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Responsiveness of *Dichrostachys cinerea* to seasonal variations in temperature and rainfall in central Namibia

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ABSTRACT

Woody plants provide natural archives of climatic variation which can be investigated by applying dendroclimatological methods. Such studies are limited in Southern Africa but have great potential of improving our understanding of past climates and plant functional adaptations in the region. This study therefore investigated the responsiveness of *Dichrostachys cinerea* to seasonal variations in temperature and rainfall at two sites in central Namibia, Waterberg and Kuzikus. *Dichrostachys cinerea* is one of the encroacher species thriving well in Namibia. A moving correlation and response function analysis were used to test its responsiveness to seasonal climatic variations over time. *Dichrostachys cinerea* growth rings showed relationships to late summer warming, lasting up to half of the rainy season. The results also revealed that past temperatures had been fluctuating and their influence on growth rings had been intensifying over the years, but to varying extents between the two sites. Temperature was a more important determinant of ring growth at the drier site (Kuzikus), while rainfall was more important at the wetter site (Waterberg). Growth ring responsiveness to rainfall was not immediate but showed a rather lagged pattern. We conclude that *D. cinerea* differentially responds to variations in rainfall and temperature across short climatic gradients. This study showed that the species, due to its somewhat wide ecological amplitude, has great potential for dendroclimatological studies in tropical regions.

1. Introduction

Dendroclimatology is used to reconstruct climatic conditions of past millennia and estimate changes in local climate by using annual tree growth rings (Bräuning et al., 2009; Karanitsch-Ackerl et al., 2017; Zulfiyor et al., 2017). In Africa, there is a paucity of instrumental climatic data across vast regions, and dendrochronology is a useful tool that can fill that gap as has been shown by Gebrekirstos et al. (2014). Such research provides assessments of past climate variations, rainfall or drought events and other unusual dynamics that are needed in guiding water resource planning and management, particularly in countries that are water stressed such as Namibia. More than 90% of the Namibian landmass is classified as semi-arid (250 mm to 500 mm rain per annum), arid (100 mm to 250 mm of rain per annum) or hyper-arid (less than 100 mm per annum) (Mendelsohn et al., 2002; Shanyengana et al., 2004; Barnard, 2012). Bräuning et al. (2009), Bräuning et al., (2009) Fichtler et al., (2004) and Krepkowski et al., (2011) have shown how temperature and rainfall variations and elevation affected the dynamics of cambial growth in tropical tree species. These studies have clearly shown that tree life forms in sub-Saharan Africa do respond to climatic signals and can reliably be used to document climatic variation over millennia. In the last few decades, Namibia has experienced more frequent drought spells, with the most devastating drought during 2018 –2019 (Moorsom et al., 1995; Shikangalah, 2020a; GRN, 2020). The average annual rainfall over two-thirds of the country has been reported to have fallen below 270 mm during the normal rainfall years in the last 60 decades (MET, 2011). Climate projections indicate a further drop in the amount of rainfall and increase in variability (UNDP, 2019) implying greater water deficit stress and additional decline in rain-fed agricultural outputs (Dube et al., 2016; Reid et al., 2008). Trends of maximum temperatures observed over the past 40 years have also shown temperatures exceeding 35 °C recorded more frequently, and a further increase of 1 °C to 3.5 °C in summer and 1 °C to 4 °C in winter is still expected (GRN, 2010; New, 2015).

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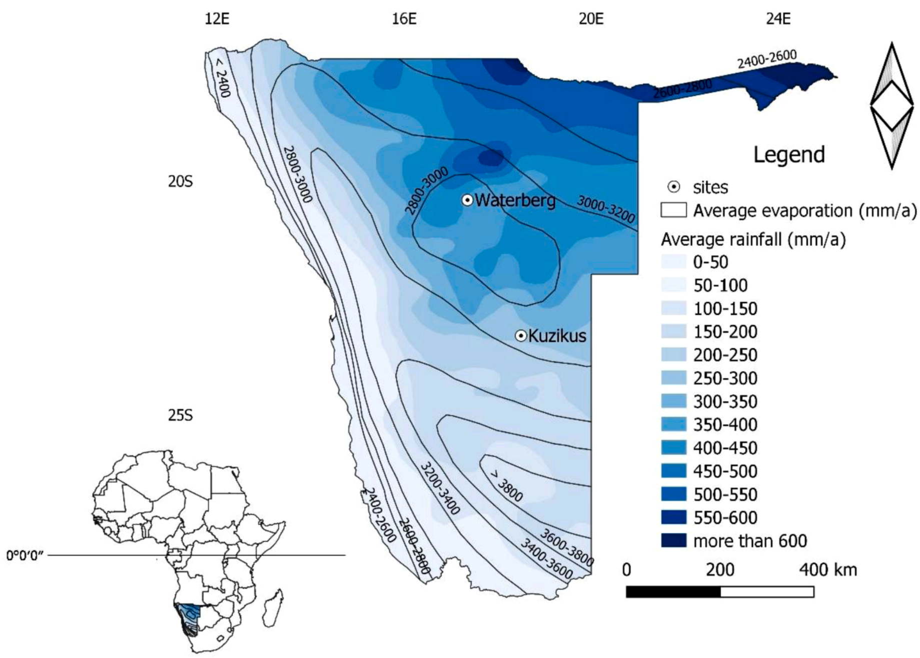
The distribution of vegetation and its survival mechanisms are governed by a combination of complex processes that are highly influenced by the climatic conditions (Gebrekirstos et al., 2006, 2008). The occurrence of frequent and severe droughts experienced are likely to cause shifts in vegetation cover depending on plant ability to adapt to drier environments (Adams et al., 2009; Allen et al., 2010; Choat et al., 2018; Case et al., 2019). A number of areas in Namibia are highly drought-stressed for vegetation to grow due to the extreme dry climate conditions, and such areas could be potential sites for climatic studies using tree rings. Encroacher species such as *Burkea africana* and *Pterocarpus angolensis*, found in Namibia have been shown to give very good climatic signals in tree growth rings (Fichtler et al., 2004). Recent studies have also highlighted how well encroaching species such as *Sengalia mellifera* and *Dichrostachys cinerea* are thriving in Namibia, despite the experienced multi-year rainfall deficits. Some woody encroachers have remarkably expanded, creating impenetrable thickets that are dominating huge areas affecting nearly 45 million hectares of land (Uchezuba et al., 2019). *Senegalia mellifera* and *Dichrostachys cinerea* are the most notorious deciduous woody encroachers among all other encroacher species and are responsible for 40% of the affected areas (Bester, 1999; Marais et al., 2015; Hauwanga et al., 2018).

A few encroachers (16 species) have been studied for dendrochronological purposes in Namibia (Shikangalah, 2020b). Most of the studies have however focused largely on age determination, identification of growth rings and to a certain extent linking the growth rings to the different amounts of precipitation (Shikangalah, 2020b). Studies on



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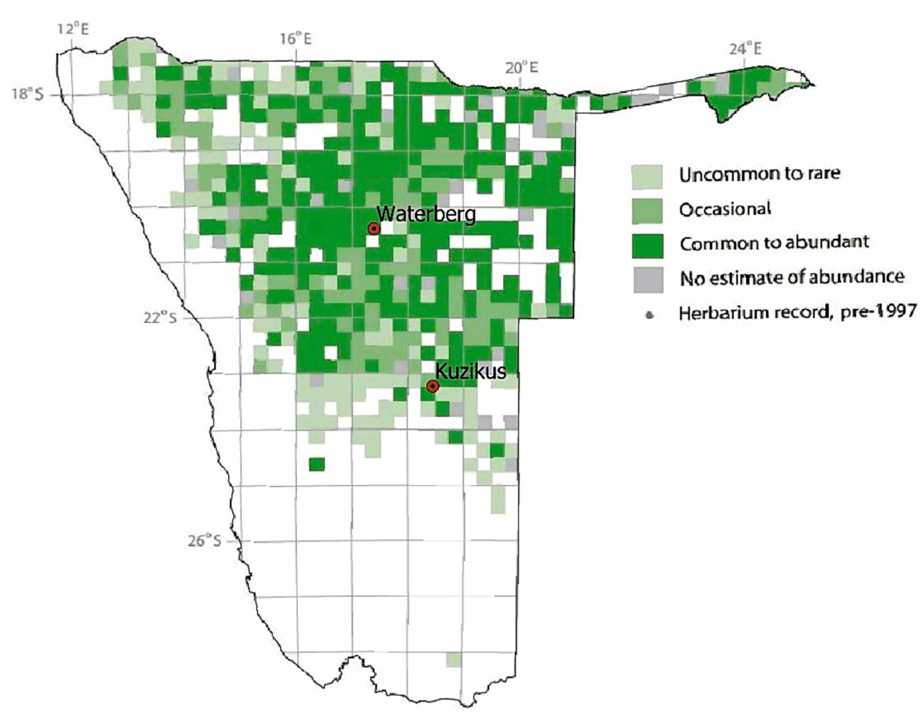


b)

Fig. 1. a. The location of the study sites on a map of evaporation rate (black line grids) and rainfall (blue theme) based on the period 1900–2001 (dataset Digital Atlas of Namibia, 2002). Fig. 1b. Occurrences of *Dichrostachys cinerea* in Namibia (Curtis and Mannheimer, 2005). Fig. 1c. Mean monthly precipitation and temperature of Waterberg and Kuzikus based on the period 1999–2019 (dataset Climate-Data.org, 2020).

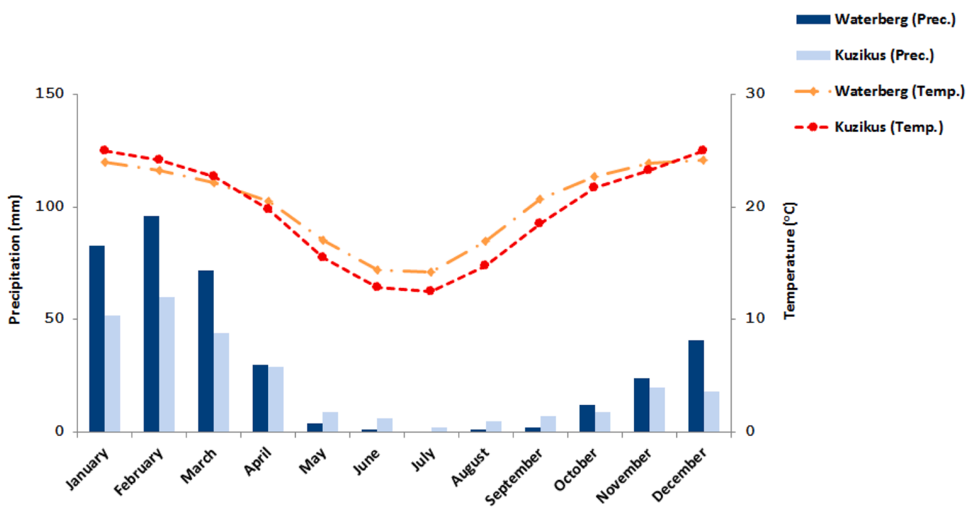


Fig. 1. (*continued*).

D. cinerea showed that the species forms distinctive rings and is more responsive to precipitation than *S. mellifera* (Cunningham and Detering, 2017; Shikangalah et al., 2020). However, very little attention has been paid to the aspect of responses to temperature. This study is aimed at investigating the responsiveness of *D. cinerea* growth rings to variations in seasonal temperature and precipitation over a period of up to forty-nine (49) years. The study used two sites that have small differences in temperature and precipitation (Fig. 1a), to determine whether small variations in these variables elicited any responses in growth rings of this species.

2. Materials and methods

2.1. Study area

Waterberg, located at 20° 25’ 0″ S and 17° 13’ 0″ E and Kuzikus, located at 23° 12’ 57″ S and 18° 27’ 22″ E were selected for this study (Fig 1a). The two study sites fall under relatively similar climatic regimes, but Kuzikus is a bit drier and hotter than Waterberg. The mean annual rainfall ranges from 300 mm to 450 mm at Waterberg and 250 mm to 300 mm at Kuzikus, whereas the mean annual potential evaporation rates are 2800 – 3000 mm and 3200 – 3400 mm, respectively. The mean monthly minimum temperatures are 14.2 °C and 12.5 °C, while the normal mean monthly maximum temperatures are 24 °C and 25 °C, respectively (Fig. 1c), with Kuzikus reaching up to 45 °C during very hot days (Geißler et al., 2019). *Dichrostachys cinerea* (Leguminosae) Wight & Arn. is well distributed in these two areas (Fig. 1b), but more abundant in areas with ample annual rainfall, lower temperature and lower evaporation rates (Fig. 1a & b).

Land use is the same in both study areas, i.e., both are used for livestock farming activities. In addition, the soils and vegetation are largely similar. The soils are red sands underlain by calcareous material, and the vegetation is characterized by trees and open shrubs mainly dominated by *Boscia albitrunca, Vachellia erioloba, Senegalia mellifera, Dichrostachys cinerea, Vachellia haematoxylon, Vachellia hebeclada*, and carpeted by grass species such as *Eragrostis spp*., *Stipagrostis spp*., *Aristida spp*., *Schmidtia kalahariensis*, and *Pogonarthria fleckii* (Mendelsohn et al., 2002; Uugulu and Wanke, 2020). The difference in vegetation is mostly in its density, which is higher at Waterberg than at Kuzikus (Mendelsohn et al., 2002).

2.2. Sampling, processing and analysis

Tree discs of *Dichrostachys cinerea* were haphazardly sampled in 2016 to analyse the relationship between interannual variation of *D. cinerea* growth rings and climate (Shikangalah et al., 2020). Sample discs were cut from each site, one sample disc from each tree was taken at a height of about 1.0 m, because rings appear more frequently near the stem base (Lamarche et al., 1982; Trouet et al., 2006). The discs were air-dried and polished with sandpaper (80–1200) to permit clear visualisation of the tree-rings. Growth rings were identified under a binocular microscope to make sure that only samples with visible rings were selected for further analysis. From a total selected sample of 32, twelve (12) were from the Waterberg site and 8 from Kuzikus site. At Kuzikus, the species is less abundant, whereas it was readily accessed at Waterberg Plateau.

Selected samples were scanned at 2400 dpi resolution and the scanned images were uploaded and analysed with WinDENDRO software, which automatically counts and dates growth rings. Using WinDENDRO, four perpendicular radii from the pith were drawn on each sample (Grudd, 2006; Heinrich et al., 2009). The identified tree-rings were then again verified under a binocular microscope, and were necessary corrected in WinDENDRO (e.g. adding the missing or removing the added false rings). In addition, the COFECHA program was used to correct, verify and validate the outputs of WinDENDRO (Holmes, 1983), which was to ensure that the quality and accuracy for all segments measured in the disc were accounted for (Grissino-Mayer, 2001). The COFECHA program creates a master chronology of all the discs and then calculates the correlation coefficients to indicate how well the inter-annual ring width variation in series correlates with the ring-width variations of the mean chronology while at the same time it identifies the incorrect dated rings, missing rings and false rings (Holmes, 1983; Steenkamp et al., 2008). A ring width index (RWI) chronology was created using the dplR package (Bunn, 2008) of R 3.4.4 (R Core Team, 2018). The chronology showed that the age of trees ranged from 22 to 38 years, covering from 1977 to 2015 (Shikangalah et al., 2020).

Tree-rings get naturally narrower as the tree gets older. To create a RWI that is not affected by age, the chronologies were detrended (Meko et al., 1995). We performed spline detrending with a 50% frequency response based on a year-to-year variability to remove biological tendencies of growth and condense the effects of endogenous stand disturbances while enhancing the common signal present in the tree-ring series (Fritts, 1976; Cook et al., 1990; Cook and Kairiukstis, 1990; R Core Team, 2018). The quality of chronologies was investigated using statistics such as Standard Deviation (SD); Mean Sensitivity (MS); and Expressed Population Signal (EPS).

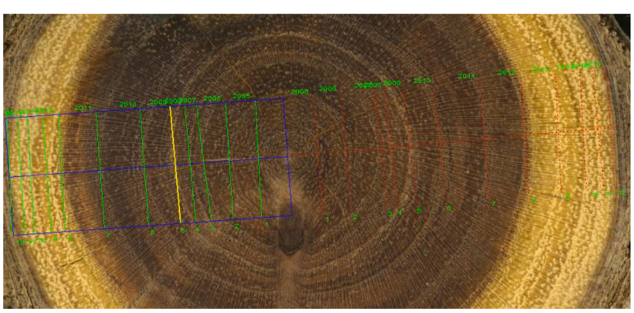
To study the source of growth variation, a mean value chronology was developed which was calculated from all individual residual series for successive 10-year periods that were lagged by intervals of one year (Bunn, 2008, 2010). Development of a master chronology also used a

Tukey bi-weight robust mean, in order to reduce the effect of outliers. Using the dplR package (Bunn, 2008) of R 3.4.4 (R Core Team, 2018), moving correlation and response analyses were used to test the responsiveness to the microclimates from 1966 to 2015. The analysis was conducted using regular bootstrapped correlation function analysis in the bootRes library package in R (Zang and Biondi, 2013, 2015; Palmer et al., 2018; R Core Team, 2018), using Pearson's correlation coefficients at the significance level of 0.05. The dcc function in TreeClim Package in R was used to calculate (potentially moving or evolving) response and correlation functions from tree-ring chronologies and monthly climatic data. The Climate Hazards Group Infrared Precipitation station data (CHIRPS) was used to benchmark climate data (Funk et al., 2015). The calculations were performed repeatedly for consecutive time windows. The dendroclimatic window period was set to -5 (previous May) to +5 (current May), with the timespan of 2 years.

3. Results

3.1. Wood anatomy of *D. cinerea*

Fig. 2a shows an image of *D. cinerea* being processed in WinDENDRO, two paths are drawn and two more followed. The demarcation of the annual tree-ring boundary was identified by means of the presence of the marginal parenchyma band. Each year is detected and dated at a marginal parenchyma band ring (Fig. 2a), as pointed by the solid arrows (Fig. 2b). For this disc, the earliest year was 2005 as marked from the centre. In Fig. 2b, broken arrows show the various tree-ring width (Fig. 2b). Each growth ring consists of two zones of vessels, a wide but low-density vessel zone that is manifested during a wet season (see the big cycles with broken line, Fig. 2b), and a thin but high-density vessel zone (small circles with solid line, Fig. 2b).



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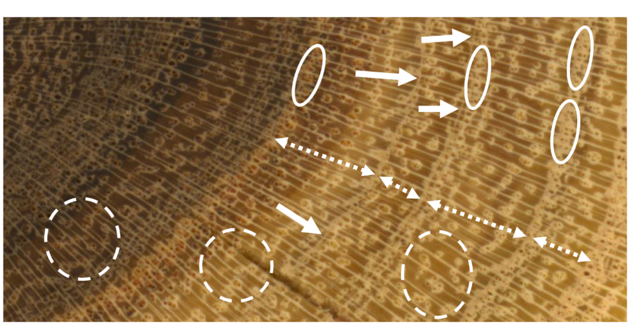


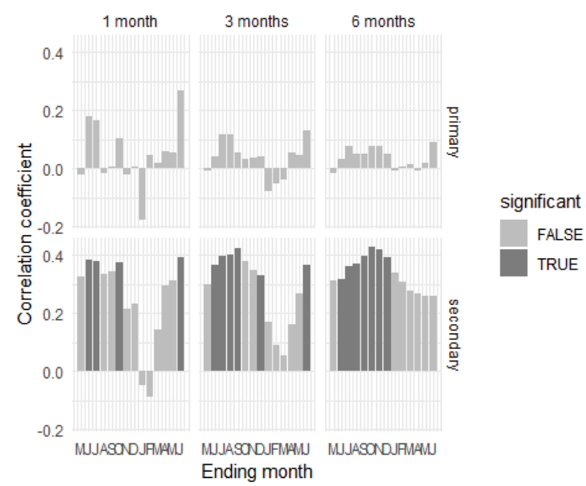
b)

Fig. 2. Wood sections of *Dichrostachys cinerea*. (a) a microscopic sample under WinDENDRO, (b) Other characteristics of the growth rings: Solid arrows show examples of marginal parenchyma band rings, pointing where one ring ends and another starts; the broken double arrows show examples of ring width, by pointing from one end to another; solid ellipses show examples of narrow zones with high-density vessels; and the broken ellipses show examples of wide zone with low-density vessels.

3.2. Correlations between ring width and climatic factors

To assess the quality of the chronology, we calculated commonly used descriptive statistic that showed that the RWI chronology is of good quality. It showed a Standard Deviation (SD) of 0.98, Mean Sensitivity (MS) of 0.45 (the measure of the relative change in ring widths from one year to another), a high Signal to Noise Ratio (SNR) of 7.1, and an Expressed Population Signal (EPS) values of 0.88 which is above the standard threshold of 0.85 EPS. Values that are above 0.85 indicate that the number of radii in the segments of the chronology is great enough to capture adequate percentage of the signal present in the fully replicated chronology (Briffa, 1995; Layme-Huaman et al., 2018).

Plots of seasonal correlations coefficients relating tree-ring width chronology to temperature and precipitation at Waterberg Plateau and Kuzikus are shown in Fig. 3. There are many months of non-significant but positive (very low) correlations are indicated between growth rings and temperature (primary variable, upper panel) at Waterberg (Fig. 3a). Precipitation (secondary variable, lower panel) and growth ring width were positively correlated with a high significance during the winter period. On the contrary, at Kuzikus the correlations between temperature and tree-ring width were negative for most of the period and



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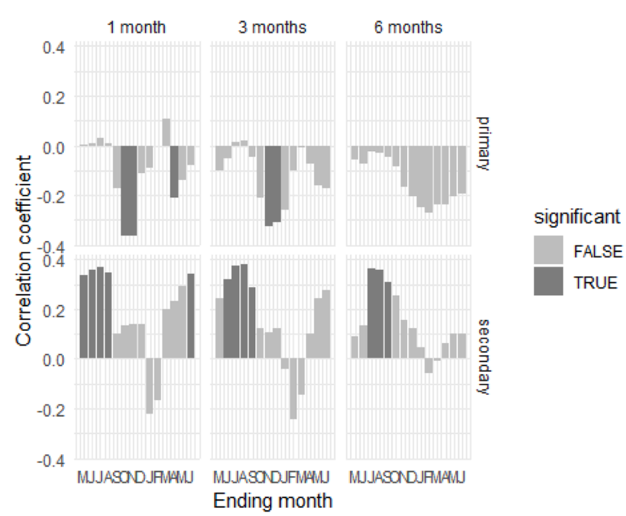

b)

Fig. 3. Seasonal correlation analysis relating ring width of *Dichrostachys cinerea* to climatic factors: (a) Waterberg and (b) Kuzikus. Temperature (primary variable, upper panel) and Precipitation (secondary variable, lower panel) composites with lengths of 1, 3, and 6 months. In the panels, TRUE ($p < 0.05$) implies significant difference and $p > 0.05$ implies no significance, therefore FALSE.

significantly negative during October, November and December, which is 50% of the rainfall period (Fig. 3b). Correlation between growth ring width and precipitation was positive and significant from May to September at Kuzikus compared to Waterberg.

The temporal stability of growth–climate correlation was further analysed using moving correlation functions with respect to temperature to gain a better understanding on its effect on growth rings (Fig. 4). The result showed mostly negative relationships before the peak rainfall period (November–January) while positive relationships occurred during the peak rainfall period (February–April) of both sites. At Waterberg site, the coefficients displayed negative correlation from November (r = -0.04), December (r = -0.09) and January (r = -0.22) (Fig. 4a), but positive from February (r = 0.05) to April (r = 0.14 to 0.24). At Kuzikus, the correlations were negative during November and December only (Fig. 4b), with a significant negative correlation in December (r = -0.27), which also corresponds with Figure 3. The overall results showed fluctuating correlations, but the correlations (both positive and negative) generally became stronger over the years at both sites.

4. Discussion

So far, only few studies analysed historical climate trends in Namibia. This study used dendroclimatology to investigate responsiveness of *Dichrostachys cinerea* to seasonal temperature and precipitation at two sites that are relatively similar in temperature regimes and less so in rainfall. The main aim was to determine the responsiveness of this species to small differences in temperature and rainfall with respect to tree ring width.

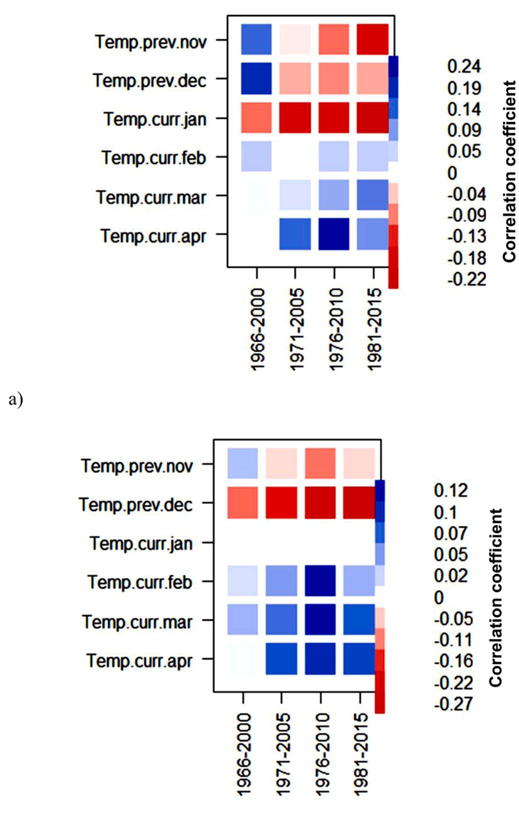

Fig. 4. Plot of moving correlation coefficient relating *Dichrostachys cinerea* tree ring width to temperature at (a) Waterberg and (b) Kuzikus), from previous (prev) year of November to current (curr) year of April. The moving correlation is carried out in windows of 35 years, offset by 5-year periods.

4.1. Influence of seasonal rainfall on ring width

The results showed that the influence of rainfall on growth rings is not immediate but rather increases over a longer period of months of rainfall, and more important during winter period than during the rainy season. This is particularly so at the site of higher rainfall, Waterberg (Fig. 3b). This could imply a lagged ring growth response to rainfall. This may be due to the water uptake of the species, taking up water with deeper roots rather than with lateral roots (Timberlake and Calvert, 1993). Although *D. cinerea* is reported to colonise mostly areas with annual rainfall of 200–400 mm (Travieso and Kaltschmitt, 2012; Fig. 1a), possibly because the leaf fraction and productivity of *D. cinerea* decline significantly with a reduction in rainfall amount (Fernández et al., 2015), making the species more vulnerable in drier sites such as Kuzikus than at wetter sites such as Waterberg. At Waterberg, the area is surrounded by a plateau and a few hills which are likely to results in significant water run-off to lower plains, where *D. cinerea* is mainly found. The runoff from the plateau would gives the plants (*D. cinerea*) additional moisture and time for water uptake. However, at Kuzikus, the area is relatively flat and water is likely to infiltrates straight downward, giving the plants a shorter period to utilize the water. In addition to these differences in topography, *D. cinerea* is also found to lack the ability to re-saturate its water status during the night unlike other plants, having lowest water potential values for midday and pre-dawn time during the dry season (Gebrehiwot et al., 2005; Gebrekirstos et al., 2006). Its growth and survival depend much on the root-suckering which normally leaves little in reserve for coping with drought stress (Wakeling and Bond, 2007; Case et al., 2020). Such a strategy may be useful to the plant in areas with ample rainfall, but less so in places such as Kuzikus, where the amount of rainfall is not only limited but it also percolates straight into lower horizons with less of it being available for plant use. Typically, such drier conditions are temporary setbacks for woody encroachers in drier savannas, however, they are also associated with high mortality of *D. cinerea* as reported by Case et al., (2020).

4.2. Influence of seasonal temperature on ring width

Several months of non-significant but positive correlations between growth rings and temperature at Waterberg Plateau (Fig. 3a) indicate minimal influence of temperature on sizes of growth rings. At Kuzikus, the correlations between temperature and growth ring width were negative 50% of the growing season because during the other half of the growing season the plants will even be without moisture (Fig. 3b). This shows how temperature is a more important determinant at Kuzikus, since high temperatures (synergistically with low moisture) reduced tree-ring growth more strongly than at Waterberg, where rainfall could have had a moderating effect on influence of temperature.

Our findings also demonstrated that at both sites the influence of temperature on growth rings has been fluctuating over the years and is getting more intense with time, reaching up to correlation coefficients of -0.27 at Kuzikus and -0.22 at Waterberg (Fig. 4). This corresponds well with the observed tendency of higher temperatures in the second half of the 20th century and a significant increase in temperature (up to 0.5 °C) experienced in Namibia (Spear et al., 2018). The average annual temperature has been increasing at a rate of 0.0123 °C over the period of 1901–2016 (GRN, 2020). For every 1 °C of temperature rise, evaporation increases by 5% (Reid et al., 2008; GRN, 2010). The increase in temperature and the subsequent high evaporation has a significant negative impact on plant productivity, more so at already drier sites like Kuzikus. According to Fernández et al., (2015), *D. cinerea* has low stomatal sensitivity to air vapour pressure deficit, which makes it more vulnerable to summer dehydration. During hot days, *D. cinerea* displays higher transpiration rate, that contributes to low productivity, while during winter and spring transpiration rate is medium to low, leading to better productivity (Fernández et al., 2015). However, trends reported by Fernández et al., (2015) were from a field experiment in southwestern Spain, and could be functionally different from what happens in arid and semi-arid tropical environments. Bhugeloo (2014) reported that *Vachellia nilotica* in northern KwaZulu-Natal (South Africa) showed that this species was not strongly influenced by changes in climatic variables. Furthermore, the negative correlation between growth rings and temperature was greater at Kuzikus than at Waterberg (Fig. 3b), probably due to the higher evaporation (and less soil moisture availability) during most of the year at Kuzikus (Fig. 1a). The higher evaporation rates, coupled with relatively longer periods of evapotranspiration water loss, resulted in reduced width of growth rings compared to Waterberg. Higher ambient temperatures are usually associated with increased evapotranspiration, thereby negatively correlating with tree-ring width. This could also explain the limited distribution and lower abundance of *D. cinerea* in that area (Fig.1b). A study of *Chukrasia tabularis* in a tropical rainforest has found similar negative correlations between growth ring and temperature (Rahman et al., 2018), where the highest negative correlation occurred when temperature-driven evapotranspiration was high. This underscores the important role temperature may play in limiting growth rings of many tropical plant species. The results imply that with the predicted climate change-induced warming in Namibia, the growth of *Dichrostachys cinerea* will likely be curtailed in drier sites but less so in wetter environments. This observation has important implications for the management of this encroacher species at various sites in Namibia.

5. Conclusions

Findings from this study have shown that *Dichrostachys cinerea* showed site-specific responses to variation of differences in rainfall and temperature between the two sites, both seasonally and over longer periods (in the case of temperature for the latter). The negative effects of summer temperatures on growth rings last up to half of the growing season at Kuzikus, which is likely to result from lower availability of soil moisture, while responses to rainfall impacts showed a lagged response at Waterberg. The results also revealed that the influence of temperature on growth rings has become stronger, possibly resulting from a rise in temperature over the years. It is recommended that older trees and a larger sample size than that used in this study should be analysed to reconstruct periods of past climate trends in order to get a more holistic understanding of regional climate change. Given that the distribution of *D. cinerea* covers the areas affected by both droughts and floods, it remains a good candidate for such studies.

Credit author statement

Rosemary Shikangalah: Conceptualization; carried out data analysis and wrote the manuscript, and contributed to refining the manuscript.

Benjamin Mapani: Conceived the research, wrote the manuscript, and contributed to refining the manuscript.

Ulrike Herzschuh: Tree rings were analyzed at her Laboratory, and she contributed to refining the manuscript.

Isaac Mapaure: Contributed to refining the manuscript.

Declaration of Competing Interest

Authors declare NO conflict of interest.

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