained from Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) (Funk et al., 2015).
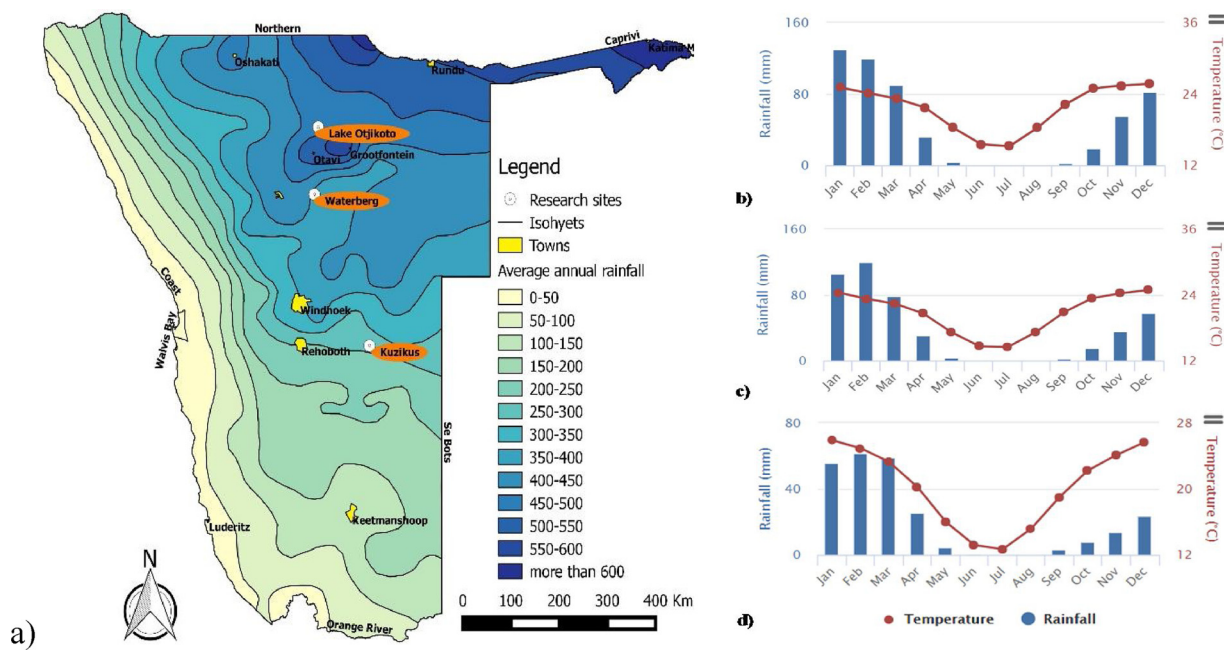
Fig. 1. Climatic conditions at the three sites: (a) Rainfall gradient, (b) Lake Otjikoto site, (c) Waterberg site, and (d) Kuzikus Farm site. Average monthly temperature and rainfall, 1901–2015 (Climate-Data.Org, 2018).
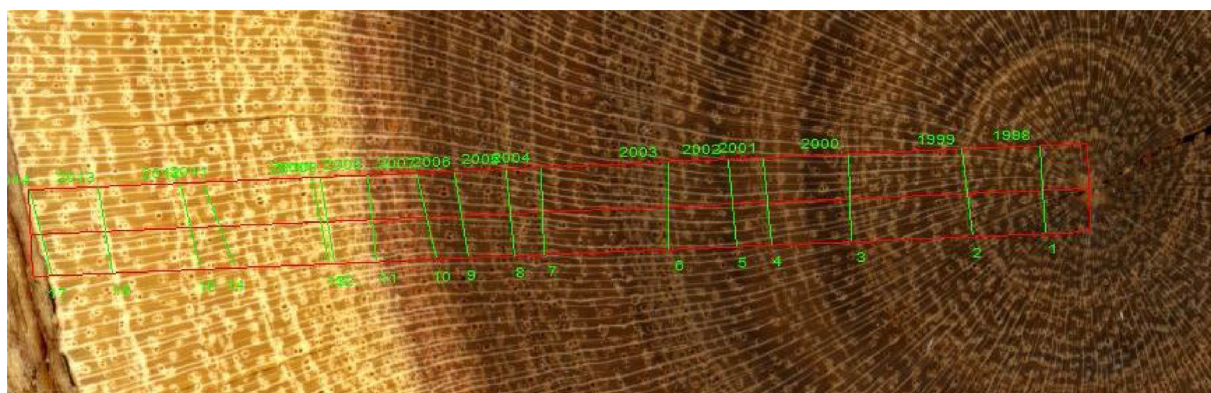

Fig. 2. An automatic marking of a sample by WinDENDRO, before correction.

Interseries mean sensitive correlations with the combined species master chronology was used to identify 6 tree cores from the three sites that closely related to the chronology. The threshold for further selection was statistical significance for both the RWI and the BAI, based on the master chronology for RWI and a BAI correlation coefficient of r > |0.3|, following Cohen (1988) recommendations.

4. Results

4.1. Wood anatomy and growth ring formation

The wood structures of *D. cinerea* and *S. mellifera* were both found to have proper ring development comprised of: a) a wide zone of large, low-density vessels that marked the wet seasons and b) a narrower zone of small, high-density vessels that marked the dry seasons (Fig. 3a & b). The two groups of layers make up one ring and together represent one wet-dry cycle (usually a year) of growth (Fig. 3). The width of the ring mainly depends on the spread of the large vessels. The layer of small vessels ends or begins with a marginal parenchyma band. Although the marginal parenchyma band was clear in both species (Fig. 3c & d), the groups of large and small vessels were not always as visible in *S. mellifera* as in *D. cinerea* (Fig. 3a & b). Furthermore, the ring widths of *D.*

cinerea were generally wider in comparison to those of *S. mellifera* for the same years and same sites, suggesting more ring growth in *D. cinerea*.

A quick report from RWI provides a visual representation of the specimen dataset in terms of segments arranged over time (Fig. 4). The results for *D. cinerea* show 32 dated series and 718 ring measurements, with an average series length of 22 years and a range of 38 years spanning from 1977 to 2015. For *S. mellifera*, the results show 37 dated series and 1086 ring measurements, with an average series length of 29 years and a range of 59 years spanning from 1956 to 2015.

4.2. Growth ring measurement, cross-dating and chronology development

Fig. 5 presents the standardized ring widths and shows the effect of age on raw ring-widths by plotting mean growth curves of all cross-sections aligned by cambial age. The cambial age curve for both species shows a typical juvenile effect, in which the tree produces wider growth-rings during its early years and narrower rings as it ages. *D. cinerea* exhibits some wide ring widths even at a mature age in 1999 and 2011 (Fig. 5a), suggesting exceptional environmental conditions in those years.

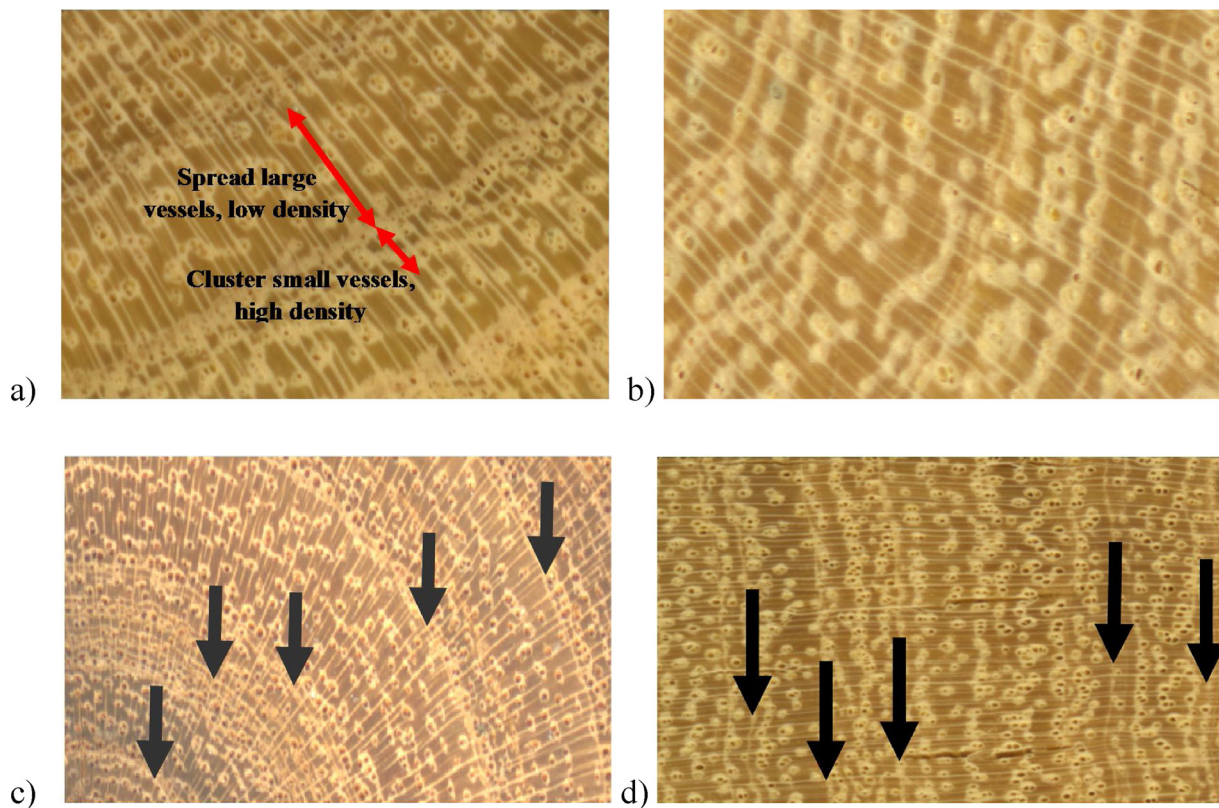Fig. 6 presents the smoothed BAI mean growth curves for each

Fig. 3. Cross-sections of tree rings showing the alternating layers of the spread of large, low density vessels and cluster of small, high density vessels of (a) *D. cinerea* and (b) *S. mellifera*. Black arrows in (c) and (d) indicate parenchyma bands in *D. cinerea* in *S. mellifera* growth rings, respectively.

species, which show a slight but constant increase with age. A dip in the curve for *D. cinerea* occurs around 1995, whereas the *S. mellifera* curve shows smooth and consistent growth throughout the period. This dip may be related the drought during the 1994–1995 rainy season at Kuzikus and Lake Otjikoto (Fig. 7a). The level of sample depth on the master chronology has highly improved from RWI in Fig. 5a & b, to BAI in Fig. 6a & b. For *S. mellifera* the value is more than twice in BAI than in RWI.

The descriptive statistics for the RWI and BAI chronologies for each species are shown in Table 1. The Standard Deviation (SD) for both species is lower in the BAI than the RWI chronology, with 0.68 and 0.98 for *D. cinerea* and 0.63 and 0.97 for *S. mellifera*. The SD was lower for *S. mellifera* than for *D. cinerea* in both cases. The Mean Sensitivity (MS) increased from 0.45 in RWI to 0.53 BAI for *D. cinerea* and from 0.36 to 0.42 for *S. mellifera*. For BAI, both species had Expressed Population Signal (EPS) values above the threshold (0.85), as well as high Signal-to-Noise Ratios (SNR). *D. cinerea* has higher values than *S. mellifera* for EPS and SNR in both RWI and BAI.

4.3. Growth rings variation along the rainfall gradient

To test the validity of the forcing factors responsible for the growth of the two species, the ring widths of six randomly selected samples, one from each site for each species, are plotted against annual rainfall. The results are shown in Figs. 7a and 7b. In Fig. 7.1a, the growth of *D. Cinerea* at Kuzikus (annual rainfall of $250-300$ mm/a) shows a positive correlation with rainfall. At Waterberg (Fig. 7a) and Lake Otjikoto (Fig. 7a), the correlation is also positive. In years when annual rainfall was received over a short period of time, resulting in runoff, the correlation is not good, for example, 2006 and 2016 at Kuzikus, 1987 at Waterberg and 2011 at Lake Otjikoto (Figs. 7a and 7b). For *S. mellifera*, the correlation at Kuzikus and Waterberg is very poor, but a weak correlation exists at Lake Otjikoto, which experiences much more

rainfall. These results show that precipitation is not the only factor controlling ring-width growth in *S. mellifera*.

A comparison of tree-ring width variations along the rainfall gradient was carried out. Fig. 8a, 8b, which includes all the specimens studied, indicates that ring growth for both species decreases along the rainfall gradient. Both show wider ring widths variation at Lake Otjikoto and narrow at Kuzikus. For *D. cinerea*, the results show strong variability of growth rings (53 %, r-squared = 0.53) at Lake Otjikoto, 30 % at Waterberg National Park, and 20 % at Kuzikus Farm (Fig. 8a). The variability of growth rings for *S. mellifera* are lower: 37 % (r-squared = 0.37) at Lake Otjikoto, 23 % at Waterberg National Park, and 17 % at Kuzikus Farm. Overall, *D. cinerea* shows higher variance than *S. mellifera* at all sites. R values (Fig. 8b) indicate a much higher variation and difference between the species at the wettest site (Lake Otjikoto) than at the driest site (Kuzikus).

Series that correlate significantly with the master chronology were analysed further. The threshold for further selection was statistically significant (p < 0.05) and a correlation coefficient of r > |0.3| to the master chronology of both the RWI and the BAI was established. Table 2 shows the six most significant samples for BAI, which are also the most significant samples for RWI. For *S. mellifera*, the *p* values for RWI appear to be more or less the same for all specimens; for BAI, the *p* values increase as the rainfall gradient decreases. For *D. cinerea*, the *p* values for BAI are also negatively related to the rainfall gradient, with the exception of one sample (ST2DC440). The *p* values for RWI are very high at Kuzikus for example in sample ST3DC01.

5. Discussion

The study presents results that focus on the wood anatomy and growth ring formation of two encroacher species in Namibia, as well as their dendrochronological potential. In both species, distinct marginal parenchyma bands are present around the rings (Fig. 3c & d). Marginal
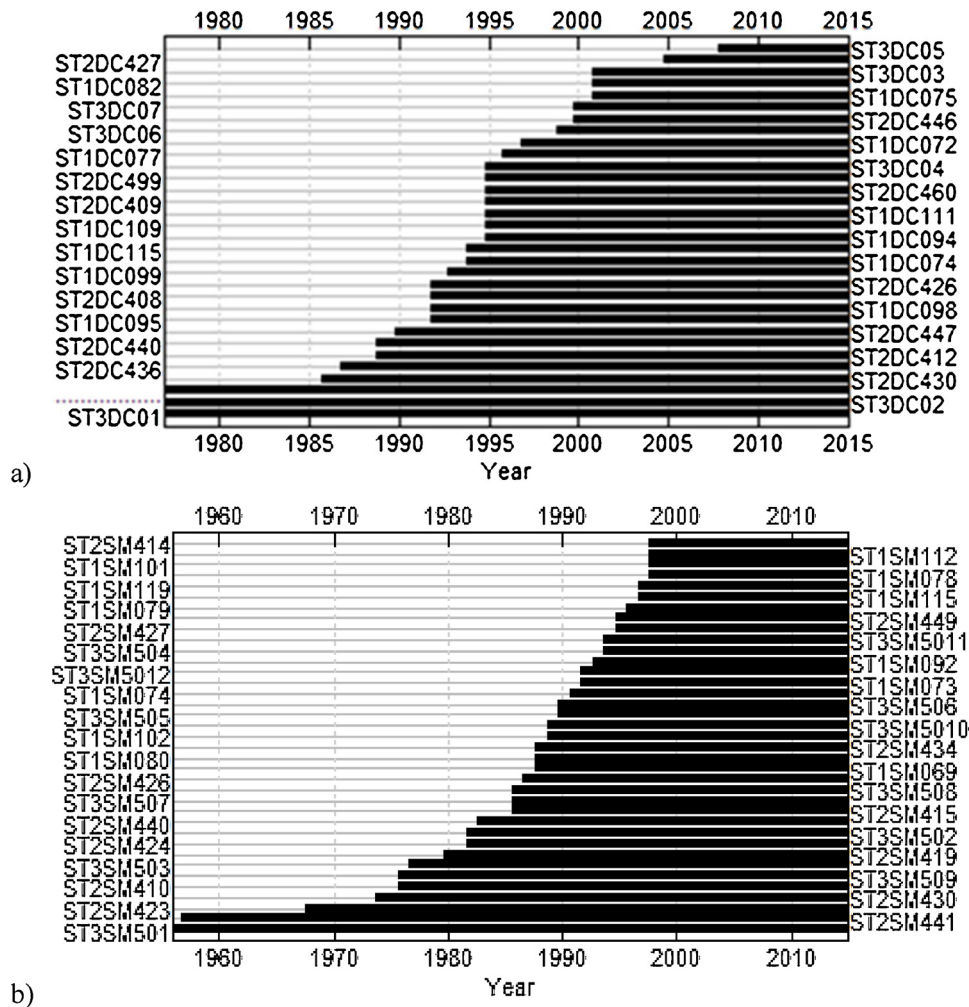
Fig. 4. Segmentation plot: a) *D. cinerea* and b) *S. mellifera* specimens. Each colour segment represents one specimen in the dataset.

parenchyma bands develop in relation to wet and dry periods, creating growth boundaries that are formed within each growth year. The number of marginal parenchyma bands corresponds to the number of peaks in annual rainfall, whereas the ring width generally corresponds to the total amount of rainfall received (Gourlay and Grime, 1994; Shorrocks, 2007; Zacharias, 2018). Our findings of tree-ring formation are similar to those of Fichtler et al. (2004).

In the chronologies, both species show a typical juvenile effect, in which they display wider growth rings at younger ages than at mature ages (Figs. 5 & 6). However, *D. cinerea* also displays wider ring widths at a mature age when above average rainfall occurs (Fig. 5a). Though age range of trees in this study was not very wide, the juvenile effect is still apparent. According to Feliksik and Wilczyński (2009), wider rings indicate good annual rainfall amounts, while narrower rings indicate poor rainfalls. Growth ring development in *S. mellifera* suggests that the trees generally add a constant ring width even during mature age, in spite of differences in annual rainfall. This suggests further that *S. mellifera* might have a unique adaptive mechanism that enables it to
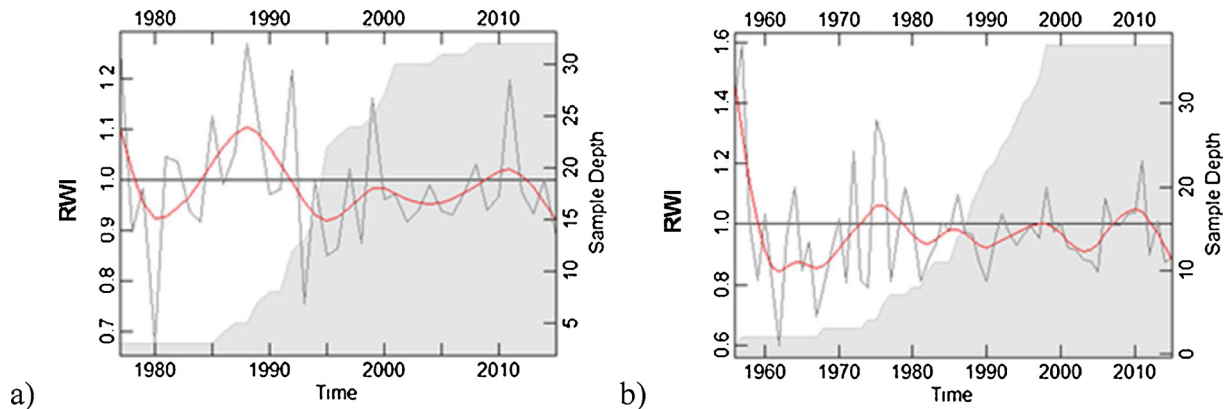

Fig. 5. Master chronologies a) *D. cinerea* and b) *S. mellifera,* showing the age effect in raw ring-widths. The graphs were produced by plotting mean growth curves aligned by cambial age.
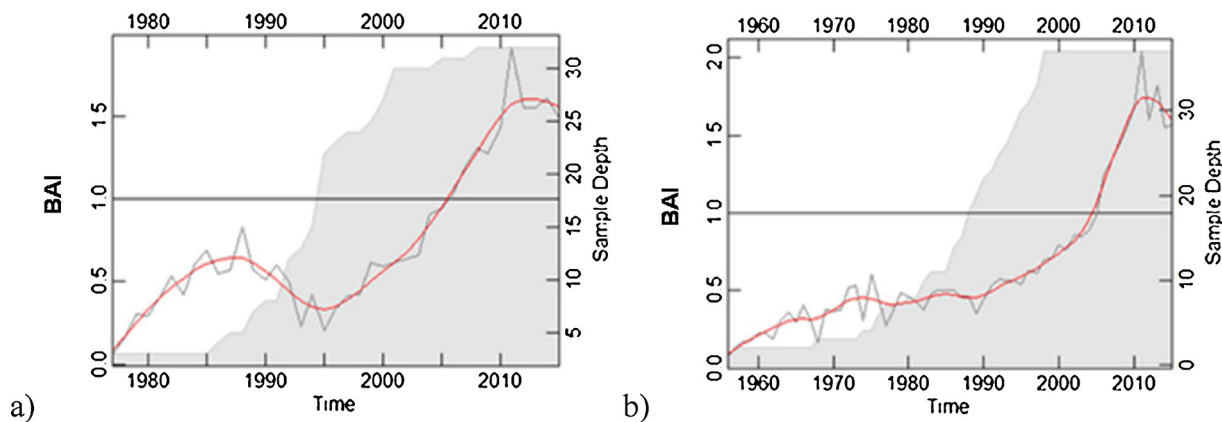
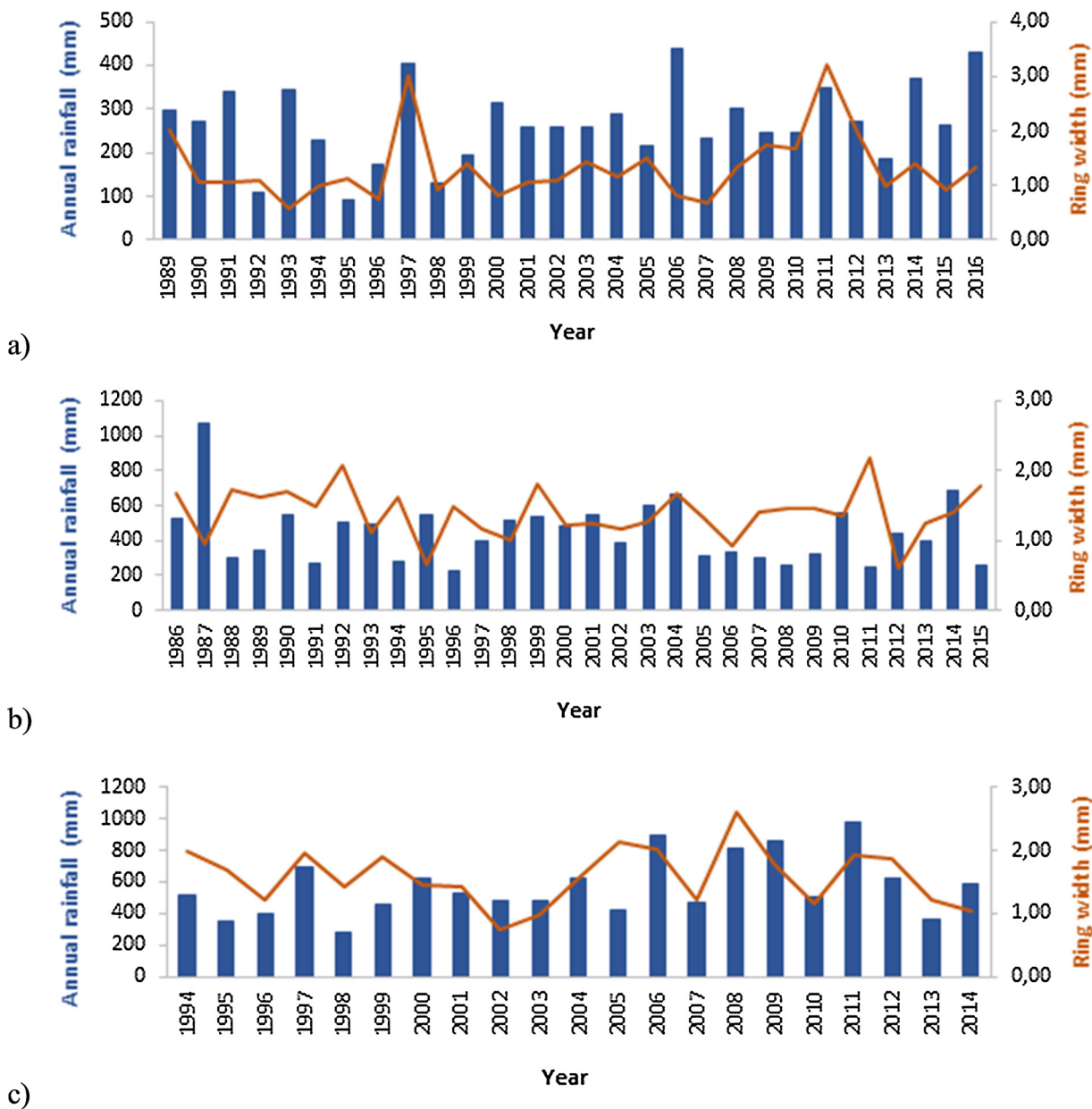**Fig. 6.** Smoothed master chronologies of the BAI mean growth curve: a) *D. cinerea* and b) *S. mellifera*.

Fig. 7a. *Dichrostachys cinerea* ring widths at: **a**) Kuzikus (250 mm), **b**) Waterberg (450 mm) and **c**) Lake Otjikoto (600 mm).
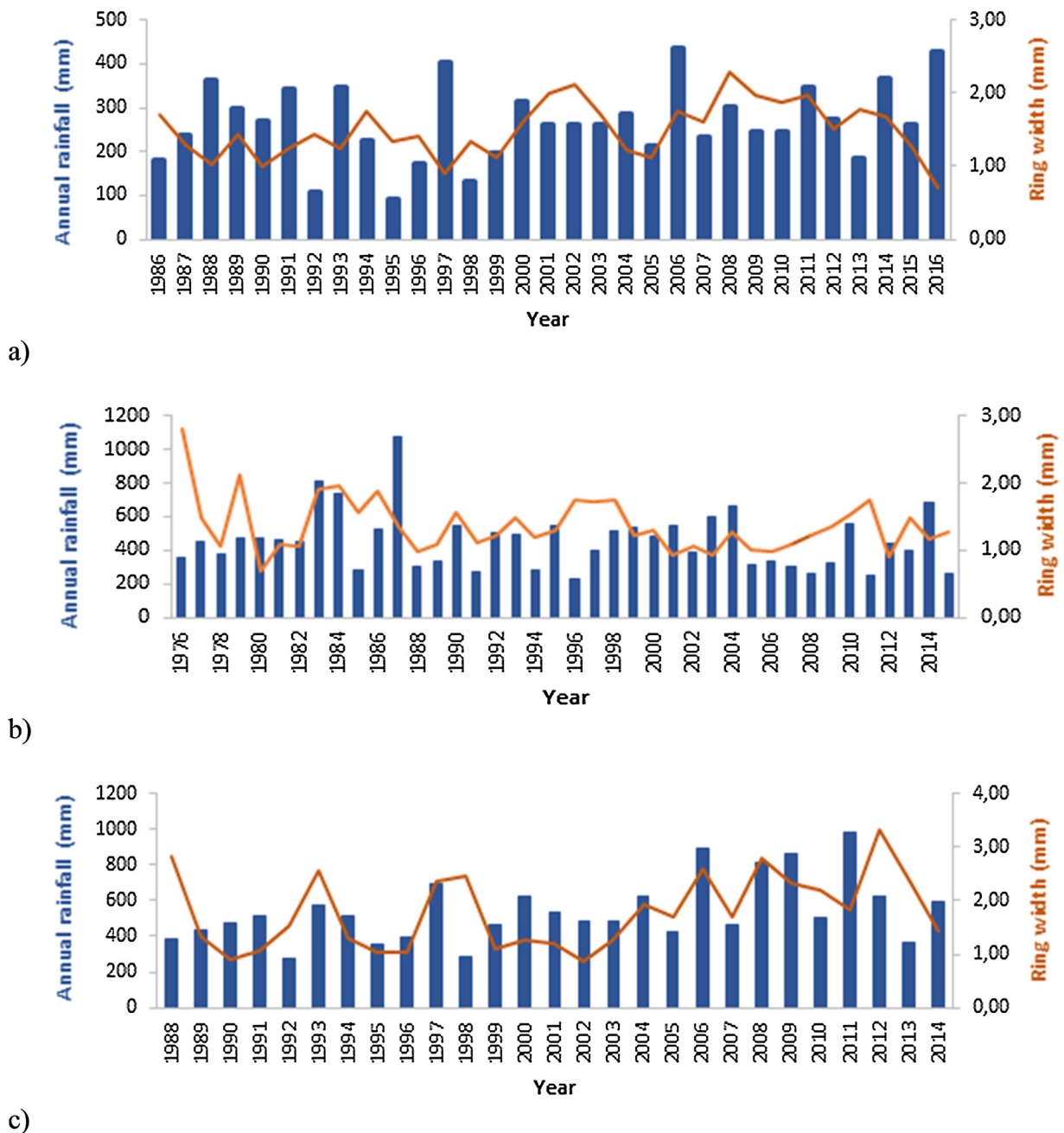
a)

b)

c)

Fig. 7b. *Senegalia mellifera* ring widths at: **a**) Kuzikus (250 mm), **b**) Waterberg (450 mm) and **c**) Lake Otjikoto (600 mm).

Table 1
Mean statistics of RWI and BAI chronologies.

Statistics	RWI		BAI	
	D. cinerea	*S. mellifera*	*D. cinerea*	*S. mellifera*
Standard Deviation (SD)	0.9814	0.9737	0.678	0.625
Mean Sensitivity (MS)	0.452	0.364	0.529	0.416
Number of cores calculated (n cores)	32	37	32	37
Mean between different cores (rbar total)	0.28	0.025	0.83	0.633
Effective signal calculated (rbar. eff)	0.28	0.025	0.83	0.633
Expressed Population Signal (EPS)	0.876	0.353	0.989	0.974
Signal-to-Noise Ratio (SNR)	7.054	0.545	88.465	36.753

alter its hydraulic pathway and/or processes during dry periods for better survival. This could explain why *S. mellifera* is highly adaptable across a wide rainfall gradient. Within the growth ring, the high-density vessels on the margins and low-density vessels at the centre of the growth ring zones in both *D. cinerea* and *S. mellifera* (Fig. 3) point to a varying water supply throughout the growth period (Novak et al., 2013). The density of the vessels is directly proportional to the size of the vessels. In the high-density zones, the vessels are smaller; in the low-density zones, they are larger. The variations in vessel density were found to be similar to those of *Rhizophora mangle* in Guaratiba, Rio De Janeiro, Brazil (Souza et al., 2016), and to those cited by Souza et al. (2016) of *R. mangle* in northern Brazil (Menezes et al., 2003). Studies of *R. mucronata* in Kenya (Verheyden et al., 2004) and *R. apiculata* in China (Yu et al., 2004) have results similar to those of our study. Groups of small, high-density vessels in tree rings are related to periods of water stress (Verheyden et al., 2004; Nath et al., 2016; Souza et al.,
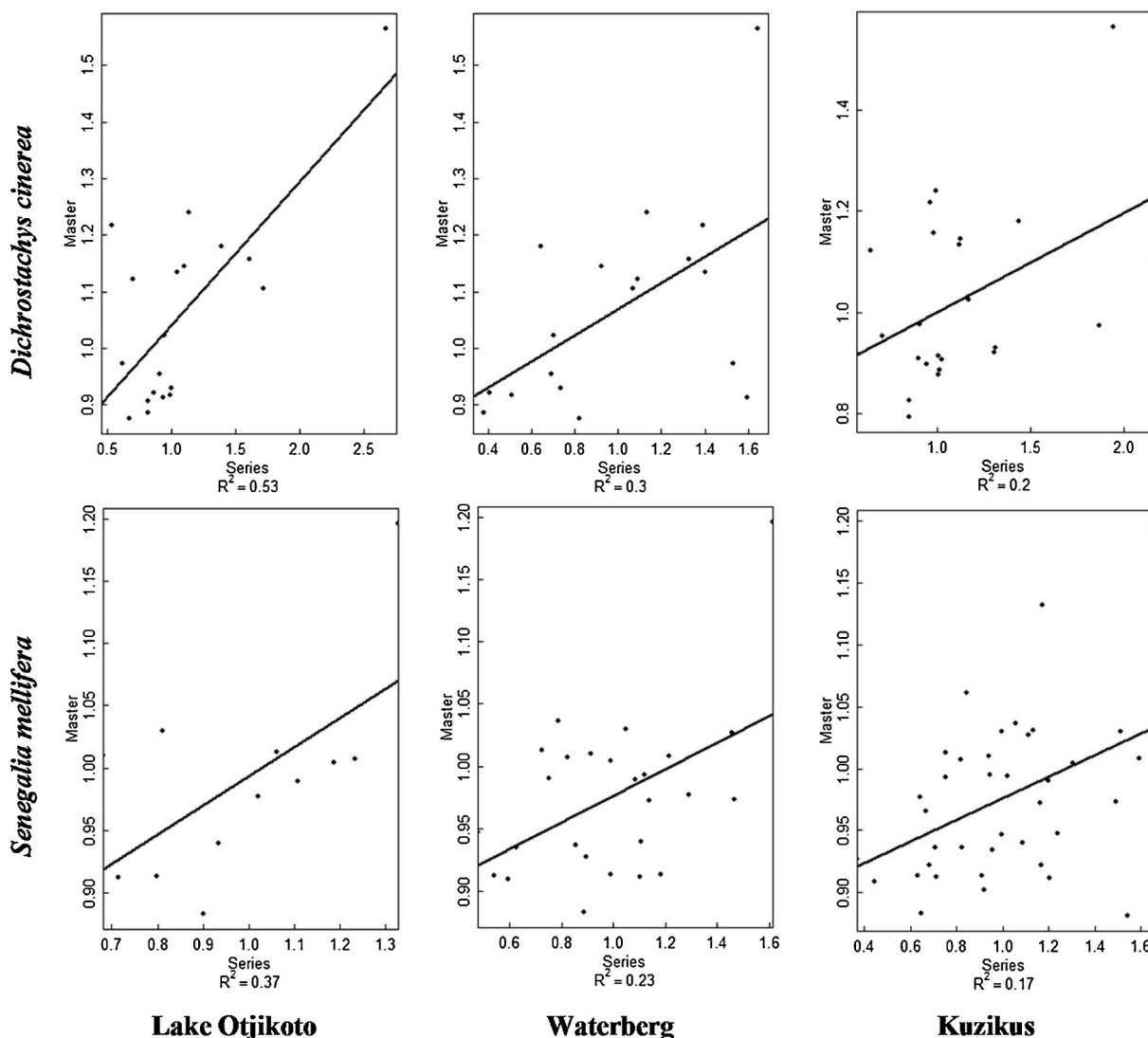
Fig. 8a. Variability of growth rings of *D. cinerea* and *S. mellifera* at the three sites.
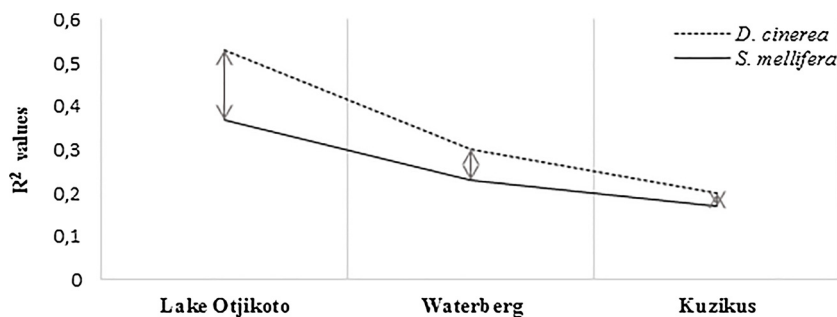

Fig. 8b. R-values differences between *D. cinerea* and *S. mellifera* at the three sites.

2016; Islam et al., 2019). Variation in the density of vessels was much better observed in the growth rings of *D. cinerea* than in those of *S. mellifera*. This suggests that periods of water stress are more clearly recorded in the growth rings of *D. cinerea* than in those of *S. mellifera*. The growth curve of *S. mellifera* in Fig. 6 is constant, whereas that of *D. cinerea* has a marked dip, suggesting that the latter was unable to access sufficient moisture to add woody matter during a particularly dry period.

D. cinerea was found to add more biomass when the amount of rainfall is high (wider rings) and to add very little biomass when

precipitation is very low. This is not the case for *S. mellifera,* which adds less biomass than *D. cinerea* but appears to do so more consistently, regardless of precipitation (Figs. 8a & 8b). Unlike *D. cinerea, S. mellifera* long tap root that penetrates deeply into the ground and is thought to be key to its adaptability in arid ecosystems. The tap root can extend to depths of more than 30 m and is supported by an extensive lateral root system (de Klerk, 2004; Namibia Agricultural Union (NAU, 2010). The lateral root system is adapted to absorb soil moisture and is useful for competing for rainfall, whereas the deep tap root can reach groundwater, especially during dry periods (Sarris et al., 2007). Due to the lack

Table 2

The six most statistically significant tree discs, two from each site and one of each species. In the sample code, **DC** stands for *Dichrostachys cinerea* and **SM** stands for *Senegalia mellifera*. *p value for correlation coefficient more than 0.3 but statistically significant for the 95 % confidence interval.

Sample code	R. Coeff (BAI)	p Value	Residual Correlation (RWI)	p Value	Site
ST1SM079	0.702	0.0004	0.789	0.00	Lake Otjikoto
ST1DC082	0.826	0.0001	0.580	0.02	Lake Otjikoto
ST2SM414	0.517	0.0139	0.550	0.02	Waterberg
ST2DC440	0.329	0.0539*	0.401	0.02	Waterberg
ST3SM505	0.415	0.0218	0.393	0.02	Kuzikus Farm
ST3DC01	0.389	0.0087	0.210	0.10*	Kuzikus Farm

of a very deep tap root, *D. cinerea* may depend entirely on rainfall (soil moisture) and therefore adds as much biomass as much as possible when moisture is available. The population of *D. cinerea* decreases significantly from the Lake Otjikoto site, where the trees are abundant, to the Kuzikus site, where the trees are scarce. In contrast, the population of *S. mellifera* is mostly constant along the rainfall gradient from Lake Otjikoto to Kuzikus Farm (Bester, 1999; Birch et al., 2017). It does, however, decrease in height along the gradient from more precipitation to less precipitation. The comparison of the two species underlines the significance of soil moisture supply for tree growth. The clayey vertisol soils at Lake Otjikoto are conducive to holding water for a longer period than the sandier soils at Kuzikus Farm. The combination of good soil and higher rainfall amounts makes the trees more dependent on rainfall, especially during dry periods. The water-holding capacity of the soil at Kuzikus Farm is naturally poor so little moisture is retained and fewer nutrients are available to the trees, resulting in narrower growth rings.

In this study, tree-ring chronologies were developed using conventional techniques to yield comparable statistical results (Fritts, 1976; Cook and Kairiukstis, 1990; Wang et al., 2005). While the SDs of both species declined, the Mean Sensitivity (MS), Expressed Population Signal (EPS) and Signal-to-Noise Ratio (SNR) improved from RWI to BAI (Table 1). The MS quantifies the annual variation in growth between two adjacent rings (Fritts, 1976; Liang et al., 2001), and increases from 0.45 to 0.53 for *D. cinerea* and 0.36 to 0.42 for *S. mellifera* indicating that there is a higher response from the former than the latter. Furthermore, for BAI, both species had EPS values above the 0.85, which is considered to be a critical threshold for climatic signals (Wigley et al., 1984; Liang et al., 2001; Zhang et al., 2013; David et al., 2018). They also both had a high SNR, which is an indicator of the strength of the common environmental signal in the tree-ring dataset (Wigley et al., 1984). These statistics indicate that the chronologies (especially the BAI) are reliable and can be used to study the correlation between tree growth and environmental signals (Wigley et al., 1984; Wang et al., 2005; David et al., 2018). The statistics also indicate that the BAI chronologies have better common environmental signals and are therefore more reliable for comparing growth ring measurements. Furthermore, the statistics show that *D. cinerea* has higher MS, EPS, and SNR than *S. mellifera*, suggesting that *D. cinerea* correlates better with environmental cues than *S. mellifera*.

6. Conclusion

This study is the first to construct a master chronology for two most aggressive encroacher species in Namibia. The study focuses on identifying how the anatomical features of *Dichrostachys cinerea* and *Senegalia mellifera* develop in arid to semi-arid environments. The study confirms that the two species form well-defined annual growth rings in response to the changes from the wet seasons to the dry seasons. The variability in ring width and the alternation between vessel layers of

high- and low-density reflect the wet and dry seasons experienced in southern Africa. These changes are more clearly recorded in specimens of *D. cinerea* than of *S. mellifera*. The master ring-width chronologies better reflect results using the BAI methodology as compared to the RWI methodology. The growth patterns of both species are suitable for dendrochronological purposes, and both species produce clear and reliable ring chronologies. However, *D. cinerea* appears to respond more sensitively to environmental cues and may therefore provide more immediate climatological information. In contrast, *S. mellifera* appears to have a more complex growth habitat, necessitating greater scrutiny to understand its multifaceted growth ring patterns. The chronologies developed in this study form the basis for further dendrochronological study of these two species in Namibia.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

References

Anchukaitis, K.J., 2017. Tree rings reveal climate change past, present, and future. Proc. Am. Philos. Soc. 161 (3), 244–263.

Barnard, P., 2012. Water and Climate Change, IBA Newsletter 2. Spring p. 3.

Bester, F.V., 1999. Major problem, bush species and densities in Namibia. Agricola 10, 1–3.

Bhugeloo, A., 2014. Assessing the Dendrochronological and Dendroclimatological Potential of Acacia nilotica (L.) in Northern KwaZulu – Natal. Pietermaritzburg, S.A.. .

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization defining the biological trend expected basal area increment. Tree- Ring Res. 64 (2), 81–96.

Birch, C., Harper-Simmonds, L., Lindeque, P., Middleton, A., 2017. Benefits of Bush Control in Namibia. A National Economic Study for Namibia and a Case Study for the Otjozonjupa Region. Report for the Economics of Land Degradation Initiative. Available from. . www.eld-initiative.org.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28 (4), 251–258.

Buras, A., Wilmking, M., 2014. Straight lines or eccentric eggs? A comparison of radial and spatial ring width measurements and its implications for climate transfer functions. Dendrochronologia 32 (4), 313–326.

Carrer, M., Urbinati, C., 2010. Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. America 85 (3), 730–740.

Chhetri, P., Shrestha, K., 2009. Dendrochronology and climate change study in Nepal: a preview. Banko Janakari 19 (2), 42–43.

Climate-Data.Org (2018). https://en.climate-data.org/africa/namibia-89/.

Cohen, J., 1988. Statistical Power Analysis for the Behavioural Sciences Hillsdale. Lawrence Earlbaum Associates, NJ, pp. 2.

Cook, E., Kairiukstis, L., 1990. Methods of Dendrochronology - Applications in the Environmental Sciences. Springer Science & Business Media.

Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. Tree-ring standardization and growth-trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology, Application in Environmental Sciences. Kluwer Academic Publisher, pp. 104–123.

Curtis, B.A., Mannheimer, C.A., 2005. Tree Atlas of Namibia. National Botanical Research Institute, Ministry of Agriculture, Water and Forestry. Windhoek.

David, A.A.J., Boura, A., Lata, J., Kraepiel, Y., Charlot, C., Barot, S., et al., 2018. Street trees in Paris are sensitive to spring and autumn precipitation and recent climate changes. Urban Ecosyst. 21 (1), 133–145.

De Klerk, J.N., 2004. Bush Encroachment in Namibia: Report on Phase 1 of the Bush Encroachment Research, Monitoring, and Management Project. Ministry of

Environment and Tourism, Directorate of Environmental Affairs. Windhoek.

FAO, 2005. Namibia: Irrigation in African in Figures, Aquastat Survey. Retrieved from. http://www.fao.org/nr/water/aquastat/countries_regions/NAM/NAM-CP_eng.pdf.

Feliksik, E., Wilczyński, S., 2009. The effect of climate on tree-ring chronologies of native and nonnative tree species growing under homogenous site conditions. Geochronometria 33, 49–57.

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

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, New York.

Fritts, H.C., 2012. Tree Rings and Climate. Academic Press, New York.

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., et al., 2015. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. Sci. Data 2, 150066 doi:10.1038/sdata.2015.66 2015. http://chg.geog.ucsb.edu/data/chirps/.

Gaspard, D.T., Venegas-González, A., Beeckman, H., Randriamalala, J.R., Tomazello-Filho, M., De Ridder, M., Ramananantoandro, T., 2018. Tree ring responses to climate variability of xerophytic thickets from South Soalara, Madagascar. Dendrochronologia 49 (March), 57–67.

Gourlay, I.D., 1995. Growth ring characteristics of some african Acacia species. J. Trop. Ecol. 11 (1), 121–140. Retrieved from. http://www.jstor.org/stable/2560149.

Gourlay, I.D., Grime, G.W., 1994. Calcium oxalate crystals in African Acacia species and their analysis by scanning proton microprobe (SPM). IAWA J. 15, 137–148.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree. Res. 57, 205e221.

Grudd, H., 2006. Tree Rings As Sensitive Proxies of Past Climate Change. Doctoral dissertation. Institutionen för naturgeografi och kvartärgeologi. https://www.diva-portal.org/smash/get/diva2:189273/FULLTEXT01.pdf.

Hauwanga, W.N., McBenedict, B., Strohbach, B.J., 2018. Trends of phanerophyte encroacher species along an aridity gradient on Kalahari sands, central Namibia. Eur. J. Ecol. 4 (2), 41–47.

Heinrich, I., Weidner, K., Helle, G., Vos, H., Lindesay, J., Banks, J.C.G., 2009. Interdecadal modulation of the relationship between ENSO, IPO and precipitation: insights from tree rings in Australia. Clim. Dyn. 33 (1), 63–73.

Hollesen, J., Buchwal, A., Rachlewicz, G., Hansen, B.U., Hansen, M.O., Stecher, O., Elberling, B., 2015. Winter warming as an important co-driver for Betula nana growth in western Greenland during the past century. Glob. Change Biol. 21, 2410–2423.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull. 43, 69–78.

IPCC, 2001. Climate change 2001: impacts, adaptation, and vulnerability. In: McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.), Contribution of Working Group II to the Intergovernmental Panel on Climate Change Third Assessment Report. Cambridge University Press, Cambridge, UK.

Islam, M., Rahman, M., Bräuning, A., 2019. Impact of extreme drought on tree-ring width and vessel anatomical features of Chukrasia tabularis. Dendrochronologia 53, 63–72.

Joubert, D.F., Rothauge, A., Smit, G.N., 2008. A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular reference to bush thickening by Acacia mellifera. J. Arid Environ. 72 (12), 2201–2210.

Le Moullec, M., Buchwal, A., van der Wal, R., Sandal, L., Hansen, B.B., 2019. Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass. J. Ecol. 107 (1), 436–451.

Liang, E., Shao, X., Lin, J., 2001. Dendroclimatic evaluation of climate-growth relationships of Meyer spruce (Picea meyeri) on a sandy substrate in semi-arid grassland, north China. Trees 15, 230–235.

Marais, E., Scott, L., Gil-Romera, G., Carrión, J.S., 2015. The potential of palynology in fossil bat-dung from Arnhem Cave, Namibia. Trans. R. Soc. South Africa 70 (2), 109–115.

Meko, D.M., Stockton, C.W., Boggess, W.R., 1995. The tree-ring record of severe sustained drought: American Water Resources Association. Water Resour. Bull. 31, 789–801.

Mendelsohn, J., Jarvis, A., Roberts, C., Robertson, T., 2002. Atlas of Namibia: A Portrait of Land and Its People Vol. 53 David Philip Publisherhttps://doi.org/10.1017/CBO9781107415324.004.

Menezes, M., Berger, U., Worbes, M., 2003. Annual growth rings and long-term growth patterns of mangrove trees from the Bragança Peninsula, North Brazil. Wetl. Ecol. Manage. 11, 233–242.

Nath, C.D., Munoz, F., Pélissier, R., Burslem, D.F.R.P., Muthusankar, G., 2016. Growth rings in tropical trees: role of functional traits, environment, and phylogeny. Trees – Struct. Funct. 30 (6), 2153–2175.

Namibia Agricultural Union (NAU), 2010. The Effect of Bush Encroachment on Groundwater Resources in Namibia: A Desktop Study. Unpublished. Windhoek, Namibia. Namibia Agricultural Union. http://www.agrinamibia.com.na/wp-content/uploads/2018/02/.

Ndunge, C.I.H., 2018. Assessment of Woody Plant and Grass Competitive Interactions Using Reciprocal Transplants Along a Rainfall Gradient in Namibian Savannas (Doctoral Thesis). University of Namibia, Windhoek, Namibia.

Novak, K., Čufar, K., De Luis, M., Sánchez, M.A.S., Raventós, J., 2013. Age, climate and intra-annual density fluctuations in Pinus halepensis in Spain. IAWA J. 34 (4), 459–474. https://doi.org/10.1163/22941932-00000037.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. Vienna, Austria, 0. Retrieved from. https://www.r-project.org/.

Rahman, M., Islam, M., Bräuning, A., 2018. Tree radial growth is projected to decline in South Asian moist forest trees under climate change. Glob. Planet. Change 170 (April), 106–119.

Rodgers, M., Bilton, M., Hauptfleisch, M., 2017. Responses and feedbacks of burrowing mammals under differently managed rangelands. Namibian J. Environ. 1 (A), 40–51.

Sarris, D., Christodoulakis, D., Körner, C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. Glob. Chang. Biol. 13 (6), 1187–1200. https://doi.org/10.1111/j.1365-2486.2007.01348.x.

Shanyengana, E.S., Seely, M.K., Sanderson, R.D., 2004. Major-ion chemistry and groundwater salinization in ephemeral floodplains in some arid regions of Namibia. J. Arid Environ. 57, 71–83.

Sheppard, P.R., 2010. Dendroclimatology: extracting climate from trees. Wiley Interdiscip. Rev.: Clim. Change 1 (3), 343–352. https://doi.org/10.1002/wcc.42.

Shorrocks, B., 2007. The Biology of African Savannahs. The Biology of Habi- Tats Series. Oxford University Press, Oxford, New York.

Shorrocks, B., Bates, W., 2015. The Biology of African Savannahs. Oxford University Press, USA.

Singer, M.C., Parmesan, C., 2010. Phenological asynchrony between herbivorous insects and their hosts: Signal of climate change or pre-existing adaptive strategy? Philos. Trans. R. Soc. B: Biol. Sci. 365 (1555), 3161–3176.

Souza, B.T., Estrada, G.C.D., Soares, M.L.G., Callado, C.H., 2016. Occurrence of annual growth rings in Rhizophora mangle in a region with low climate seasonality. Ann. Braz. Acad. Sci. 88 (1), 517–525.

Staudinger, M.D., Grimm, N.B., Staudt, A., Carter, S.L., Chapin, F.S., Kareiva, P., et al., 2012. Impacts of Climate Change on Biodiversity, Ecosystems, and Ecosystem Services: Technical Input to the 2013 National Climate Assessment. Retrieved from. Cooperative Report to the 2013 National Climate Assessment. http://ec.europa.eu/eurostat/statistics-explained/index.php/Waste_statistics.

Steenkamp, C.J., Vogel, J.C., Fuls, A., Van Rooyen, N., Van Rooyen, M.W., 2008. Age determination of Acacia erioloba trees in the Kalahari. J. Arid Environ. 72 (4), 302–313.

Stoffel, M., Bollschweiler, M., 2010. Tree-ring reconstructions in natural hazards research. Preface 2355–2357.

Strohbach, B.J., 2000. Vegetation degradation trends in the northern Oshikoto Region: III. The Terminalia prunioides woodlands and Andoni grasslands. Dinteria 26, 76–92.

Turpie, A.J., Midgley, G., Brown, C., Barnes, J., Pallett, J., Desmet, P., et al., 2010. Climate Change Vulnerability and Adaptation Assessment for Namibia'S Biodiversity and Protected. Ministry of Environment and Tourism, Directorate of Parks & Wildlife Management.

Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2004. Growth rings, growth ring formation and age determination in the mangrove Rhizophora mucronata. Ann. Bot. 94, 59–66.

Visser, M.E., Both, C., Lambrechts, M.M., 2004. Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35, 89–110.

Wang, T., Ren, H., Ma, K., 2005. Climatic signals in tree ring of Picea schrenkiana along an altitudinal gradient in the central Tianshan Mountains, northwestern China. Trees 19, 735–741.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average values of correlated time series, with applications in Dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201–213.

Wils, T.H.G., Robertson, I., Eshetu, Z., Sass-Klaassen, U.G.W., Koprowski, M., 2009. Periodicity of growth rings in juniperus procera from Ethiopia inferred from cross-dating and radiocarbon dating. Dendrochronologia 27, 45–58.

Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo forest reserve in Venezuela author (s): Martin Worbes published by: British Ecological Society Stable URL: http://www.jstor.org/stable/2648. J. Ecol. 87 (3), 391–403.

Yu, K., Zhao, J., Liu, T., Wang, P., Qian, J., 2004. Alpha-cellulose δ 13C variation in mangrove tree rings correlates well with annual sea level trend between 1982 and 1999. Geophys. Res. Lett. 31 (L11203).

Zacharias, M., Weijers, S., Löffler, J., 2018. Growth rings in bush species of the South African savannah. Afr. J. Ecol. 56 (2), 399–403.

Zhang, T., Liu, Y., Yu, S., Qin, L., 2013. A tree-ring based temperature reconstruction for the Kaiduhe River watershed, northwestern China, since A. D. 1680: Linkages to the North Atlantic Oscillation. Quat. Int. 311, 71–80.