

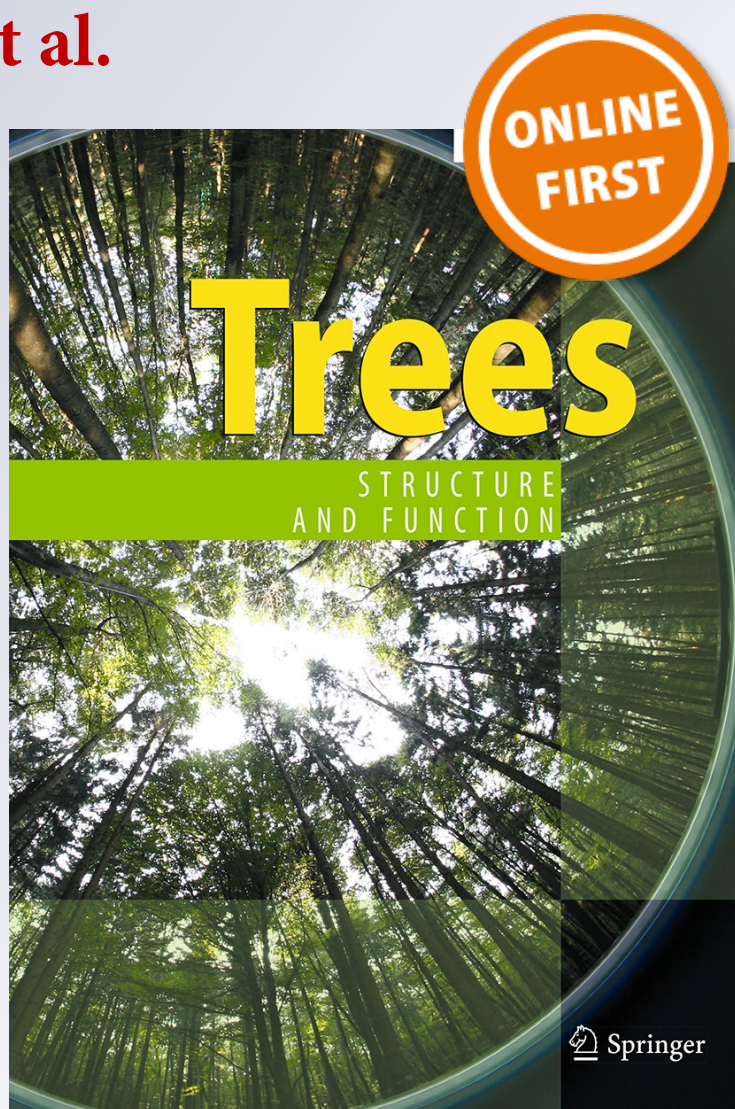
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savannas of the Volta basin, Ghana*

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Influence of climatic factors on tree growth in riparian forests in the humid and dry savannas of the Volta basin, Ghana

Emmanuel Amoah Boakye^{1,3} · Aster Gebrekirstos² · Dibi N'da Hyppolite¹ · Victor Rex Barnes³ · François N. Kouamé¹ · Daouda Kone¹ · Stefan Porembski⁴ · Achim Bräuning⁵

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Abstract

Key message The paper demonstrates the prospects and applications of dendrochronology for understanding climate change effects on riparian forests in the savanna landscape.

Abstract Riparian trees in savannas have a potential for dendro-climatic studies, but have been neglected hitherto. We examined ring-width series of *Azelia africana* (evergreen) and *Anogeissus leiocarpus* (deciduous) to study the influence of climatic factors on the growth of riparian trees in the humid (HS) and dry (DS) savanna zones of the Volta basin in Ghana. A total of 31 stem discs belonging to *A. africana* and *A. leiocarpus* were selected from HS and DS to establish species-specific local chronologies of tree growth. Each individual of *A. africana* and *A. leiocarpus* from the two savanna sites showed distinct growth rings. Cross-dating of individual tree-ring patterns was successful using standard dendrochronological techniques. The mean annual growth rates of *A. africana* in the HS (1.38 ± 0.09)

and DS (1.34 ± 0.08) were not statistically different. Furthermore, mean annual growth rate of *A. leiocarpus* in the DS (3.75 ± 0.27) was higher than in the HS (2.83 ± 0.16) suggesting that species in drier environment can have higher growth rates when sufficient soil moisture is available. The growth rates of both species at the same sites were different, which might indicate different water use strategies. High correlations of individual tree-ring series of *A. africana* and *A. leiocarpus* trees at HS and DS suggest a strong climatic forcing controlled by the seasonal movement of the inter-tropical convergence zone. The annual growth of *A. africana* and *A. leiocarpus* at both the HS and DS was significantly correlated with local temperature and precipitation. The negative correlations of the growth of the two tree species to global sea surface temperatures were however, indications that the growth of riparian forests can be impacted during El Niño-Southern Oscillation years. The result of our study shows that riparian trees in the humid and dry savanna zones of West Africa can be successfully used for dendrochronological studies.

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✉ Emmanuel Amoah Boakye
eaaboakye@yahoo.com

¹ WASCAL Graduate Research Programme on Climate Change and Biodiversity, Université Felix Houphouët Boigny, Abidjan, Cote d'Ivoire

² World Agroforestry Center, Nairobi, Kenya

³ Faculty of Renewable Natural Resources, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

⁴ Institute of Biosciences, University of Rostock, Rostock, Germany

⁵ Institute of Geography, Friedrich-Alexander-University Erlangen-Nürnberg, Erlangen, Germany

Keywords Riparian forests · Humid savanna · Dry savanna · Dendrochronology · Tree growth · West Africa

Introduction

Forests growing along waterways (also known as riparian forests) are vulnerable to the effects of climate change (Rayner et al. 2003; Scherer-Lorenzen et al. 2005). The reason is that any changes in climatic variables such as precipitation, air temperature, wind speed and solar radiation affect the hydrology of rivers and the riparian forests which depend on regular flooding cycles for maintaining

tree composition and growth (IPCC 2013; Sambare et al. 2011). Previous studies have revealed that drought conditions result in the loss of species and reduce moisture availability of riparian forests (Sambare et al. 2011; Mantyka-Pringle et al. 2012). Other studies have also demonstrated the negative effect of excess rainfall causing long-term flooding of riparian areas which limits nutrients availability to plants (Schifman et al. 2012). Long-term drowning is reported to have effects on photosynthesis and consequently, the growth rate of riparian tree species (Schifman et al. 2012). Understanding the responses of tropical riparian trees to climate change is important since they sequester large amounts of carbon and transpire considerable amounts of water (IPCC 2013) which is of extreme relevance for regional water cycles.

Dendrochronology is a discipline that allows dating of tree growth rings to the year of their formation. The dated rings have the utility of detecting climatic signals that are common for a population of trees (Gebrekirstos et al. 2014). Comparing various natural archives such as ice cores, lake and ocean sediments and corals (McCarroll and Loader 2004), trees have great advantages for climatic studies (Schweingruber 1988; McCarroll and Loader 2004; Gebrekirstos et al. 2011), because trees are widespread so that it is possible to examine geographical variations of changing environmental conditions. It is also possible to create chronologies of trees with overlapping life times and to analyze the variability within the measurements (Gebrekirstos et al. 2008; Puchacofrep et al. 2015). Ratios of stable isotopes in tree rings cellulose provide another possibility of studying the physiology of riparian trees in relation to environmental changes (McCarroll and Loader 2004; Gebrekirstos et al. 2014).

Studies have proven the existence of annual rings in tree species in tropical regions from arid (Fichtler et al. 2004; Schöngart et al. 2006; Gebrekirstos et al. 2008, 2014) to humid zones (Trouet et al. 2010; Groenendijk et al. 2014; Sleen et al. 2015). Such studies have shown that many tree species growing in tropical regions characterized by one severe dry season per year form annual rings. Unlike for temperate zones, few studies have been conducted for tropical regions (Worbes 2002; Schöngart et al. 2006), despite the numerous reports on the potential of tropical trees for climatic and environmental studies (Worbes 2002; Gebrekirstos et al. 2011). This research gap is partly caused by the limited technical facilities and financial resources in tropical countries. In addition, the difficulty for accessing forest stands and low sampling replication because of the high species diversity that comes along with low abundances of individuals of any particular species in most tropical forests have hampered tree ring research (Worbes 2002).

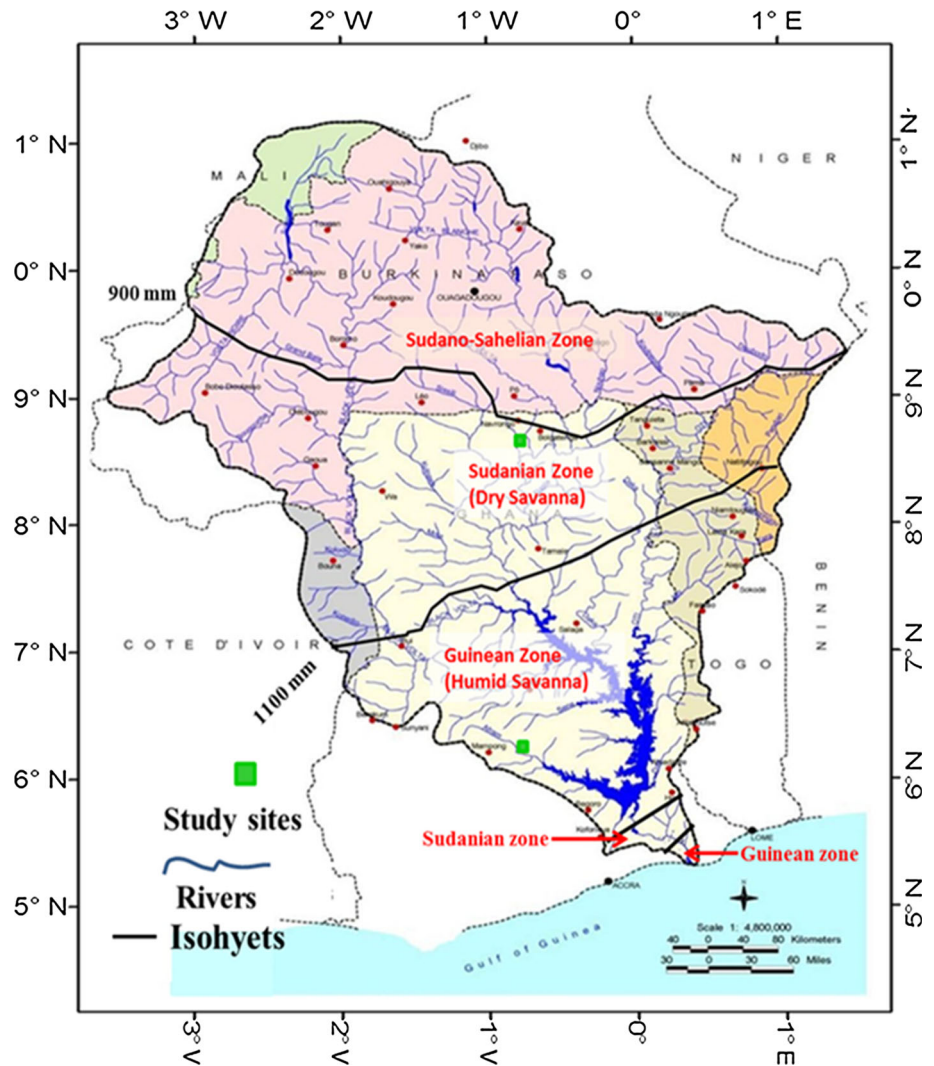
Leaf phenology (i.e., seasonal variations in leaf area) of plants influences carbon assimilation (Caldararu et al. 2014). Phenological cycles are highly dependent on climate and the timing and spatial patterns of phenological dates may change significantly in response to changes in climate (Krepekowski et al. 2013). In the present study, we compared the variation in radial growth of two broad leaved tree species belonging to different plant functional types, i.e. *Azelia africana* (evergreen), and *Anogeissus leiocarpus* (deciduous) within the Volta sub-basin of Ghana. The Volta basin is one of the largest river basins in sub-Saharan Africa and covers approximately 400,000 km². The water resources of the basin are shared by six countries: Benin, Burkina Faso, Côte d'Ivoire, Ghana, Mali and Togo. Approximately, 42 % of the basin is in Ghana (UNEP-GEF 2012). It is divided into three main agro-ecological zones: the Sudan-Sahel savanna, the Sudan savanna and Guinea savanna. The Sudan-Sahel savanna is predominantly desertification-prone. The Sudan savannas are found in the northern parts of the basin. The Guinea savanna consists of a mosaic of forests and savanna woodland (de Condappa and Lemoalle 2009; UNEP-GEF 2012; Callo-Concha et al. 2012). To assess the effect of climate change on riparian forest ecosystems of different ecological zones within the Volta sub-basin in Ghana, we included two riparian forests in our sampling design, one in the humid Guinea zone which is characterized by humid savanna growing outside of the riverine areas, and one in the dry Sudanian zone which is characterized by dry savanna. Since riverine ecosystems are partly decoupled from the surrounding vegetation due to the dominance of the river hydrology on the soil moisture regime, we hypothesized (1) that the annual growth patterns of riparian trees (*A. africana* and *A. leiocarpus*) in the dry and humid savanna zones are similar, making them useful for tree ring research; (2) there exist significant relationships between climatic factors and annual growth rates of riparian tree species.

Materials and methods

Study area

The study was conducted in linear strips of riparian forests along the Afram and Tankwidi rivers (riparian reserves), located in the humid (Guinean) and dry savanna (Sudanian) zones of the Volta basin of Ghana, respectively (Fig. 1). The two rivers are similar in terms of width (8–12 m) and major soil conditions of floodplain regions which are characterized by Luvisols (Konate and Kampmann 2010). Luvisols are soils with sub-surface accumulation of clay and organic matter, high activity clay and high base saturation. Beside their fertility, Luvisols have favorable soil

Fig. 1 Location of the two study sites in different climatic zones of the Volta basin in Ghana, West Africa (Source: de Condappa and Lemoalle 2009)



physical structure with high porosity, and are well drained and well aerated (Konate and Kampmann 2010).

Forty-seven percent of the woody plants in the Afram riparian forests belong to the Fabaceae and Combretaceae, with an average tree density of 545 ± 18 individuals per hectare. In the case of the Tankwidi riparian forests, 49 % of the species belong to Fabaceae and Rubiaceae, with a mean tree density of 355 ± 21 individuals per hectare. In both of the Afram and Tankwidi riparian forests, about 58 % of the tree individuals are in lower diameter class (5–20 cm) than in higher diameter classes (>20 cm) (Boakye et al. 2015, 2016).

The spatial and temporal distribution of precipitation patterns in the Volta basin of Ghana are influenced by the inter-tropical convergence zone (ITCZ), the northeast trade winds, and atmospheric disturbances originating in the tropical Atlantic Ocean. These disturbances are modulated by the sea surface temperatures (SST), both in the tropical

Atlantic and the equatorial Pacific that determine wetter and drier years in the study sites (Odekunle and Eludoyin 2008). Analysis of weather data from Ejura and Navrongo Meteorological Stations of Ghana Meteorological Agency reflects differences in absolute values and temporal patterns of precipitation and temperature in the two savanna zones (Fig. 2). The humid savanna has a mean annual maximum temperature of 32°C and a mean annual precipitation of 1100 mm, with an eight-month long rainy season (monthly precipitation sums exceeding 60 mm) lasting from March to October and somewhat lower precipitation rates in July and August. In contrast, the dry savanna has a mean annual maximum temperature of 36°C and a mean annual precipitation of 800 mm, with a shorter rainy season lasting from April to October. The two riparian forests dry out during the prolonged dry season from November to April for the Tankwidi catchment and November–February for the Afram catchment.

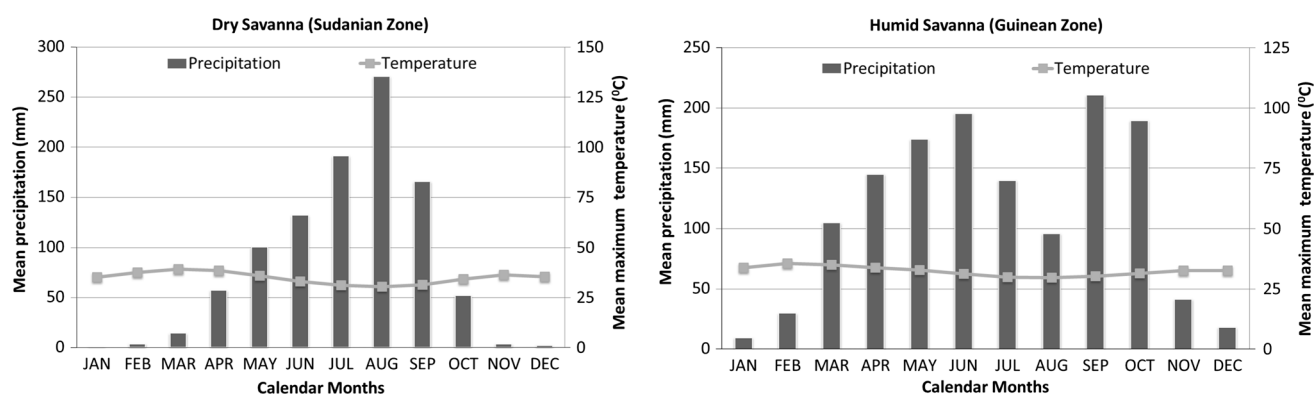


Fig. 2 Seasonal patterns of mean monthly precipitation and maximum temperature (averages of 1961 to 2012) of the dry and humid savanna zones

Methods

Sample collection

Since no previous dendrochronological studies have been carried out in the humid and dry savanna zones of Ghana, it was first necessary to identify the riparian woody species that produce discernible rings. Therefore, during the intensive fieldwork for inventorying riparian woody species in 2013, a Haglof increment borer of 5 mm diameter was used to extract sample cores of all woody species in both the Afram (humid savanna, HS) and Tankwidi (dry, DS) riparian forests for visual inspection. The targeted species common to both riparian forests in the humid and dry savanna zones were *Azalia africana*, *Anogeissus leiocarpus*, *Azadirachta indica*, *Daniellia oliveri*, *Diospyros mespiliformis*, *Khaya senegalensis*, *Mitragyna inermis*, and *Vitex doniana*. After scanning through the sample cores of the different riparian trees, two species that displayed clearly visible growth rings, and were common to both savanna types and quite dominant in both forest ecosystems were selected. These species were *A. africana* and *A. leiocarpus*. According to the classification of (Sarmiento and Monasterio 1983) and Seghieri et al. (2012), *A. leiocarpus* is considered as deciduous species with a short leafless period of 3–4 months. *A. africana* is a semi-evergreen species, shedding its leaves during a period no longer than 2 months. Both *A. africana* and *A. leiocarpus* have socio-economic importance and are used for furniture, firewood and charcoal production. The foliage of *A. africana* is used as source of fodder for livestock whereas the seeds of *A. leiocarpus* are used in traditional medicine (Andary et al. 2005; Gérard and Louppe 2011).

For a thorough study, a total of 31 stem discs of *A. africana* (HS = 8, DS = 7) and *A. leiocarpus* (HS = 7, DS = 9) within the diameter class of 25–40 cm were collected along the Afram (HS) and Tankwidi (DS) rivers.

The discs were collected at breast height, approximately 1.3 m from the base of all trees. In order to minimize edge effects, samples were collected at a minimum distance of 10 m from the river but within a 50 m riparian buffer zone. For each disc collected, the following information was recorded: (1) species name; (2) location; (3) date collected; (4) species and site characteristics (i.e., tree height, diameter, canopy density and ground slope).

Sample preparation

Standard dendrochronological methods were used to prepare the stem discs for measurement at the tree ring laboratory of Friedrich-Alexander University of Erlangen-Nürnberg, Germany. After air-drying the discs, they were polished mechanically and with sandpaper of progressively finer grit up to a grain of 1000. Wood dust was removed from the vessels with compressed air to improve visibility of the growth zone boundaries. In some cases, the surfaces of the wood samples were moistened to increase the contrast between different wood tissues and the distinctiveness of growth zones.

Growth ring measurements

Prior to growth ring measurements, thin sections of 10 to 20- μ m thicknesses were cut from samples each of *A. africana* and *A. leiocarpus* (both humid and dry savanna) with a microtome to take microscopic pictures and to characterize the nature of their rings boundaries (Worbes and Fichtler 2010). The sections (Fig. 3) were stained with solutions of safranin and astra blue, and dehydrated by washing with increasing concentrations of ethanol, following standards procedures (Gärtner and Schweingruber 2013). The micro-sections were subsequently used to describe the wood anatomical features by following the classification in Schweingruber et al. (2006).

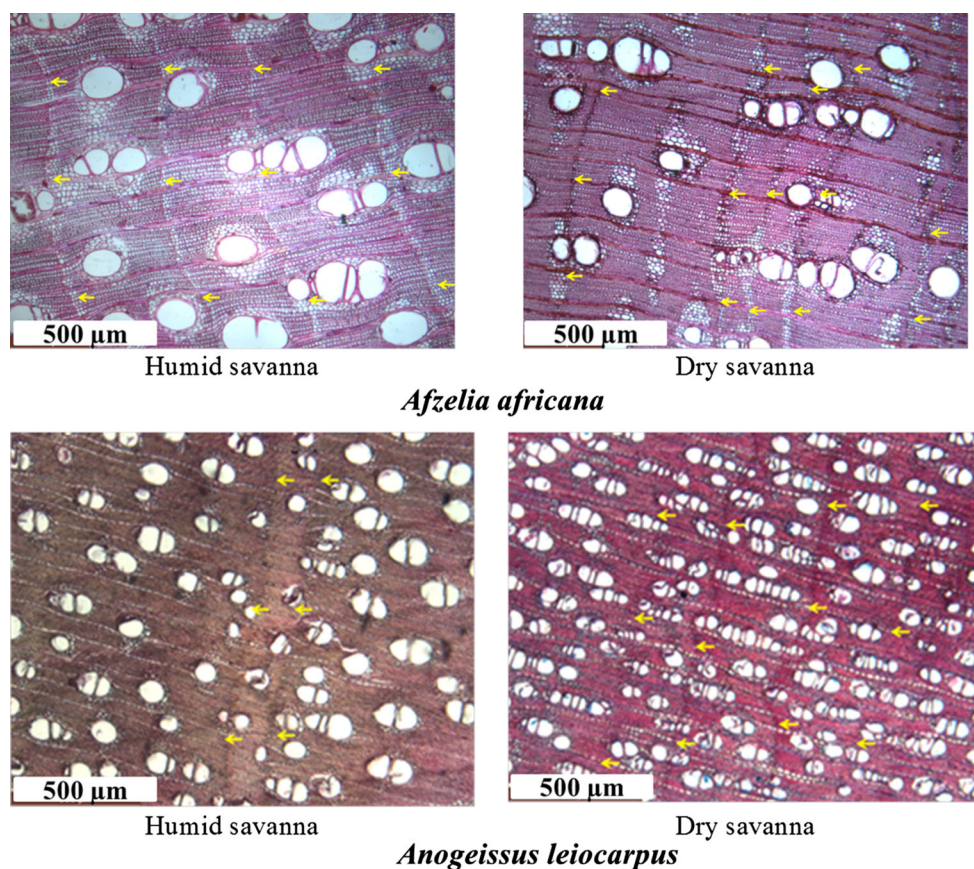


Fig. 3 Transverse sections of *Afzelia africana* and *Anogeissus leiocarpus* in the humid and dry savanna zones of Ghana. Yellow arrows mark annual growth ring boundaries

During the measurements (31 discs), each ring was marked on a sample disc on 2–4 radii and every tenth ring was interconnected between the different radii. This procedure helped to detect wedging rings, discontinuous growth zones as well as verifying the existence of each ring round a disc. When all rings on a disc were detected and ring numbers and characteristics matched along different radii, ring width was measured along 2–4 radii of each stem disc. All ring widths were measured perpendicular to ring boundaries to the nearest 0.01 mm along the pre-determined radii along a straight line using a semi-automated device (LINTAB 6, Rinntech, Heidelberg Germany). LINTAB consists of a stereoscope and a moveable board linked to a distance measuring device and a computer (Rinn 2012).

Mean curves were produced for each disc and per species for each study site (termed chronologies) using the radii after visual cross-dating with reference to pointer years (the position of very narrow or very wide rings to link rings detected on different radii). In addition to visual cross-dating (Stokes and Smiley 1968), all ring-width series were statistically (Cook et al. 1990) cross-dated using

computer program Time Series Analysis and Presentation (TSAP). Two statistical indicators were used to evaluate the match between the time series: the “Gleichläufigkeit” (GLK; equivalent to a sign-test) which reflects the percentage of ring-width oscillations in the same direction in two time series within a certain period (Eckstein and Bauch 1969) and the “*t*-value” (Baillie and Pilcher 1973). These statistics were used for selecting the best correlated series included in building sites chronologies.

Measuring signal strength and chronology reliability

Mean interseries correlation was used as a measure of the strength of the common growth signal within a chronology. This index was calculated over a moving 30-year window with sample replication of five. Expressed Population Signal (EPS) (Wigley et al. 1984) measures the chronology reliability, if it reflects a hypothetically perfect or true chronology. EPS is a function of the interseries correlation and the series replication. EPS ranges from zero to one, the recommended threshold to be exceeded for acknowledging a chronology as “robust” is 0.85 (Wigley et al. 1984).

Data analysis

Comparison of radial growth

The study compared the mean radial growth (ring widths) among the species using *t* test in Statistical Package Software for the Social Sciences, Version 17 after testing for normality. Results were considered significant at $p \leq 0.05$.

Climate-growth relationships

Before assessing the relationship between climatic parameters and radial growth of the trees, individual growth ring width series were detrended and standardized using the dendrochronology program library in *R* statistical software “dplR” (Bunn 2008, 2010). The detrending is the estimation and removal of the tree’s natural biological growth trend. The standardization is done by dividing each series by an estimated growth trend to produce dimensionless growth series free of autocorrelation caused by internal biological growth trends. The final mean chronology is a dimensionless ring-width index (RWI). In this study, a Spline function was used to fit each raw mean ring-width series with a frequency response of 0.50 % at wavelength of 0.67 of each tree-ring series length.

Pearson correlation analysis was conducted with a significance of 5 % separately for the RWI of each species (*A. africana* and *A. leiocarpus*) of the humid and dry savanna zones to climatic parameters (Total monthly and yearly averages of precipitation and mean monthly maximum temperature). The quarterly precipitation values of the previous year starting from the beginning of the rainy season (April) were also correlated with the growth of trees. The climate data covering the period 1961–2012 were obtained from the Ejura (1 km to study site) and Navrongo (3 km to study site) Meteorological Stations of the Ghana Meteorological Agency for the humid and dry savanna zones, respectively. The correlation analyses were conducted in GraphPad Prism 6.

Spatial correlation analyses of RWI and Hadley Centre Sea Ice and Sea Surface Temperature (HadISST1) ($p \leq 0.05$) were also carried out with the KNMI Climate Explorer (Royal Netherlands Meteorological Institute 2015). The SST dataset were downloaded from the Climate Research Unit of the University of East Anglia. This was done for *A. africana* and *A. leiocarpus* in both the dry and humid savanna zones.

Results

Characteristics of growth rings

Both *A. africana* and *A. leiocarpus* in the humid and dry savanna zones showed distinct growth rings (Fig. 3). The

growth rings of *A. africana* are formed by marginal bands of axial parenchyma and were more distinct. The vessel size of *A. africana* appeared to be larger than those of *A. leiocarpus*. The color of the wood is light-brown to red with coarse-grained, rough, hard wood texture. The wood structure is diffuse porous and vessels are circular to oval-shaped and occur solitary or in small groupings of 2–3 vessel elements in radial arrangement surrounded by paratracheal aliform or confluent parenchyma which are effective seals and protect the vessels from accidental air leak. The vessel size of *A. africana* in the humid savanna was visibly larger than those of the dry savanna zone. In some instances, wedging rings occurred and were determined by analyzing several radii on each stem disc. The ring widths were variable comprising both extremely narrow and wide rings.

The wood color of *A. leiocarpus* is light-brown and darkens towards the pith. The species was characterized by a weak ring porous vessel distribution with no specific differences in pore size (Fig. 3). Vessels are solitary or aligned in radial groups of up to more than 10 elements. Interestingly, trees growing in the dry savanna show higher numbers of vessel arranged in radial groups than in the humid savanna. The vessel sizes of *A. leiocarpus* in the dry savanna appear to be much smaller than in the humid savanna, which may be an interesting effect to be studied quantitatively in the future. The ring boundaries of the species are demarcated by alternating bands of radially flattened fibres with thickened cell walls but appeared less distinct than those of *A. africana*. Wide rings were generally distinct, but distinctiveness declined with decreasing ring width. *A. leiocarpus* rarely shows wedging rings, and if present they were determined by following the same procedure as in *A. africana*.

Cross-dating

Cross-dating between radii of the same discs was successful for both *A. africana* and *A. leiocarpus* in the humid and dry savanna zones, with significant TV-BP and GLK values (Table 1). In the humid savanna zone, cross-dating of *A. africana* was successful for 7 out of 8 trees varying in lengths between 55 and 95 years. For *A. leiocarpus* of the same site, cross-dating was successful for 5 out of 7 trees also varying in length between 40 and 77 years. In the case of the dry savanna zone, cross-dating of *A. africana* was successful for 6 out of 7 trees of lengths ranging between 32 and 102 years. For *A. leiocarpus* of the dry savanna zone, cross-dating was successful for 7 out of 9 trees of lengths ranging between 26 and 42 years. In order to have an even number of cross-dated individuals for comparative analysis, the five best cross-dated individuals of each species were used for calculating mean ring width series site

Table 1 Characteristics of tree ring series of *Azelia africana* and *Anogeissus leiocarpus* in the dry and humid savanna zones of Ghana

	Dry savanna		Humid savanna	
	<i>A. africana</i>	<i>A. leiocarpus</i>	<i>A. africana</i>	<i>A. leiocarpus</i>
No. of trees	7	9	8	7
No. of dated trees	6	7	7	5
Total chronology length (years)	102	42	92	77
Diameter range (cm)	22–33	28–32	20–36	31–39
Mean GLK	79	72	77	73
Mean TV	4.8	3.6	4.2	3.7
Mean ring width	1.34	3.75	1.38	2.83
Standard error	0.08	0.27	0.09	0.16

chronologies. All individuals that were less than 30 years in age were excluded from chronology building.

Radial growth of *A. africana* and *A. leiocarpus* in the humid and dry savanna zones

A comparison of the annual radial growth variations of *A. africana* and *A. leiocarpus* is presented in (Table 1, Fig. 4). The results showed no significant difference ($p = 0.75$) in the mean growth of *A. africana* between the humid and dry savanna zones during the 67-year study period (1946–2012) (Fig. 4a). This 67-year period is beyond the juvenile phase (below 30 years) of the plants. In the case of *A. leiocarpus*, the mean growth rate in the dry savanna was significantly ($p = 0.02$) higher than in the humid savanna zone (Fig. 4a). For both the dry and humid savanna zones, the mean annual growth rate of *A. leiocarpus* was significantly ($p < 0.05$) higher than for *A. africana* (Fig. 4b).

Relationship of ring width of *A. africana* and *A. leiocarpus* in the humid and dry savanna zones

The detrended ring width (RWI) (Fig. 5) of *A. africana* in the humid savanna had the highest mean inter-series correlation ($r_{bar} = 0.76$) and EPS (0.94). This was followed by *A. leiocarpus* in the dry savanna ($r_{bar} = 0.69$, EPS = 0.92). The inter-series correlation and EPS values of the *A. africana* ($r_{bar} = 0.64$, EPS = 0.90) and *A. leiocarpus* ($r_{bar} = 0.63$, EPS = 0.89) respectively in the dry and humid savanna zones were similar, indicating a strong common environmental forcing of ring-width patterns of all trees.

When comparing the detrended time series of *A. africana* and *A. leiocarpus* in the humid and dry savanna zones, the correlation of RWI of *A. africana* and *A. leiocarpus* collected from the same sites was weak. Actually, we found a 1-year time lag of the tree ring patterns in some years (Fig. 5b). Nevertheless, correlation of *A. africana* and *A. leiocarpus* between the humid and dry savanna

zones (Fig. 5a) was strong as the species of the riparian habitats showed similar growth variability.

Species response to climatic parameters

Correlation of annual growth increments with precipitation

The annual growth index series of *A. africana* and *A. leiocarpus* were positively correlated with the annual average precipitation (Fig. 6). In the dry savanna, *A. africana* and *A. leiocarpus* responded strongly to precipitation in April, May, June and August. *A. leiocarpus* was positively correlated with June and August precipitation and negatively correlated with precipitation in April. The growth of *A. africana* was positively correlated with precipitation in May and negative in June.

In the case of the humid savanna, *A. africana* and *A. leiocarpus* generally showed a positive correlation with precipitation for most months, except for March. In both the humid and dry savanna zones, the quarterly precipitation values of the previous years had a weak correlation with *A. africana*, but a strong correlation with *A. leiocarpus*.

Correlation of annual growth increments with temperature

We observed a strong negative correlation between the detrended annual tree growth increments and temperature for both the humid and dry savanna zones (Fig. 7). In the dry savanna, *A. africana* and *A. leiocarpus* were correlated to temperature in January, April, August, September and November. In the case of the humid savanna, *A. africana* and *A. leiocarpus* were strongly correlated to temperatures in January, February and April.

Correlation of detrended tree annual growth increments with sea surface temperature

The study observed a non-significant negative correlation between precipitation and temperature data of both Ejura

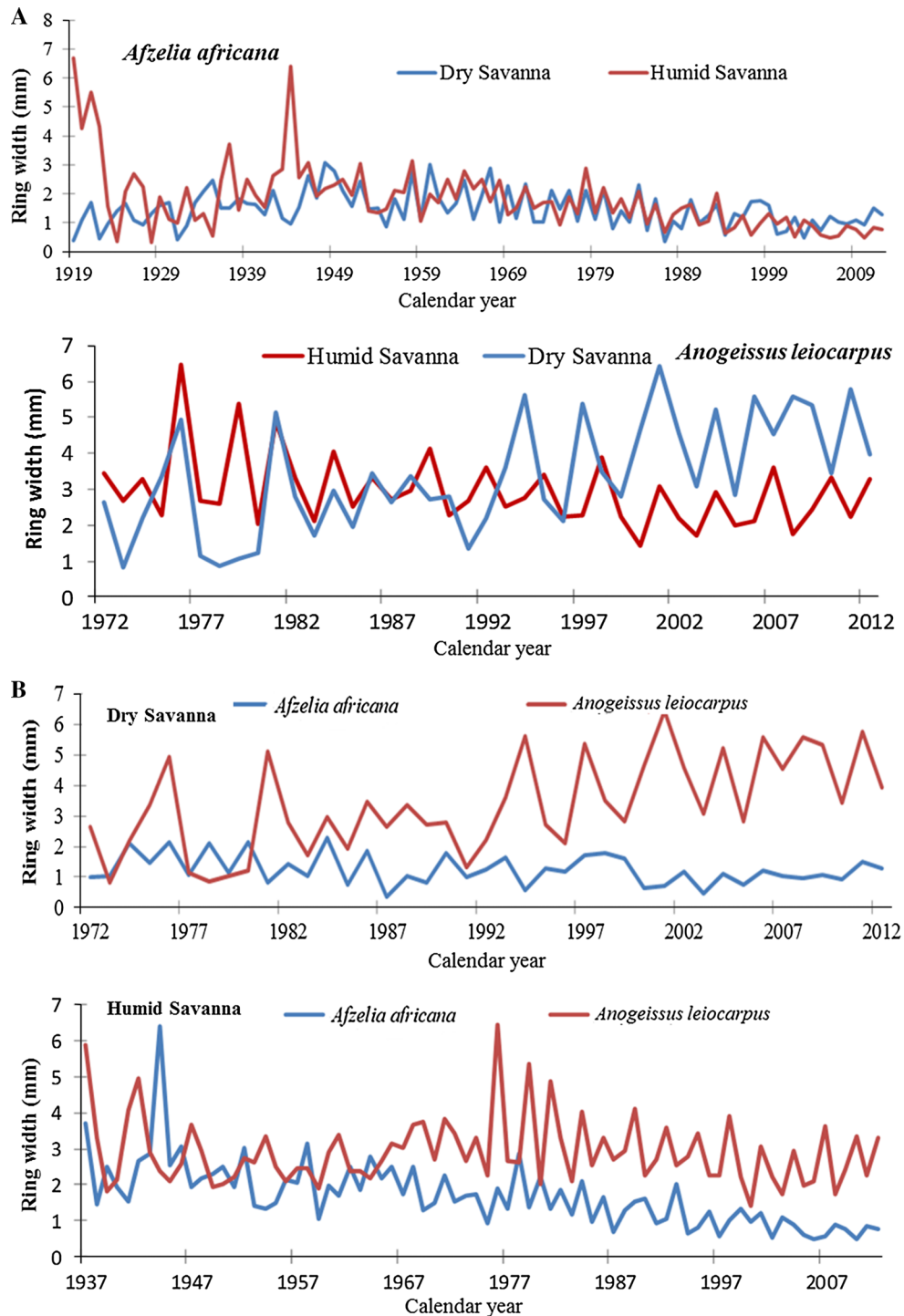
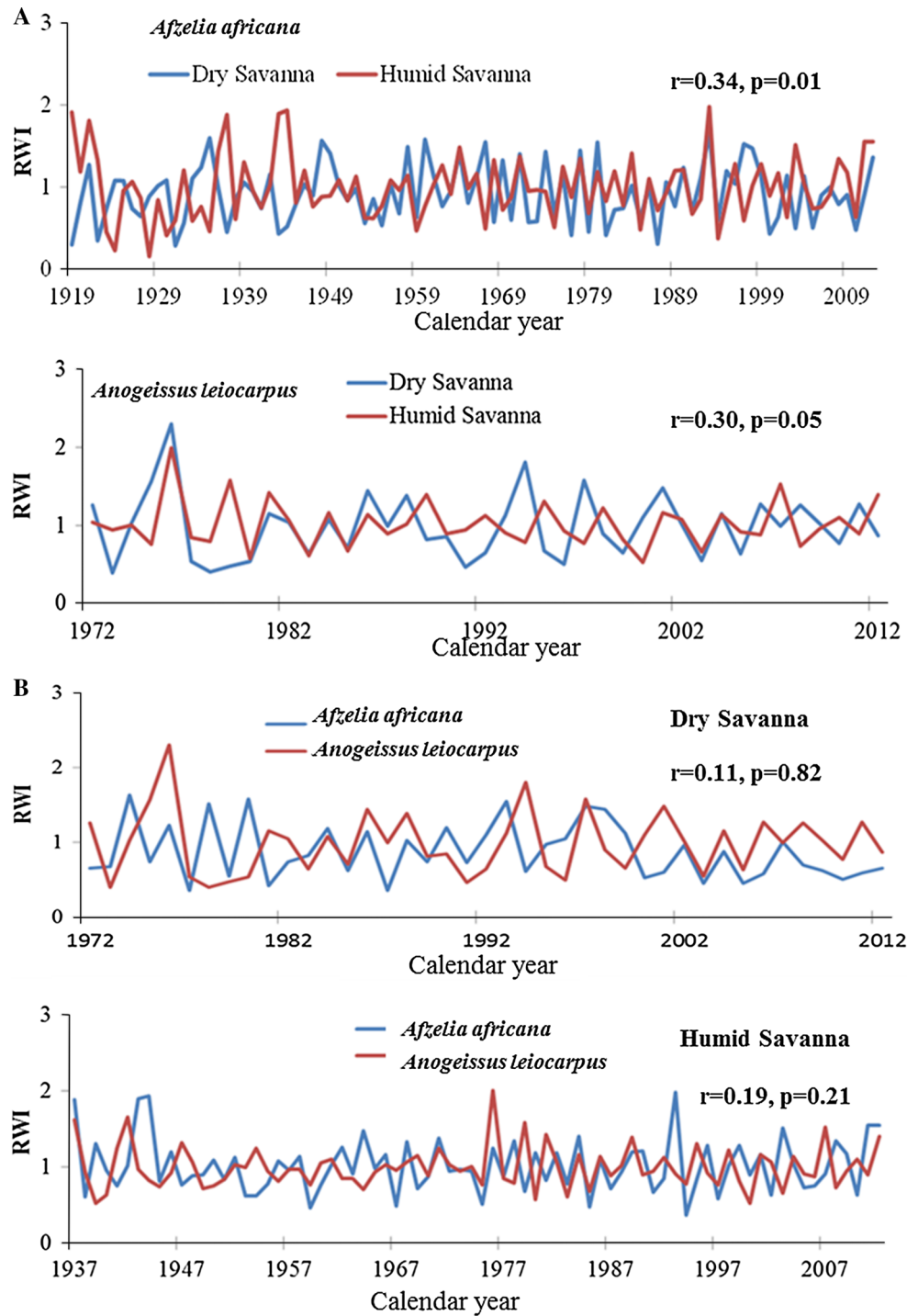


Fig. 4 Comparison of ring widths of *Afzelia africana* and *Anogeissus leiocarpus* in the dry and humid savannas zone of Ghana

($r = -1.41$, $p = 0.33$) and Navrongo ($r = -0.13$, $p = 0.56$) weather stations. There was a weak positive correlation of mean annual precipitation data from Ejura ($r = 0.31$, $p = 0.03$) and Navrongo ($r = 0.33$, $p = 0.04$) weather stations with annual SSTs from 1961 to 2012. Similarly, mean annual maximum temperature showed

highly significant correlations with SSTs for Ejura ($r = 0.59$, $p = 0.00$) and Navrongo weather stations ($r = 0.51$, $p = 0.00$). In contrast, the annual growth index (RWI) of the two species from the humid and dry savanna zones showed significant negative correlations with the annual SST (Fig. 8). In both the humid and dry

Fig. 5 Correlation coefficients of detrended growth chronologies (RWI) of *Azelia africana* and *Anogeissus leiocarpus* in the dry and humid savannas of Ghana



savanna zones, *A. africana* was more sensitive to inter-annual SST changes than *A. leiocarpus*. *A. africana* showed strong negative correlation patterns in the equatorial Atlantic as well as in the Pacific and the Indian Oceans. The correlation of SSTs with growth of *A. leiocarpus* from the humid savanna was slightly negative. The correlations of SSTs with *A. leiocarpus* of the dry savanna were only significant in the Pacific and Indian Oceans.

Discussion

Wood anatomical features

A. africana (evergreen) and *A. leiocarpus* (deciduous) in both the humid and dry savanna zones (Fig. 3) showed distinct growth rings resulting from the periodicity of growth dormancy induced by seasonal precipitation

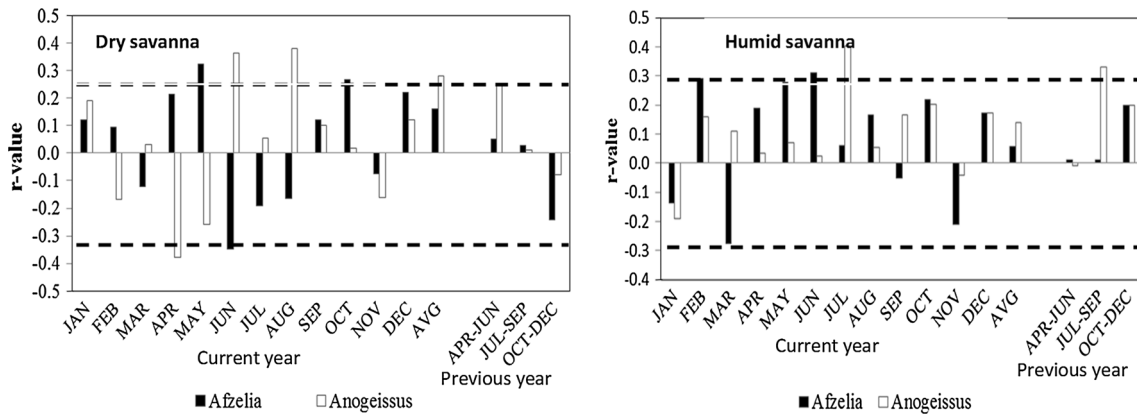


Fig. 6 Correlation of detrended annual growth increments of *A. africana* and *A. leiocarpus* from the dry and humid savanna and precipitation. The variables used are monthly precipitation data

(January to December) of the current and previous years as well as yearly average (AVG) for each savanna type. Dashed horizontal lines indicate significance ($p \leq 0.05$)

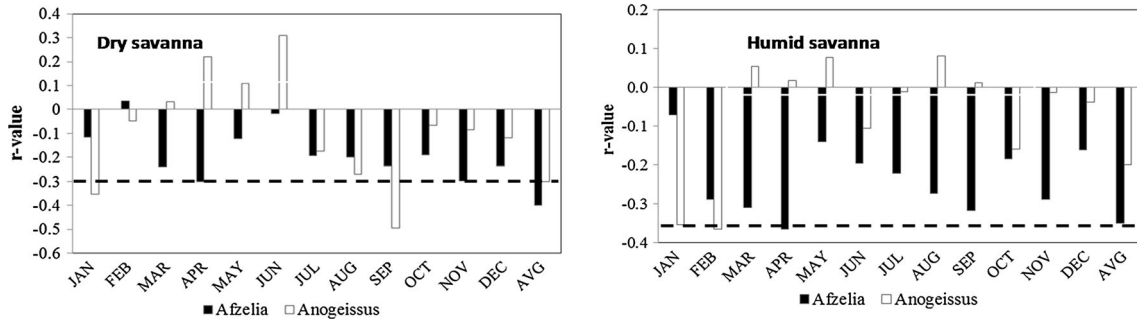


Fig. 7 Correlation of detrended annual growth increments of *A. africana* and *A. leiocarpus* from the dry and humid savanna to maximum mean monthly temperature (January to December) and

yearly average (AVG) data of climatic stations of each savanna types. Significance levels are shown as dashed lines ($p \leq 0.05$)

patterns with a distinct dry season (Schöngart et al. 2006). A dry season of more than 3 months with less than 60 mm of monthly rainfall is found to be sufficient to invoke cambial dormancy (Gebrekirstos et al. 2008). Generally, during the dry season, when plant water potential reaches the permanent wilting point, deciduous species shed their leaves. At this period both evergreen and deciduous species enter a state of cambial dormancy, which implies formation of visible growth boundaries (Gebrekirstos et al. 2008). Previous studies in Benin and Cote d'Ivoire have also found the formation of growth rings in *A. africana* and *A. leiocarpus* and other tropical savanna tree species (Schöngart et al. 2006).

The growth rings of *A. africana* (Fig. 3) marked by parenchyma bands are more distinct than those of *A. leiocarpus* formed by tangential bands of fibres. Their distinctiveness is controlled by the differences in wood anatomy which are defined by the genetic constitution of the species (Gebrekirstos et al. 2008). On the one hand, the primary function of parenchyma is starch storage for bridging the dry season. Parenchyma bands can promote

conduction when growth is renewed and the provision of starch can support rapid flushes of growth, flowering, and fruiting (Schöngart et al. 2006). On the other hand, fibres provide mechanical support and stability to the tree. The vessels grouping of *A. africana* and *A. leiocarpus* indicates a special adaptation of the species that facilitate transportation of water. In contrast to *A. leiocarpus*, *A. africana* maintains large vessels for the transportation of a large volume of water. *A. leiocarpus* maintained a higher number of smaller sized vessels in order to ensure sufficient transportation of water and minerals for tree growth while at the same time minimizing the risk of cavitation during the dry season (Gebrekirstos et al. 2008; Tomlinson et al. 2014).

Cross-dating

The successful cross-dating of ring width patterns of individuals of the same species (*A. africana* and *A. leiocarpus*) in the humid and dry savanna zones were indications that one ring is formed per year and that a common

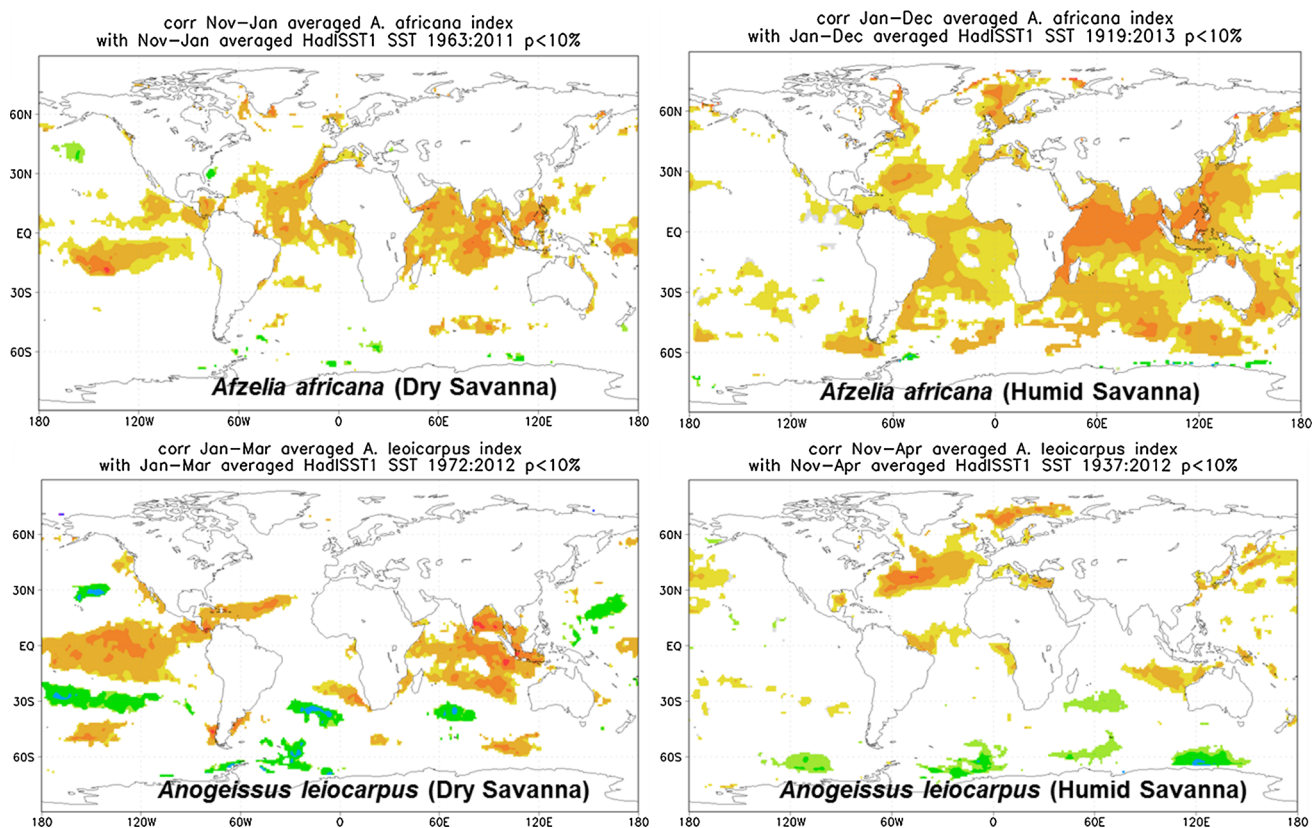


Fig. 8 Spatial correlations of detrended annual growth increments of *Afzelia africana* and *Anogeissus leiocarpus* of the dry savanna to sea surface temperatures (SSTs). Scale bars show correlation coefficients with a significance level ≤ 0.05

environmental factor (climate) strongly influences tree ring formation. The GLK and t values (Table 1) of the cross-dating process in this study were above the threshold generally applied in dendrochronology in temperate and boreal regions ($t > 3.5$ and $GLK > 70\%$) (Trouet et al. 2010). The high EPS of the chronologies of *A. africana* (HS = 0.94, DS = 0.90) and *A. leiocarpus* (HS = 0.89, DS = 0.92) in both the humid and dry savanna zones exceeded the recommended threshold of 0.85 (Wigley et al. 1984). This means that the chronologies of both species in both environments are reliable, sufficiently well replicated and show consistency in the ring-width variations found among the trees.

The significant correlations of the standardized time series of both *A. africana* and *A. leiocarpus* trees between the humid and dry savanna zones (Fig. 5a) suggested that the growth of the species is influenced by a similar climatic factor that controls precipitation in the Volta basin of Ghana, which is the movement of the inter-tropical convergence zone (ITCZ) (Schöngart et al. 2006). ITCZ is the inter-phase of two air masses: the North-East Trade Winds and the South-West Monsoons. The North-East Trade Winds, known as the Harmattan, blow from the interior of the African continent and are dry and dusty. In contrast, the

South-West Monsoons blow over the seas and are moist. ITCZ moves northwards and southwards across the study area from about March to October when precipitation is received in the region (Odekunle and Eludoyin 2008; UNEP-GEF 2012).

The weak correlation between ring-width variations of *A. africana* and *A. leiocarpus* at the same site (Fig. 5b) could be attributed to differences in water use strategies resulting in different responses to local climatic conditions. Although species specific rooting depth ranges were not reported in the literature, Hasselquist et al. (2010) indicated that evergreen species of Mexico have the capacity to use deeper ground water to overcome seasonal water limitation than deciduous trees. Similarly, Gebrekirstos et al. (2006) from Ethiopia and Jackson et al. (1995) and Meinzer et al. (1999) from Panama showed that evergreen species tap deeper water sources compared to deciduous species.

Radial growth

The higher mean annual growth of *A. leiocarpus* (deciduous) compared to *A. africana* (evergreen) in both savanna types (Table 1, Fig. 4b) may be explained by its high specific leaf area to maximise light interception and higher

nitrogen concentration per leaf unit, allowing for higher photosynthetic rates (Ruiz-Robledo and Villar 2005). These factors coupled with the intensification of precipitation regimes in recent times (since 1990s) (Descroix et al. 2009; Panthou et al. 2014; Nka et al. 2015) could have contributed to the sudden rise in the growth of *A. leiocarpus* during the period between 1992 and 2012 (Fig. 4). Generally, the deciduousness of plant species is a strategy to avoid drought stress and then maximize resource capture during a short growing season. Deciduous species normally have high root water contents and such water storage in roots has been found to increase drought survival (Poorter and Markesteijn 2008). Furthermore, deciduous species allocate substantial carbohydrate resources as storage in their roots to support seasonal regrowth at the expense of allocation to leaf mass (Poorter and Markesteijn 2008). The evergreen *A. africana* however, needs high biomass investment in enduring organs, and has to minimize cavitation and transpiration in order to extend the functional longevity of its leaves to persist under dry conditions (Tomlinson et al. 2014).

The lack of significant differences in the mean growth of *A. africana* between the humid and dry savanna zones (Gebrekirstos et al. 2008) and the high growth rate of *A. leiocarpus* in the dry savanna in comparison to the humid savanna (Table 1, Fig. 4a) is an indication that both species can reach high growth rates under suitable water conditions. Tomlinson et al. (2014) indicated that species in drier environments tend to have small leaf sizes which result in thinner boundary layer and therefore allow greater vapour pressure for photosynthesis and greater sensible heat loss. The smaller leaf size also allows a species to precisely adjust its leaf area under variable water supply conditions at low cost by rapidly dropping or producing leaves. Furthermore, dry savanna species are known to have higher leaf phosphorus and potassium contents for controlling the turgidity of stomatal guard cells that regulate gas exchange and transpiration through the stomata. Increased nutrient concentrations may allow trees to close down water loss rapidly under low water conditions. Maintaining cellular turgor through increased solute concentration can also help plants to cope with water stress. The lower growth rates of *A. leiocarpus* in the humid savanna may also be a result of competition of the species with others for sunlight in that comparably dense forest stands (Fichtler et al. 2004; Gebrekirstos et al. 2008; Niles et al. 2010).

Climate-growth relationships

The growth of *A. africana* and *A. leiocarpus* in the dry and humid savanna showed positive correlations with annual mean precipitation (AVG) (Fig. 6) because precipitation is important for maintaining high water levels of rivers and

groundwater recharge for tree growth. There were however, variations in the response of the species to monthly precipitation values. The two species primarily showed positive correlations with some of the months between May and October because those months fall within the rainy season where plants are photosynthetically active. Anyomi et al. (2007) also reported significant positive correlation of the growth rings of *Tectona grandis* with rainy season precipitation for the savanna zone in Ghana. A second feature in the precipitation correlation function (Fig. 6) is the negative growth response of *A. africana* for both the humid and dry savanna zones during the rainy season months of June and May, when the continuous rains may result in flooding of the riparian area. According to Schifman et al. (2012), flooding creates a subsidy of high water and nutrient availability to individual terrestrial plants in riparian forests. Conversely, long-term soil moisture saturation induces soil anoxia, which limits nutrient availability and gas exchange for plants and consequently hinders the growth of trees. Growth of the previous year had little influence on the growth of the following year of the riparian trees. Instead, they were much more sensitive to environmental conditions during the current growing season.

Temperature (Fig. 7) principally had negative correlations with the growth of *A. africana* and *A. leiocarpus* because plant transpiration and respiration increase with increasing temperature, resulting in a higher loss of assimilated carbon as a source of energy (Fichtler et al. 2004; Schöngart et al. 2006). During very dry periods the reduced water availability cause stomata closure to reduce excessive transpiration and consequently a reduction in photosynthetic capacity and growth. The response of tree growth to temperature was pronounced in the humid savanna with the strongest effect recorded within the dry season between January and April. Anyomi et al. (2007) however, reported positive effects of temperature and sunshine hours during the rainy season on the growth of *Tectona grandis* in the same savanna zone. This relationship was not surprising given that trees are photosynthetically active during the rainy season.

Sea surface temperatures (SST) are seen as the one of the best climate predictor variables. Consequently, tropical Atlantic SSTs account for the largest proportion of the variability observed in West African precipitation (Odekunle and Eludoyin 2008). In spite of this, SSTs had a weak positive correlation with precipitation amounts at the climatic stations Ejura and Navrongo in the humid and dry savanna zones of Ghana, respectively (Fig. 8). According to Balas et al. (2007), the positive effect of warm SSTs on precipitation is strong in coastal areas and weakens further inland. Regional SSTs however, showed a strong negative correlation with the growth of *A. africana* in both the humid

and dry savanna and even with little effect for *A. leiocarpus* in the two savanna types. On the one hand, flooding resulting from excess precipitation limits plants growth (Schifman et al. 2012). On the other hand, the negative correlation of tree growth with Pacific SSTs is explained by precipitation deficits in West Africa during warm Pacific SSTs; implying reduction in tree growth (Schöngart et al. 2006; Odekunle and Eludoyin 2008). Tree growth also revealed a negative link with Indian Ocean SSTs. This is in accordance with the results of Balas et al. (2007) who observed a growing importance of the Indian Ocean in controlling rainfall variability in the West African sub-region. Tropical-extra tropical climate links have been suggested by Deser et al. (2004) and D'Arrigo et al. (2005) by the movement of the Gulf stream that distributes heat across the globe, and by the El Niño-Southern Oscillation (ENSO) that causes torrential rainfall in parts of South America and droughts in the sub-Saharan Africa during El Niño events (Schöngart et al. 2006; Gebrekirstos et al. 2008).

Conclusions

The annual nature of the tree rings of *A. africana* and *A. leiocarpus* and the possibility of cross-dating confirms the first hypothesis of this study. This implies that there is a high potential for dendrochronological studies of riparian trees in the humid and dry savannas zones of Ghana. Although species specific, the correlation patterns of local precipitation and temperature with the growth of the trees is in agreement with the second hypothesis of our study. These findings suggest that there are opportunities for climate reconstruction and future projections of the impact of climate change on riparian ecosystems using tree rings as proxies.

Author contribution statement E. A. Boakye data collection, analysis and drafting of manuscript, A. Gebrekirstos research design, data analysis, development and finalization of manuscript, D. N. Hyppolite research design and data collection, V. R. Barnes research design, data collection and development of manuscript, F. N. Kouame research design, data collection and development of manuscript, D. Kone development of manuscript, S. Porembski research design and development of manuscript, A. Bräuning research design, data analysis, development and finalization of manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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