Effects of flow alteration on Apple-ring Acacia (*Faidherbia albida*) stands, Middle Zambezi floodplains, Zimbabwe

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ABSTRACT

The impounding of the Zambezi River by Kariba dam has regulated the river discharge of the Middle Zambezi river. This has been implicated in the failure of regeneration of *Faidherbia albida* in the downstream flood plain. This study aimed (1) to assess the effect of the altered flow regime of the river on the establishment and growth of *F. albida* on the Middle Zambezi floodplain and islands and (2) to test the potential of dendrochronology in detecting the age and long-term growth rates of *F. albida* in response to flow regime.

Results indicated an uneven age distribution of *F. albida* stands on relatively 'new islands', dominated by young trees, while the floodplain and the 'old island' exhibited an even-aged stand but with a lack of regeneration, and a dying-off of older trees. The lack of *F. albida* establishment on the floodplain was linked to the decreased occurrence of flooding events, associated with a decrease in alluvial deposits, soil moisture and groundwater recharge. These effects may be enhanced by impact from browsers on regeneration of trees. Tree-ring analyses revealed the presence of distinct annual growth rings in *F. albida* and the applicability of dendrochronology for estimating *F. albida* population dynamics. The trees on the 'new islands' are younger and grow faster than those on the floodplain. Lack of competition and possible favourable moisture conditions suggest beneficial conditions for establishment and growth of the trees on the islands. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS   dam-impact; dendrochronology; *F. albida*; floodplain ecosystem; flow regime; Middle Zambezi; regeneration; stand structure

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INTRODUCTION

The construction of dams to meet human needs, such as water, energy and food, modify the natural flow of rivers, decrease peak flows, floodplain inundation and downstream sediment supply (Attwell, 1970; Shafroth *et al.*, 2002; Elderd, 2003). Changing the hydrological character of rivers impacts biogeochemical, physical and biotic interactions (Poff *et al.*, 1997; Naiman *et al.*, 1999; Thoms, 2006) and the livelihoods of rural communities dependent on ecosystem services (Ncube *et al.*, 2012).

Flooding regimes are central in determining the spatial and temporal dynamics of floodplain ecology. Changes in river flows, water quality and sediment transport can alter habitat and the germination and growth of riparian vegetation (Elderd, 2003; Mallik and Richardson, 2009; Xiaoyan *et al.*, 2010). Since the construction of the Kariba

dam in 1958, the ecological function of the Middle Zambezi floodplains has been reported to be deteriorating (Attwell, 1970). One notable observation attributed to the effects of the dam is the failure of *Faidherbia albida* trees to regenerate on the floodplain in the last few decades (Dunham, 1989a), although young trees are observed on the islands within the river channel.

F. albida, a riparian tree species native to the Middle Zambezi floodplains, has a so-called reverse phenology, with leaves in the dry season that are shed in the wet season (Barnes and Fagg, 2003). Dry season growth relies on uptake of water from deep soil layers, making the tree a facultative phreatophyte (Roupsard *et al.*, 1999). *F. albida* can develop a deep tap root of up to 30 m to exploit groundwater (Barnes and Fagg, 2003). Establishment of *F. albida* seedlings requires ample soil moisture during early growth to enable rapid tap-root development into groundwater before surface layers dry out. The specific growth pattern of the species makes it an important source of forage for browsers, when other foliage during the dry season is limited (Attwell, 1970; Du Toit, 1984).

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To better understand forest ecosystems, dendrochronology provides a method to estimate tree age, long-term radial growth dynamics and age–diameter relationships (Fichtler *et al.*, 2003; Rozendaal and Zuidema, 2011). Variation in ring width of riparian trees can help understand the impact of stream-flow regulation on tree growth and the environmental factors driving radial growth (Wils *et al.*, 2010). Dendrochronology requires the presence of distinct annual rings, which are mostly indicated by specific wood-anatomical structures indicating ring boundaries (Worbes and Fichtler, 2011). The distinctness of growth rings largely depends on the seasonality of growth-determining factors and especially the length of unfavourable growth conditions leading to cambium dormancy (Worbes, 2002). Periodic growth stops, especially when related to leaf deciduousness, are likely to result in distinct growth boundaries. The ease at which rings can be detected varies among species and their specific wood anatomy and is often complicated by phenomena such as missing, wedging or double rings (Gourlay, 1995; Eshete and Ståhl, 1999; Wils *et al.*, 2009, 2011).

The work presented here aims to understand the effect of the altered flow regime downstream of the Kariba dam (1958), on the *F. albida* stand structure on the Middle Zambezi floodplain and islands. The actual stand structure was assessed by recording tree height, diameter and density in plots on the islands and the floodplain along a transect perpendicular to the river. To assess the relationships between stand structure and browsers, we monitored the browser density along the same transect. Moreover, we tested the potential of dendrochronology for detecting age and growth dynamics of *F. albida* by investigating stem discs from four trees, two growing in the floodplain and two on the islands.

Study area and site conditions

The study was completed on the Mana floodplains and islands within the Zambezi river channel, about 150 km downstream of Kariba Dam (Figure 1). The floodplains are within Mana Pools National Park, a prime wildlife attraction in Zimbabwe, with high densities of browsers comprising mainly elephants (*Loxodonta africana*), impala (*Aepyceros melampus*) and buffalo (*Syncerus caffer*) (Zimbabwe Parks and Wildlife Management Authority, 2009). Within this area, the Zambezi River is characterized by a wide, shallow channel, with many mid-channel islands of varying age. These islands are both vegetated and non-vegetated, indicating their relative age. The total length of the floodplain is about 91 km, and the average width is approximately 3 km. Most islands are narrow and long, but some, such as the Chikwenya Island, with a maximum width of about 2 km, are wider.

The younger, and closest to the river, alluvial deposits of the floodplains are covered by *F. albida* woodland. Slightly higher parts of the floodplain support more diverse *Kigelia africana*, *Trichelia emetica* and *Lonchocarpus capassa* woodlands. Seasonally flooded channels are habitat for perennial species such as *Vetiveria nigritana* and *Setaria sphacelata* (Du Toit, 1984). The main vegetation types inland, beyond the floodplain, are *Colophospermum mopane* woodlands, mixed-species layered dry forests ('jesse bush') and various fairly open mixed-species deciduous woodlands.

Temperatures in this area range between 18 and 40 °C, averaging between 21 and 32 °C, with cool and dry winters from May to July, rising to 40 °C between August and October (Figure 2), that precede the October to April rainy season. Rain usually comes as short, intense thunder-showers, which are highly variable among years, with
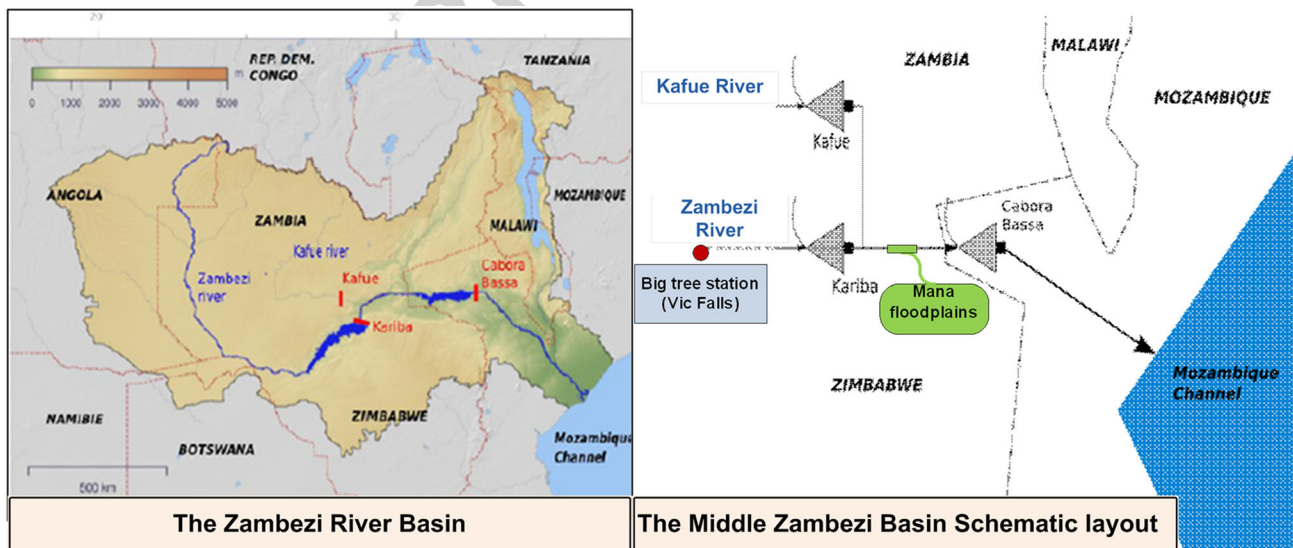

Figure 1. Location of Mana Pools National Park and Middle Zambezi Floodplains.
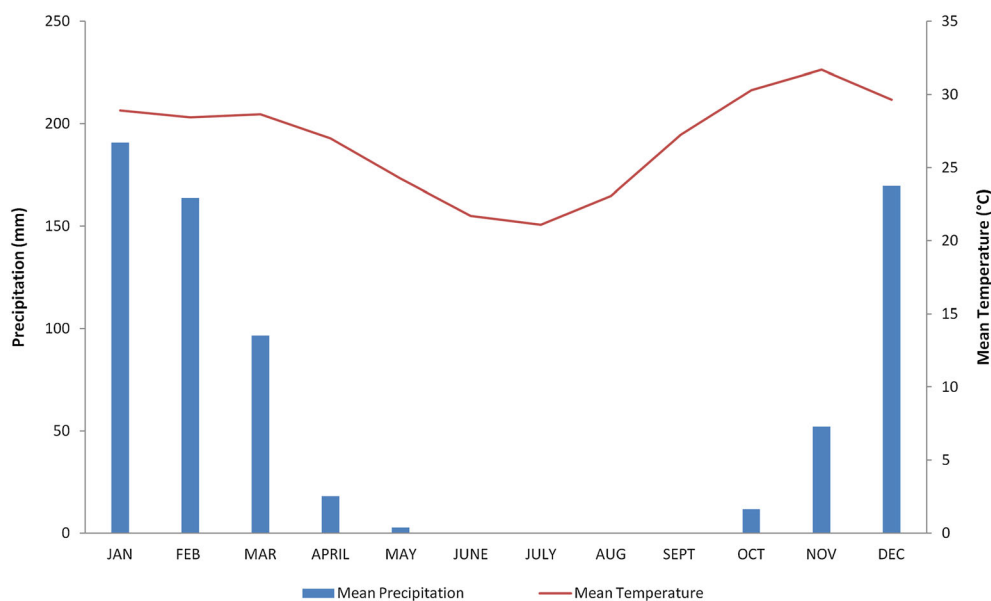
Figure 2. Climatic diagram for Mana Pools National Park.

annual means of about 750 mm at Mana Pools National Park, Nyamepi Camp (Zimbabwe Parks and Wildlife Management Authority, 2009).

Before the dam was filled, unregulated downstream flows steadily increased through the wet season, with two distinct high-flow periods annually. The lesser flood occurred around February and the higher flood, partly inundating the floodplain, occurred around April (Ncube *et al*., 2012). Since the filling of the dam in 1959, flows have been regulated for power generation purposes, through two power stations: Kariba North (established 1976/1977) and Kariba South (established 1960), respectively. Flooding events now depend upon the opening of the floodgates by the Zambezi River Authority, according to hydropower generation operating rules. The influence of these stations on downstream flows has been monitored using flow gauges (Zimbabwe Parks and Wildlife Management Authority, 2009). The consequence to the river in the Mana Pools area can be observed most clearly from around 1980 onwards where a more constant flow regime of around $1200 \, m^3 \, s^{-1}$ with occasional peaks representing spillage through the floodgates is evident. This trend is observed after Kariba North was established and in a period of low flow in the region (Ncube *et al*., 2012). This new regime is mismatched to the natural flooding regime (Attwell, 1970; Ncube *et al*., 2012).

METHODS

Stand structure sampling and data collection

Transects of equal width were established on Mana floodplains and islands within the channel perpendicular

to the river (Figure 3). Transects on the floodplain were 1·3 km long from the river bank, except transect 4 of 1·6 km, because of the absence of *F. albida* trees close to the riverbank, and transects 7 and 8 of 0·2 and 0·7 km, respectively, because the floodplain width is narrower here than at other sites. The distance between transects was determined by the distance between islands with *F. albida* trees.

Three $30 \, m \times 30 \, m$ vegetation plots were established on each transect. One plot was set on the island and two on the floodplain. Floodplain plots were separated equidistantly from each other along transects, except for transects 7 and 8. In each plot, tree species were identified, and the diameter of *F. albida* at breast height (dbh), 130 cm above the ground, was measured with a calliper. The height of the *F. albida* trees was measured using an electronic clinometer (Haglof Electronic Clinometer). Browsers sighted along the transect and surrounding visible areas were counted between 0700 h and 1700 h from 5 to 10 December 2011, according to the road strip count methodology for wildlife census (Dunham and Tsindi, 1984; Dunham, 1994). Tree diameters and heights from both island and floodplain sites were pooled into 10-cm-wide and 5-m-high frequency distribution classes, respectively. For all tree species, the frequency of occurrence was calculated as follows:

$$\text{Species Frequency} = \frac{\text{No. of plots in which a species occurs}}{\text{Total number of plots}} \times 100$$

The species distribution of the floodplain plots closest to the river was compared with those found in the island plots.
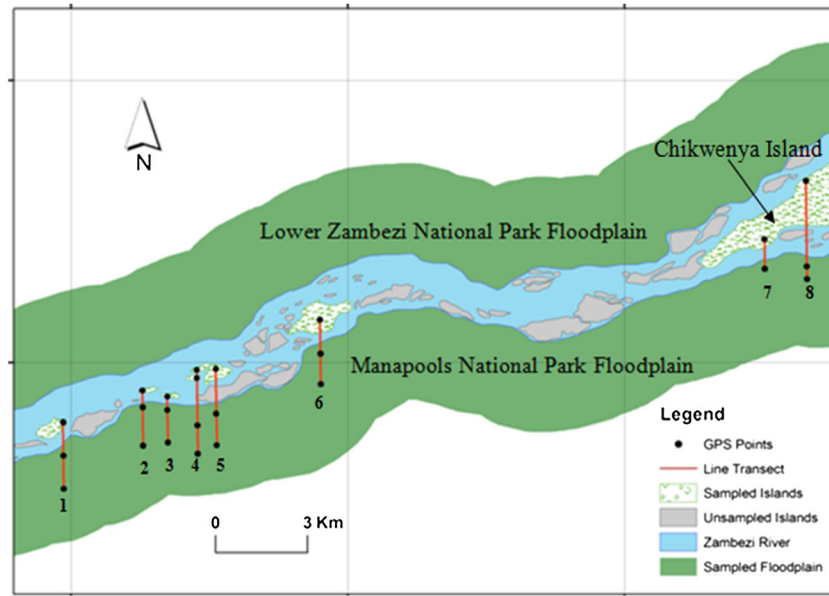
Figure 3. An illustration of the layout of the sampled transects on the Middle Zambezi floodplains and islands within the river channel. Dots represent the position of the sampled plots, and red lines represent the belt-transect.

The relative frequency of browsers sighted was calculated as follows:

$$\text{Relative Frequency} = \frac{\text{Frequency of a species}}{\text{Total frequency of all species}} \times 100$$

Dendrochronology sampling and data collection

To limit the impact of the study within a protected national park, only eight-stem discs of *F. albida* were collected from four fallen trees: two from the island and two from the floodplain. Two-stem discs with a thickness of about 5–7 cm k; were collected from each tree. One disc was cut at the base of the tree below 50 cm height and another at about 2 m height from the base. The discs were air dried for 6 weeks. Two slices, approximately representing half of the disc, were extracted to reduce weight during transportation to the laboratory.

Disc slices were mechanically sanded, using sandpaper of increasing grit size up to a grade of 800, until a smooth finish was achieved. The wood-anatomical structure was screened macroscopically for concentric growth boundaries, which were subsequently marked on the discs. Ring widths were measured along three radii per stem segment to the nearest 0·01 mm using a LINTAB measuring table associated with the program TSAP (both RinnTech, Heidelberg). Tree ring series were visually cross-dated among radii of the same tree to produce ring-width mean ring-width series for every individual tree, and age was determined. The mean curves of the two floodplain and island trees were mutually cross-dated. Ring-width series were statistically described to assess basic information on growth

level and variation (TSAP-Win™, Rinntech). These data were then directly related to available river discharge records for the Zambezi (Main stem flow gauge: 1907–1958 Victoria Falls, 1958–2008 Kariba; Kafue flow gauge: 1907–2008 Kafue (Zimbabwe Parks and Wildlife Management Authority, 2009)). Plotting these results together, correlations and trends could be investigated. Additionally, for the four dendro-dated trees, age–diameter relationships were estimated using cumulative growth curves.

RESULTS

F. albida stand structures

The frequency distribution of *F. albida* dbh on the floodplain (Figure 4a) indicates an absence of young trees as no trees were sampled with a diameter below 50 cm. The majority of the floodplain trees dbh were concentrated within 70 to 120 cm, with a declining frequency of trees with dbh above 120 cm. Mean dbh was 100 (±30 SD) cm. The average density of trees per sampled plots was 3 (±1 SD), equivalent to 33 stems ha^{-1}.

Diameter and height distribution results for islands are presented in two parts. Results for the 'old island', Chikwenya Island, are shown separate from the six relatively 'new islands' (Figure 3). Chikwenya Island showed more similarities in *F. albida* stand structure to the floodplain sites than the new islands. Chikwenya Island had no *F. albida* trees with a diameter of <20 cm (Figure 4b). Trees were concentrated within the 20–60 cm range with the majority of trees within the 51–60 cm class. Tree density was eight stems per plot (89 stems ha^{-1}), which was higher than on the floodplain.
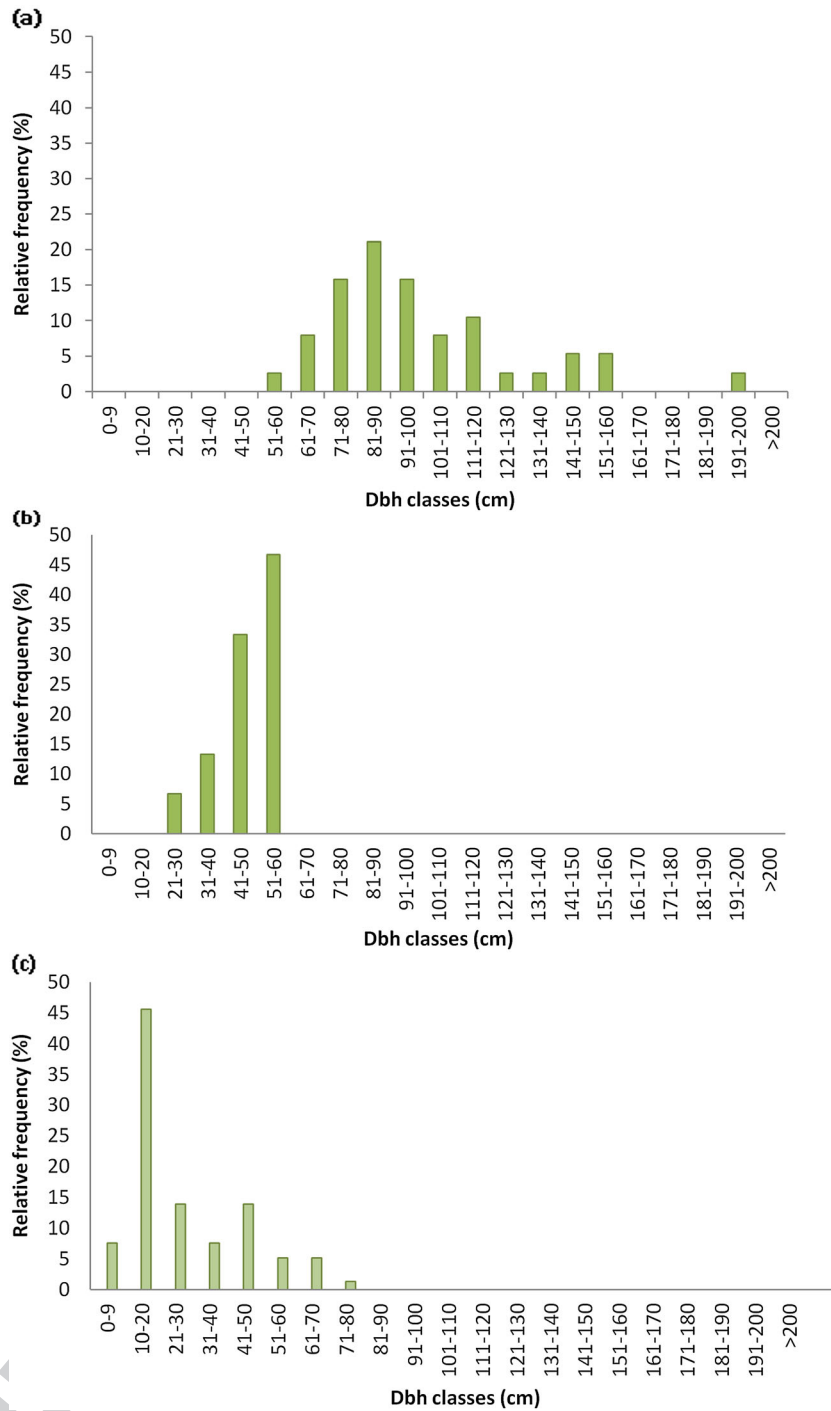
Figure 4. Dbh size distribution of *F. albida* trees on (a) Mana floodplains, (b) Chikwenya Island (old island) and (c) Middle Zambezi islands (new islands) (December 2011). $n = 38, 15, 79$.

Conversely, diameter distribution of the new island trees comprised many small and a few big trees (Figure 4c), reflecting a developing young tree stand and successful post dam regeneration. The majority of the trees were concentrated in the range of 10–60 cm, with the highest frequency occurring in the class 10–20 cm. The tree density on the new islands was higher than floodplain tree density, that is, 11 stems per plot (122 stems ha^{-1}).

Height distribution

The majority of trees on the floodplain were above 10 m high, with 40% occurring within the distribution class

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F5 16–20 m (Figure 5a). The highest height recorded was 24 m, with no *F. albida* trees <6 m. Mean tree height on the floodplain was 17 ($\pm$4 SD) m. Chikwenya Island had no *F. albida* trees <6 m high (Figure 5b). The majority of trees were within the range of 16–20 m, and the highest recorded was 22 m. Height distribution on 'new islands' trees reflected a young stand, with the majority of trees (65%) within 0–5 m (Figure 5c). The remaining trees were >5 m high, with the tallest tree recorded of 14 m. The height distribution suggests an uneven-aged young stand, supporting the dbh distribution.

Species composition

F. albida was the most frequent species (Figure 6) recorded. **F6** On the floodplain, *T. emetica* and *Croton megalobotrys* were sub-dominants, and *Friesodielsia pavatum*, *K. africana* and *Cleistochlamys kirkii* are also present. On the islands, *T. emetica* and *Cassia* spp. were sub-dominants, with *Crombretum mossambicense* and *K. africana* also present.

Relationship between browsers and stand structure

The most frequent browsers sighted on the floodplain were buffalo and impala, which occurred with similar frequencies,
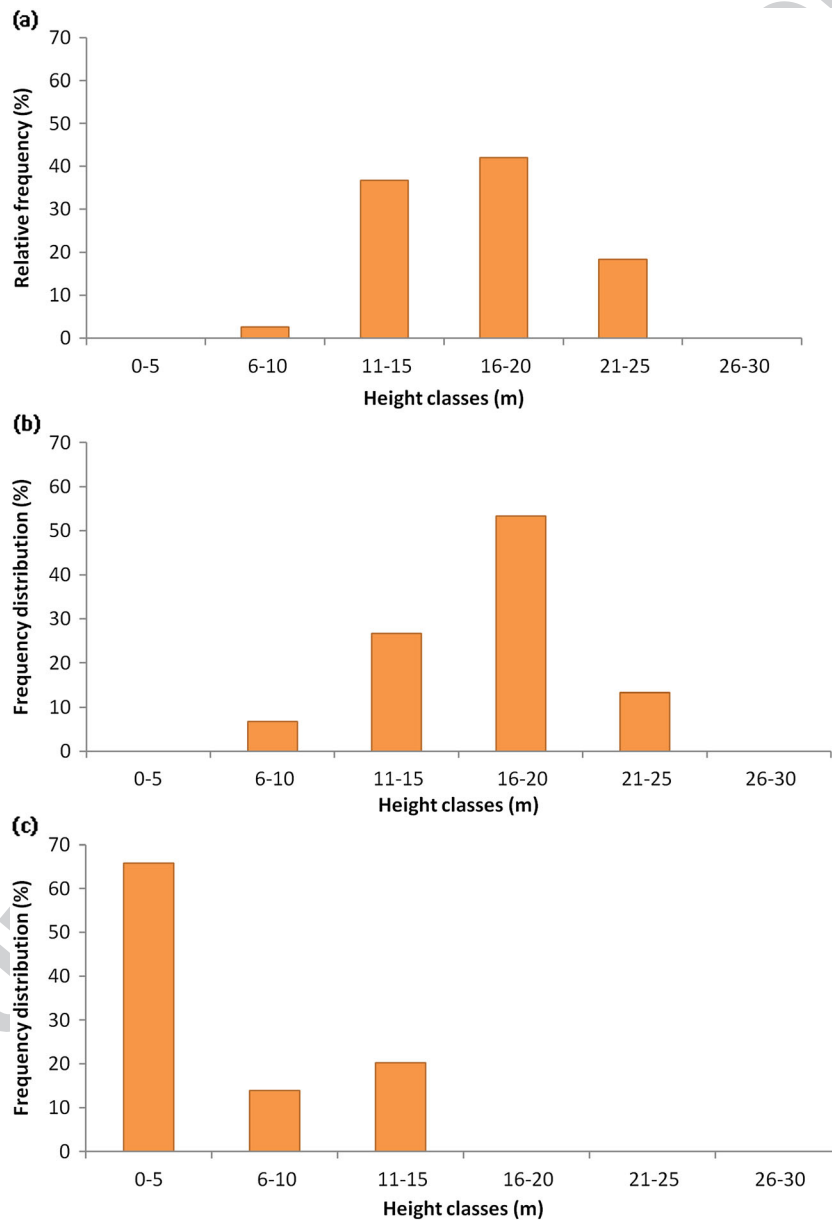

Figure 5. Frequency distribution of the height classes of the *F. albida* trees on (a) Mana floodplains, (b) Chikwenya Island (old island) and (c) Middle Zambezi islands (new islands) in December 2011. *n* = 38, 15, 79.
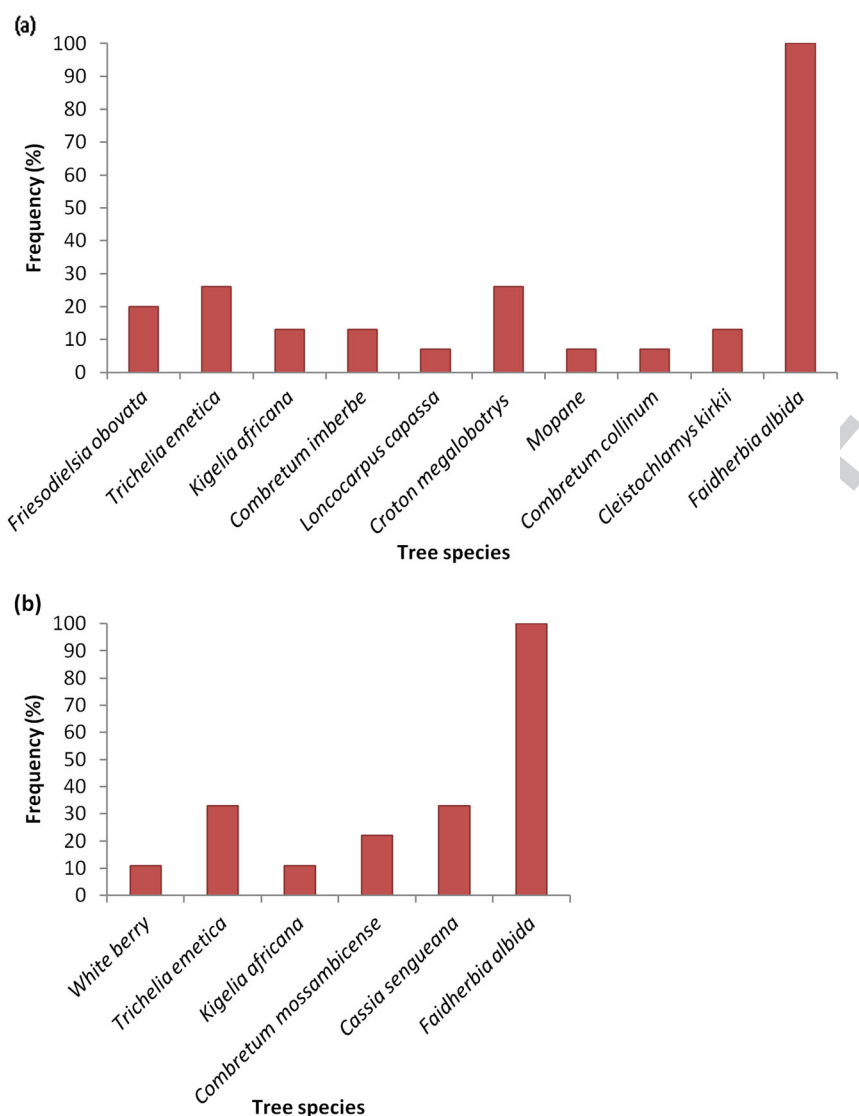
Figure 6. Frequency of occurrence of trees and shrubs on the sampled Mana floodplains plots (a) and Middle Zambezi islands plots (b) in December 2011. *n* = 8, 8.

of 40% and 38%, respectively (Figure 7a). Elephants were the third most frequent browser sighted. On Chikwenya Island, *Impala* had the highest recorded frequency (70%) followed by waterbuck (*Kobus ellipsiprymnus*) with 20% (Figure 7b). On the new islands, buffalo had the highest frequency (30%), but hippopotamus (*Hippopotamus amphibious*) (50%) and elephants (20%) were also common (Figure 7c). Almost every sampled tree at all sites showed signs of elephant damage. The majority of *F. albida* trees on the floodplain had debarking scars, whereas on the islands, the damage was mostly broken branches with a few debarking incidences.

Detection of growth rings and compilation of ring-width series

The sapwood of *F. albida* is yellowish beige, and older trees contain golden to dark brown heartwood. On the polished wood surface, alternating bands of dark fibre and light parenchyma cells are obvious (Figure 8). The water conducting vessels are embedded in the parenchyma bands, and the small rays are almost invisible. Growth rings are marked by a change in the spacing of tangential parenchyma bands in combination with decreasing thickness of the fibre bands in combination with a thin marginal parenchyma band, which is formed at the end of a growing season. This type of marker is described in Worbes and Fichtler (2011) as a combination of type B (marginal parenchyma bands) and C (recurring parenchyma and fibre bands of different width). In some cases, changes in the pattern of parenchyma bands were combined with variations in vessel distribution, especially in rings formed during the juvenile phases of the tree, that is, the first 20 rings around the pith. At the beginning of a growth ring,
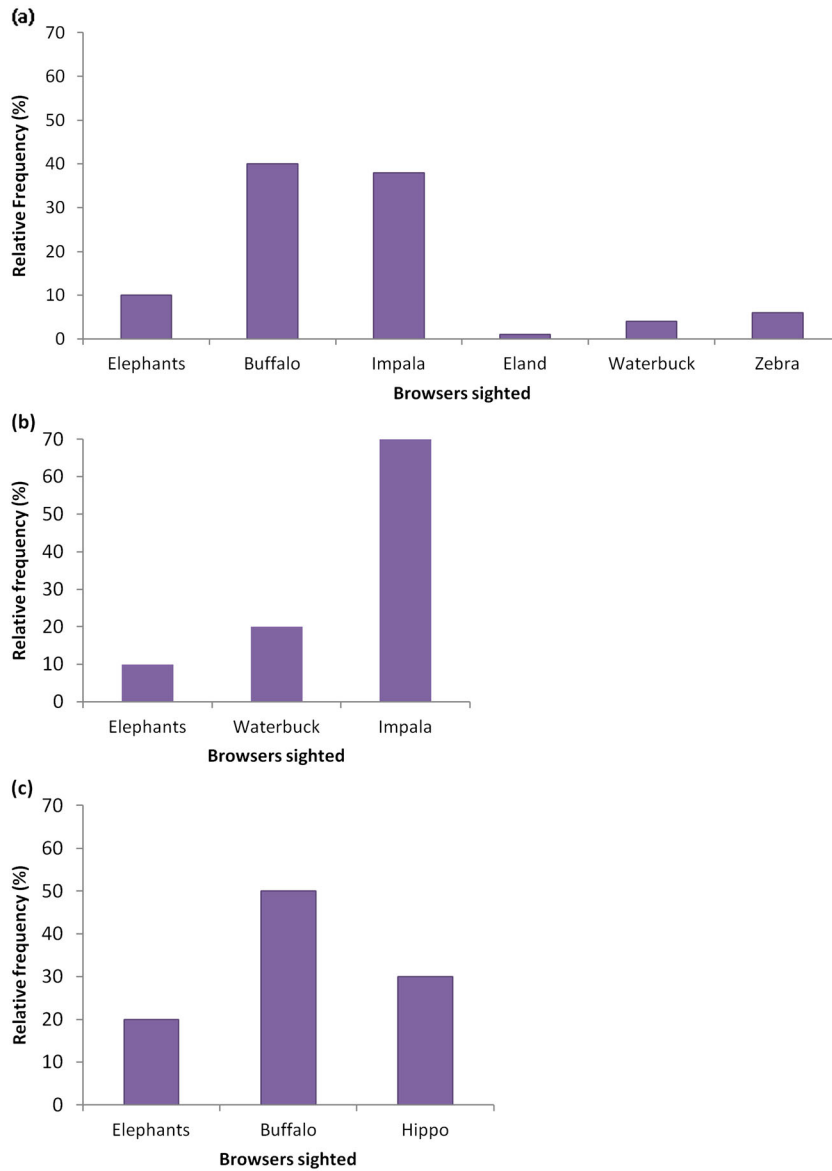
(a)

(b)

(c)

Figure 7. Relative frequency of browsers sighted on both the floodplain (a) and islands (b) during the collection of field measurements from 5 to 10 December 2011. $n = 98, 34$.
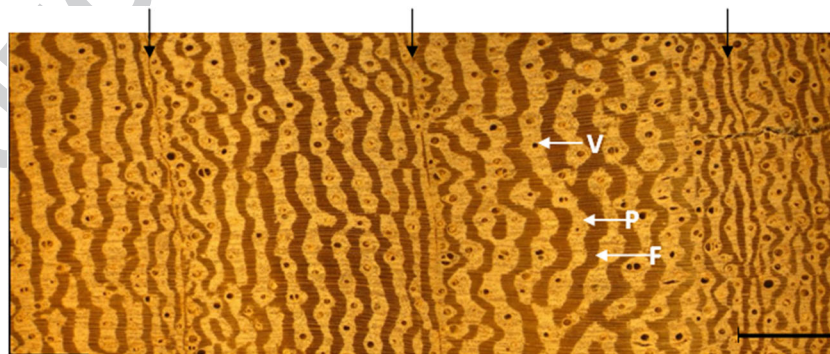

Figure 8. *F. albida* macroscopical; black arrows indicate annual ring boundaries, and white arrows indicate different cell types. F = Fibre, P = Parenchyma, V = Vessels. Black scale bar is 1 mm.

vessel density was highest with a decreasing trend towards the ring boundary.

The distinctness and width of rings can vary considerably within a growth layer around the circumference. Both young and old trees showed density variations, often referred to as double or false rings as well as partly missing or wedging rings. Ring wedging tended to be more frequent in older trees with narrow rings towards the outer parts of stem discs.

Ring-widths series of the three radii measured per tree could be crossdated. However, crossdating of mean curves of the two floodplain trees was difficult because of the generally low growth level of both trees resulting in a less pronounced annual variation in the ring-width pattern. The two island trees yielded short time series, which could not be crossdated.

Age determination and radial growth patterns of selected floodplain and island trees

From the ring-width series, it can be concluded that the two large floodplain trees with both having a dbh of 52 cm are about 103 and 84 years old, whereas the two island trees were very young, 16 and 10 years old, respectively (Table I). As stem discs are taken at 50 cm, ring counts had to be adjusted by 2 years, on the basis of the assumption that the fast initial radial growth also points to fast height growth. **T1**

The four investigated floodplain and island trees also strongly differ in average radial growth rate, with the younger island trees showing much fast growth. Radial growth rates of the island trees strongly exceed those of the juvenile growth of the floodplain trees (Table I, Figure 9). **F9** The low average annual growth rates of the older floodplain trees, that is, between 2·58 and 3·14 mm, are mainly attributed to an ontogenetic trend in radial growth. During the establishment and juvenile phase, both floodplain trees were growing fast, but over the last decade, ring width was noticeably lower, especially in floodplain tree 1 (Table I, Figure 9). However, it also becomes obvious that ontogenetic growth trends can differ between trees; in floodplain tree 2, the growth level abruptly declines after approximately 20 years of fast juvenile growth, whereas tree 1 shows a drop in growth level after about 50 years (Figure 9).

Table I. Sampling and chronology characteristics of *F. albida* on Middle Zambezi floodplains and islands.

Study site	Sample no.	Tree	Tree dbh (cm)	Age[a] (years)	Mean ring width (mm)	Standard deviation	Mean ring width first 10 years (mm)
Floodplain	2	1	52	103	2·58	1·91	5·07
		2	52	84	3·14	2·30	5·83
Islands	2	1	29	16	9·69	4·76	9·68
		2	13	10	6·48	6·88	6·48

[a] Tree age is estimated as number of counted rings plus 2 years to correct for sampling height of 50 cm.
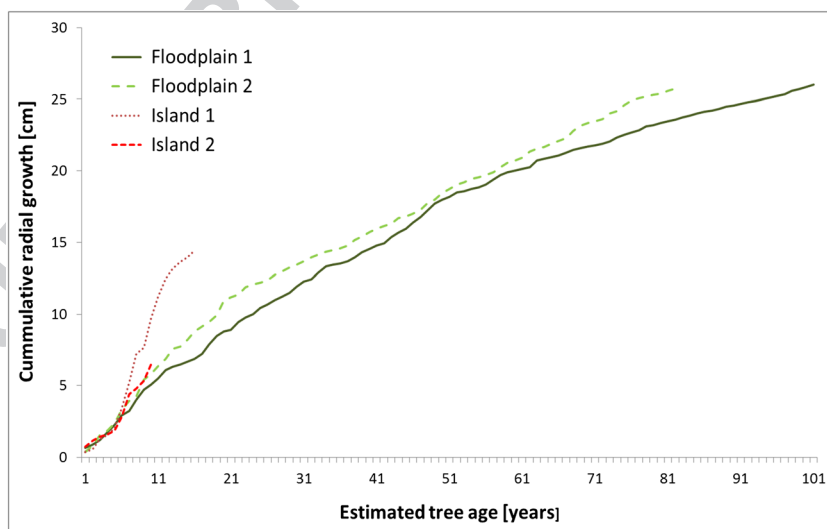

Figure 9. Tree age compared with cumulative stem radial growth of *F. albida* growing on Mana floodplains (floodplains 1 and 2) and Middle Zambezi islands (islands 1 and 2). Each line represents an individual tree.

F. albida radial growth dynamics

Mean growth rates (Table I) estimated for floodplain trees, trees 1 and 2, were 2·58 and 3·14 mm year^{-1}, respectively. Mean growth rates for island trees, trees 1 and 2, were 9·69 and 6·48 mm year^{-1}, respectively. For floodplain trees 1 and 2, mean growth rates for the first 10 years were 5·07 and 5·83 mm year^{-1}, respectively. Island trees 1 and 2 had 9·68 and 6·48 mm year^{-1}, respectively. Growth trajectories suggest that a 25-cm radius (50-cm diameter) of floodplain trees corresponds to trees of about 100 years old (96 years for tree 1 and 79 years for tree 2).

Relationship between radial growth and river discharge

Owing to the low sample size, no statistical analyses could be used to assess the relationship between environmental factors, including river discharge, and annual or decadal variation in radial tree growth. However, via visual comparison between patterns in ring-width series and river discharge, an indication can be observed between sudden changes in both records. During the pre-dam period between 1930 and 1950, a positive relationship between annual variation of ring width, especially of floodplain tree 2, and river discharge can be observed (Figure 10). However, this relationship declined a couple years before the dam was constructed in 1958. A lack of abrupt and synchronous changes in the two ring-width series does not implicate an influence of the changed flow regime after 1958, although there was a slight tendency of a gradual decrease in ring width in tree 1 (Figure 10).

DISCUSSION

F. albida stand structure

The absence of trees with small diameters and the dying-off of older trees indicated by the scattered occurrence of trees with large diameters on the floodplain indicate a forest stand lacking regeneration. Chikwenya Island has an *F. albida* stand structure similar to the floodplain with absence of trees in the lower dbh classes (0–30 cm) and in the lower height classes (0–10 m). However, unlike the floodplain, characterized by trees with large diameters, the highest dbh on Chikwenya was 60 cm (Figures 4 and 5). In contrast, the clustering of new islands' tree diameters within the lower class ranges signifies a young and regenerating forest (Bragg *et al.*, 2012). Island stands density was highest and with the lowest stand density observed on the floodplain. The floodplain density (33 stems ha^{-1}) was comparable to other studies (Roupsard *et al.*, 1999; Ndava, 2005; Ncube *et al.*, 2012), whereas the densities on the islands (Chikwenya and the new islands, 89 and 122 stems ha^{-1}, respectively) were significantly higher. This may be attributable to lower browsing pressure. *F. albida* tree can grow to heights of 30 m (Barnes and Fagg, 2003), but no sampled trees were taller than 25 m on the floodplain, implying this to be the maximum attainable height on this site, with some trees reaching senescence (Figure 5).

In this study, a floodplain tree of about 52 cm dbh was found to be around 100 years, indicating an annual growth rate comparable to those found in natural stands of Senegal
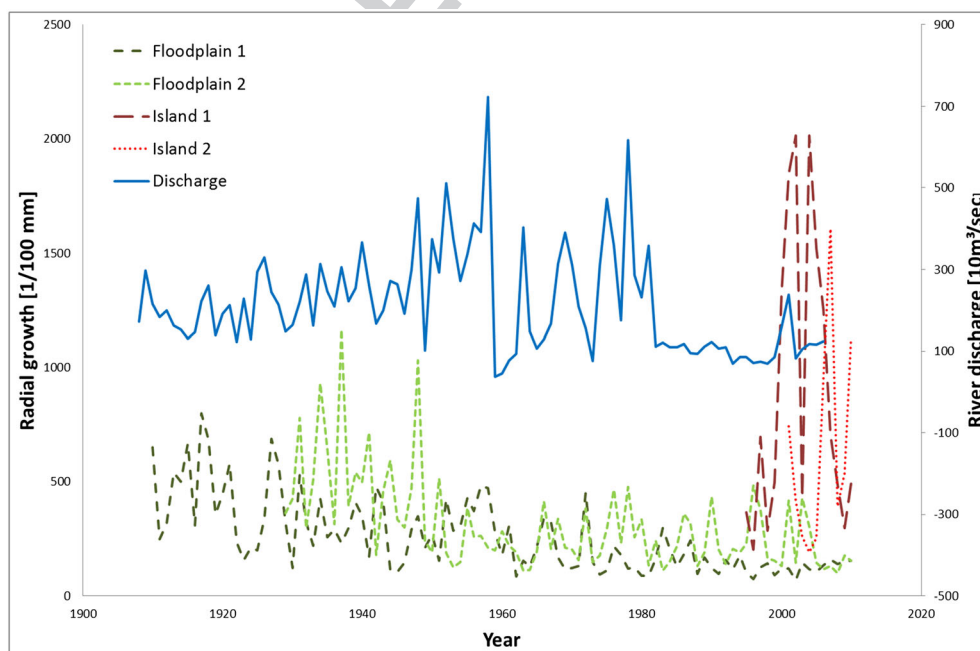

Figure 10. Tree-ring mean curves of the four sampled trees in comparison to Middle Zambezi river discharge.

by Mariaux in 1966 (Wood, 1989) and in Burkina Faso by Depommier and Detienne in 1996 (Barnes and Fagg, 2003) (Table I). An island tree with a dbh of about 29 cm was found to be 16 years old, which resembles an age–diameter relationship similar to those from agro forestry sites (Wood, 1989; Gourlay, 1995; Barnes and Fagg, 2003). Overall, sampled floodplain trees were older than the island trees, and island trees grew faster than the two investigated floodplain trees that grew in their juvenile phase (Figure 9). Growth rates of the island trees are comparable to managed sites, suggesting optimal conditions for establishment and growth. The age–diameter relationship found for islands tree is also comparable with the growth rate of the tree observed by several researchers and concurring with a consensus that the tree reaches senescence at about 80–100 years (Baumer, 1983; Sturmheit, 1990; Sterck *et al.*, 1991; Barnes and Fagg, 2003) and at diameters of about 200 cm (Fagg and Stewart, 1994). However, Barnes and Fagg (2003) considered that the tree can live to over 100 years, concurring with reports of *F. albida* trees in Zambia over 150 years (Wood, 1989) and of a tree that was noted in Libya by Oundey in 1822, which was still alive in the late 1960s (Wickens, 1969).

Relationship between browsers and stand structure

The floodplain site and Chikwenya Island, accessed easily by browsers, had an older age-stand compared with the more difficult to access islands, which also had good regeneration (Figures 7 and 9). In the dry season, browsers congregate on the floodplain because of its proximity to water and availability of forage (Dunham, 1994). Chikwenya Island is a permanent habitat of a browser population, whereas only a few animals cross to the rest of the islands, mostly during the dry season. Browsers mostly affect *F. albida* seedlings if cropped before they reach permanent groundwater, after which they can coppice from repeated cropping. Elephants have been documented to have high impact on *F. albida*. In Ruaha National Park, Tanzania, 40% mortality of the tree and lack of regeneration were attributed to high elephant population (Barnes and Fagg, 2003). However, in this study, despite almost every sampled tree showing signs of elephant damages, regeneration was taking place on the 'new islands', suggesting elephants might not be solely responsible for the lack of regeneration. In Chobe National Park, Botswana, the survival of *F. albida* seedlings in designated plots was negatively related to impala densities and unrelated to densities of other browsers such as elephants and kudu (Moe *et al.*, 2009). In this study, high impala densities were recorded on both the floodplain and Chikwenya Island. On Mana floodplain, however, Dunham (1994) reported a failure of *F. albida* regeneration in parkland protected from browsers. Although Barnes and Fagg (2003) suggest that *F. albida* cannot regenerate under

its own canopy, it is also known that *F. albida* is dependent upon browsers for seed dispersal because of the need for digestion of the seed coat (Lamprey, 1967; Barnes and Fagg, 2003; Or and Ward, 2003). This implies that regeneration of *F. albida* requires low to moderate densities of browsers, which may not be the case in highly protected nature reserves dependent on tourist revenue.

Some of the vegetation species on the Mana floodplain such as *K. africana*, *T. emetica* and *L. capassa* have been reported to follow *F. albida* in succession (Barnes and Fagg, 2003) (Figure 6). Assuming that is the case, *F. albida* may not then regenerate well on floodplains with established woodland.

Links between flow regime and stand structure establishment and growth

Regeneration of *F. albida* is episodic, following the creation of bare habitats of alluvial deposits after large floods. Trees can establish on new alluvial deposits where there is reduced competition (Barnes and Fagg, 2003). The construction of Kariba dam reduced the downstream floodplain inundation and subsequent sediment deposition (Attwell, 1970). Because sediment deposition is a result of large floods and inundation events, the absence of such floods may deprive the tree of a seedbed (Figure 10).

Successful establishment of *F. albida* requires enough moisture to grow tap roots fast enough to reach groundwater before surface layers dry out (Barnes and Fagg, 2003). The timing of the pre-dam flooding event in April, at the beginning of the rainy season, is likely to have provided the moisture required by the seedlings' taproot to reach groundwater. Besides recharging the soil moisture and alluvial aquifer, large flooding events also reduce competition by scouring off flood-intolerant species (Poff *et al.*, 1997). Following dam construction, the absence of

Figure 11. Showing *F. albida* tree fallen into the river channel after the soil has been eroded – bank erosion (December 2011).
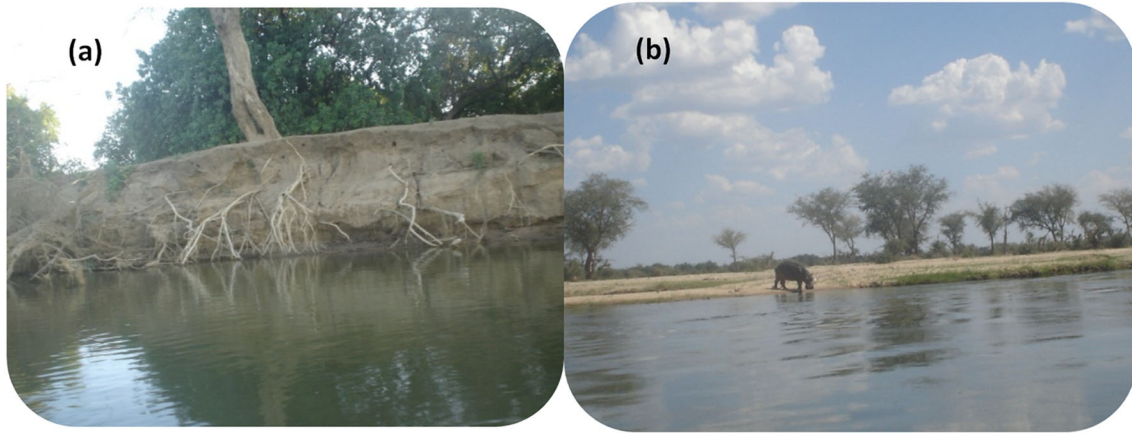
Figure 12. Steep gradient between some parts of the river bank and the floodplain (a) and gentle gradient between the river and most islands (b).

flooding would favour other vegetation species such as *C. megalobotrys* (Dunham, 1989b) and *Indigofera shrubs* (Ncube *et al.*, 2012), and increased bank erosion may have led to the loss of young *F. albida* (Dunham, 1989a; Ncube *et al.*, 2012) (Figure 11).

The development gradient of the tree vegetation on Mana floodplain increases with distance from the river, with young trees found close to the river bank. Bank erosion increases the gradient between the river and floodplain, causing steep banks in areas with significant topographical change between floodplain and river channel (Figure 12a). On the islands, a gentle gradient between the river and islands, and low topography, allows the inundation of large parts of the island during flood events, promoting soil moisture and early tree growth (Figure 12b).

Aerial photographs have shown that since the Kariba dam construction, outflow has eroded, deposited and reconfigured some of the old big islands into small new ones (Mubambe, 2011). These disturbances provide the tree with new habitat to colonize. Chikwenya Island is older than the other islands and was present before dam construction.

Outlook – potential of dendrochronology

F. albida exhibits distinct growth rings, which resemble those observed by other researchers (Giffard, 1971; Gourlay, 1995). Seeing the presence of distinct annual changes in leaf phenology, it can be assumed that these growth layers are annual (Roupsard *et al.*, 1999; Rozendaal and Zuidema, 2011). However, to understand dynamics in annual ring formation and environmental factors driving it, either pinning or microsampling should be applied (e.g. Rossi *et al.*, 2006; Tolera *et al.*, 2013). Variation in ontogenetic trends as well as problems of growth-ring detection especially in slow growing older trees are common phenomena in tropical tree species (Worbes, 2002; Dunisch *et al.*, 2003; Sass-Klaassen *et al.*, 2008). Establishment of reliable diameter–age relationships for *F. albida* will therefore require a large and systematic

sampling campaign whereby trees of different diameters are sampled in different habitats (Brienen *et al.*, 2012).

CONCLUSIONS

The alteration of the Middle Zambezi flow regime shaped *F. albida* stand structures on the middle Zambezi islands and Mana floodplain by affecting the trees' habitat and soil moisture availability. The construction of Kariba dam reduced the downstream floodplain inundation and subsequent sediment deposits, depriving the tree of suitable seedbeds on the floodplain. The reduction of floodplain inundation events may have reduced the early dry season soil moisture recharging of the floodplain. Conversely, the altered morphology of the river as a result of the dam created new islands, providing an ideal habitat for the establishment of *F. albida* populations. Additionally, the absence of young *F. albida* trees on the floodplain can be linked to the growth pattern of the tree as a pioneer species where it is being succeeded by species reported to follow it in succession such as *T. emetica.* Browsers feeding habits potentially play a major role in structuring these stands. *F. albida* forms distinct annual growth rings, and this study has demonstrated that dendrochronology can be applied to gain information on population dynamics and tree growth in relation to environmental factors.

Ecohydrol. (2014)

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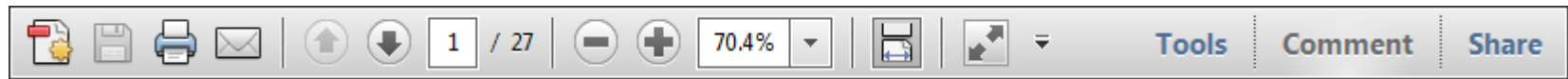
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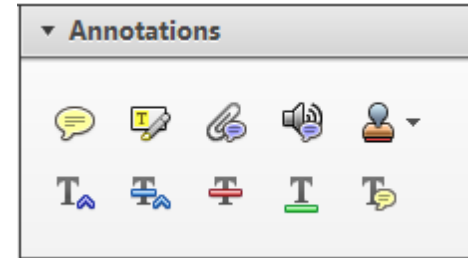
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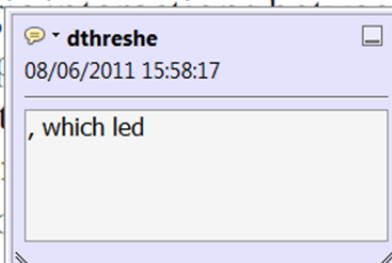
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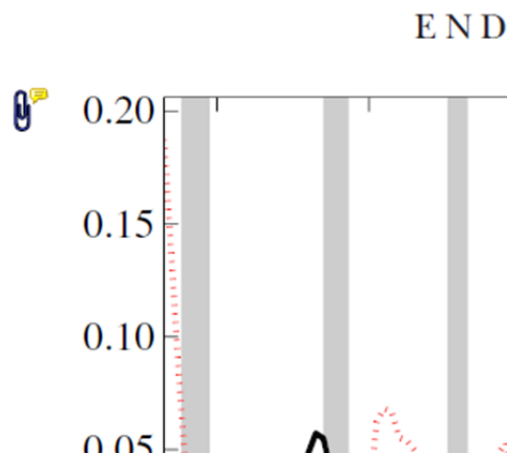
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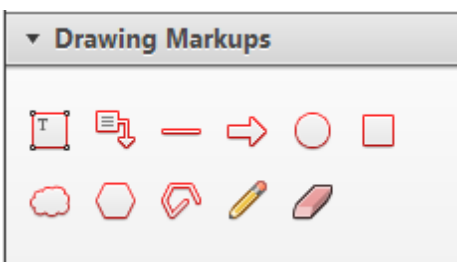

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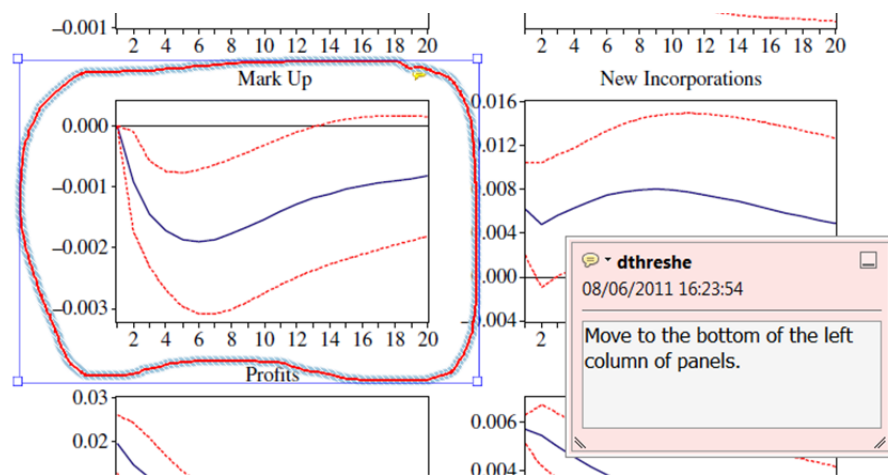
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