



The effects of floods, droughts and elephants on riparian tree mortality in a semi-arid savanna

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ARTICLE INFO

Keywords:

Faidherbia albida
Ficus sycomorus
Philenoptera violacea
Vachellia xanthophloea
Xanthocercis zambeziaca
Limpopo River

ABSTRACT

Riparian forests have declined around the world over the past century. This is mostly attributed to alteration of river flow regimes and abstraction of alluvial groundwater, although in Africa damage from elephants is often considered the primary cause. Large stands of riparian forest along the Limpopo River in Mapungubwe National Park (South Africa) were transformed to woodland between 1990 and 2005, and water stress resulting from reduced river flows and abstraction, an extreme flood and canopy infestation by climbing plants were identified as contributing causes. Recent recolonization of the area by elephant has created an additional potential driver of mortality. To determine if tree losses have continued and gain further insights into the causes - particularly the relative importance of water stress versus debarking by elephant - tagged trees were surveyed annually from 2011 to 2022. Rates of mortality were higher than in the previous decade for four of the five dominant tree species. Bank erosion from flooding remained a cause but accounted for far less mortality than in the past. For individuals not lost to floods, survival analysis indicated that low rainfall was the primary driver of mortality. Canopy infestation by climbers did not decrease survival, and while elephant damage was common for all species and most likely killed some individuals, it had far less effect than our measures of water availability. Isotopic analysis of xylem, soil, river and groundwater revealed few differences in source water use between species, and marginal contributions from the alluvial aquifer. All species relied on deep soil water, illustrating a key linkage between rainfall and survival under the current hydrological regime. Persistence of the remaining large trees at this site is highly unlikely, considering the altered flow regime of the river and likelihood that future climate change will exacerbate water stress. Given the degree of ecosystem change over the past four decades, future conservation should shift focus to the recruitment and establishment of other large tree species, particularly those tolerant of water stress and elephant browsing.

1. Introduction

Riparian ecosystems make significant contributions to biodiversity at the regional scale (Sabo et al., 2005; Tockner and Stanford, 2002) and often act as corridors that link plant and animal populations in fragmented landscapes (Naiman et al., 2005). This is particularly evident in arid- and semi-arid regions, where rainfall is inadequate to support forests but floodplains of large rivers support forests that differ substantially in composition and functioning compared to the surrounding savanna, grassland or shrubland ecosystems (Busch and Smith, 1995; Hughes, 1988; Patten, 1998; Sabo et al., 2005).

Many riparian forests have declined in cover over the past century

(Douglas et al., 2016; Kibler et al., 2021; O'Connor, 2010; Patten, 1998; Webb and Leake, 2006). While a number of causes have been identified (Naiman et al., 2005), abstraction from alluvial aquifers and reduced flooding frequency have been identified as primary in most cases (Cattolotti et al., 2015; Douglas et al., 2016; Keram et al., 2021; de Resende et al., 2019; Rood and Heinze-Milne, 1989; Rood and Mahoney, 1990; Wen et al., 2009). Riparian aquifers in arid and semi-arid regions are often the only source of water for large-scale agriculture or industry, and as a result often experience high levels of abstraction. Reduced frequency of floods that inundate floodplains, as a result of upstream impoundments and abstractions, can increase mortality and reduce recruitment of riparian trees by reducing water availability in alluvial

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<https://doi.org/10.1016/j.foreco.2023.121264>

Received 16 March 2023; Received in revised form 5 July 2023; Accepted 9 July 2023

Available online 20 July 2023

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soils (Greet et al., 2022; Moxham et al., 2018). Increased frequency and intensities of droughts, as predicted by global climate change models (Dai, 2011; Ncube et al., 2013; Trenberth et al., 2014), may now be exacerbating water stress and increasing rates of mortality of riparian trees, or will in the near future. In Africa, damage resulting from foraging by elephants has also been identified as a cause of riparian tree mortality, as well as limiting recruitment of juvenile trees, leading to conversion of forests and woodlands to open savannas or grasslands (Barnes, 1983; Gandiwa et al., 2011; Laws, 1970; Skarpe et al., 2004).

“Lowveld Riverine Forests” have been classified as a threatened ecosystem in South Africa due to their decline over the past century (Driver et al., 2012). They typically occur as narrow bands along

seasonal and perennial rivers within semi-arid or arid landscapes, and likely make a disproportionately large contribution to broader-scale biodiversity and primary productivity. Remaining patches of these forests are also a key tourist attraction for Mapungubwe National Park (MNP), part of a World Heritage Site and regional protected area spanning Botswana, Zimbabwe, and South Africa. Within MNP, the largest section of forest was transformed from near closed-canopy forest to open woodland between 1990 and 2005, following a period of stable cover over the previous 35 years (O’Connor, 2010). This was attributed to water-stress following a severe drought (during which river flow ceased for the first time in recorded history) and exacerbated by water abstraction from the alluvial aquifer. Infestations of climbing plants may

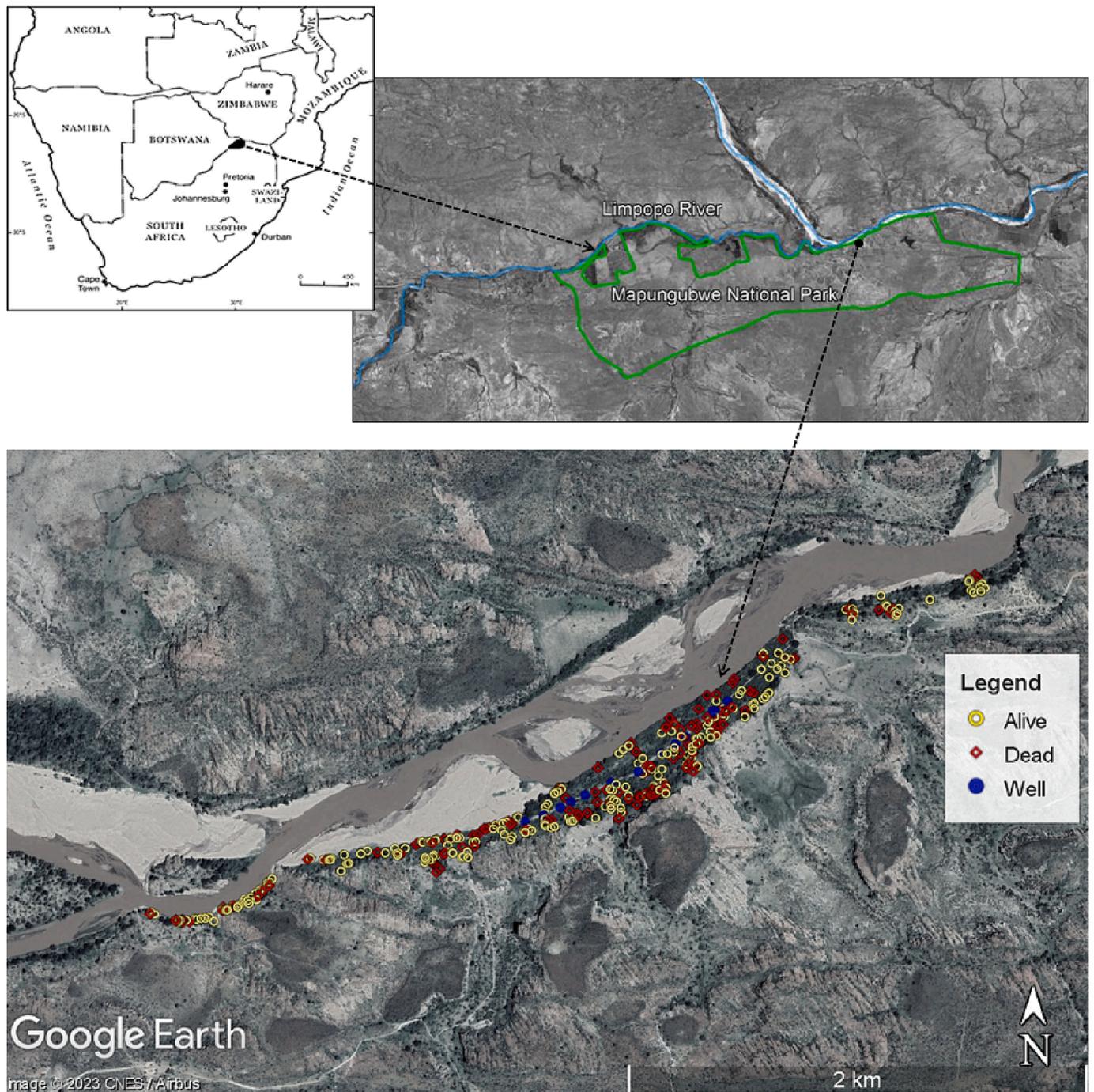


Fig. 1. Map of the Greefswald section of Mapungubwe National Park, showing the location of the tagged trees on the southern floodplain of the Limpopo River, as well as active wells. “Dead” refers to tagged trees that died between 2011 and 2022, and “Alive” to those still living in 2022.

have contributed to the mortality of two species, while river bank erosion during an extreme flood was the primary cause for a third. These causes of decline are likely to have persisted since O'Connor (2010). Furthermore, a new potential agent of mortality has emerged as a result of the return of elephants to the area. Finally, an additional, untested explanation for the loss of the riparian forest at the site is simply that cohorts of adult trees have reached the end of their natural lifespans, as has been suggested for similar sites when dramatic losses of riparian forest have occurred (Young and Lindsay, 1988). The current population declines would then be a result of a lack of recent recruitment rather than any anthropogenic acceleration of mortality.

Identifying current rates and causes of mortality, in MNP as well as many other protected areas, is important for conserving the remnants of these ecosystems and informing any efforts to restore them. As elephants now frequent the riparian areas of MNP, as they do in many African riparian forests, it is particularly pertinent to determine whether the persistence (or restoration) of riparian forests is even possible given the current elephant densities and hydrological regime.

In this study we expanded on the earlier study of O'Connor (2010), using annual measurements of the same riparian trees and incorporating new data on elephant damage, river flows, rainfall, and tree source-water use (using stable isotope analysis).

The aims were firstly, to determine if rates of tree mortality have changed since 2005. Secondly, to disentangle the various potential causes of current mortality: 1) water stress from water abstraction, 2) water stress from low rainfall, 3) water stress from a lack of floodplain inundation, i.e. a lack of moderate floods, 4) erosion of the floodplain by large floods, 5) elephant damage, 6) infestation by climbers, and 7) old age.

2. Materials and methods

2.1. Site description

The study site was located within the Greefswald section of MNP, South Africa (Fig. 1). MNP and much of the surrounding region consists of arid savannas covering sandstone hills and dolerite ridges. The site was located on a large floodplain approximately 2.5 km long and between 50 and 290 m wide, situated between the macrochannel of the Limpopo River and a ridge of sandstone. This has a cross-section gradient of 3% and is generally flat with a few minor channels that flow during inundation. The width of the river macrochannel varies between 280 and 390 m, and is flat and shallow with extensive sediment deposits.

The soils of the floodplain consist of unconsolidated alluvium, with an alluvial aquifer that varies in depth from 8 to 20 m. There is a clear and abrupt transition from woodland to savanna, where the alluvial deposits abut against the surrounding sandstone geology.

Rainfall is strongly seasonal with more than 75% of the annual mean of 364 mm falling in the mid-summer months from November to February (2001–2022). The flow of the Limpopo River is similarly seasonal, with discharge often falling below 1 m³/s by the end of the dry season but exceeding 1000 m³/s in the mid wet season. Flooding of the site is similarly variable, with full or partial inundation occurring multiple times in some years, but not at all in others. Catchment scale models indicate current flows are well below natural flows, particularly in winter, and there are over 60 dams upstream of the study site, and widespread abstraction for domestic, industrial and agricultural use (Aurecon, 2013).

Within the central portion of the study site, where the width of the floodplain is greatest, water is abstracted from the alluvial aquifer to supply a diamond mine located 25 km to the south. Approximately 2.2 million m³ is abstracted annually, with 9 to 15 groundwater pumping wells active depending on the season (Fig. 1). Water-table declines resulting from this were conservatively estimated at 1–2 m (Brown and Erasmus, 2004) but the widths of the cone-of-depression around each

well are not known.

In 1990, and for at least 45 years prior to that, the floodplain was dominated by the large riparian forest trees described below, with near complete canopy cover (O'Connor 2010). By 2005, high rates of mortality had transformed this to an open woodland, at by the start of this study, a previously sub-dominant species, *Croton megalobotrys* Müll. Arg., was the most common woody species. This species grows as shrubs and short trees, rarely reaching heights greater than 10 m. The herbaceous layer consisted of dense but patchy swards of *Panicum maximum* Jacq. or *Cenchrus ciliaris* L. interspersed with extremely dense, impenetrable swards of *Panicum deustum* Thunb., often taller than 2 m.

Elephant densities in MNP, counted annually at the end of the dry season, increased from approximately 0.02 / km² in 2000 to 1.1 / km² in 2014 (Selier and Page, 2014).

2.2. Focal species

As O'Connor (2010) found considerable variation in rates and causes of mortality amongst the various riparian tree species at the site, we included all species with a sufficient number of replicates to allow for statistical analysis. Of these five species, *Ficus sycomorus* L. subsp. *sycomorus* and *Vachellia xanthophloea* Benth are common species of African floodplain forests, typically occurring along perennial rivers and around wetlands and lakes, and often in areas that are seasonally inundated (Furness and Breen, 1980; Schmidt et al., 2002; White et al., 2019; Whittington et al., 2016). *Faidherbia albida* (Del.) A. Chev typically forms dominant stands on sandbars of large African rivers (Barnes and Fagg, 2003). *Philenoptera violacea* (Klotzsch) Schrire and *Xanthocercis zambesiaca* (Baker) Dumaz-le-Grand are common along perennial rivers, but also occur in drier habitats, such as along ephemeral rivers or on termitaria in upland areas of mesic savannas (Schmidt et al., 2002). *Faidherbia albida* and *P. violacea* have been shown to utilize ground-water, although neither are obligate phreatophytes (February et al., 2007). *Faidherbia albida* and *V. xanthophloea* are deciduous, and the former is the only species known to have reverse phenology, losing its leaves in the wet season and flushing new leaves in the dry season (Roupsard et al., 1999).

In 2011, the abundance of each species varied with distance from the river channel within the study site (Figure S1). *Ficus sycomorus* occurred predominantly on the edge of the macro-channel, or along drainage lines that flow during floods. *Vachellia xanthophloea* was most abundant in the outer half of the floodplain. *Faidherbia albida* was spread throughout the floodplain but was more common on sandy areas close to the channel. *Philenoptera violacea* and *X. zambesiaca* occurred mainly in the outer half of the floodplain, with the largest individuals of the latter typically located on the boundary of the floodplain.

2.3. Field measurements

In July 2011, 259 of the remaining trees from O'Connor (2010) were located, geotagged with a handheld GPS, marked with a metal tag, and assessed for vitality, elephant damage, climber infestation and canopy dieback. This was done in the mid to late dry season (July to September), and repeated each year up to 2022. An absence of leaves and small twigs was used as the indication of mortality, and any individuals recorded as dead in one year were checked again the following year for possible resprouting. For assessment of elephant damage, debarking of the primary stems (trunks) was recorded as the percentage of the circumference from which bark had been removed, and the percentage of the height of the primary stems (between the ground and the first branch) from which bark had been removed. Uprooting, snapping or pushing over of any primary stems was also recorded, as was breakage of large branches. Climber infestation was measured as a visual estimate of the percentage of the canopy covered by climbers. Dieback was the percentage of the canopy with dead branches or twigs. Some additional individuals were also tagged and assessed, in the same manner, in order

to increase the sample size for certain species (5 *V. xanthophloea* and *F. albida*; 2 *P. violacea*, *F. sycomorus* and *X. zambesiaca*). All individuals included in the study were taller than 10 m in 2011, and the tallest individuals were approximately 30 m in height.

Stem circumferences and tree heights were measured in 2011, 2015 and 2019. As many of the trees fork close to the ground, circumferences were measured as close to the ground as possible, but above any buttress roots or basal swellings. If more than one primary stem was present, each was measured separately, and basal area was calculated for each (on the assumption of a circular cross section) and summed to get a single area for each individual. Height was measured to the highest leaf on an individual, using a laser clinometer (Vertex Laser Geo, Haglöf Sweden AB).

For comparison with mortality data presented in O'Connor (2010), mortality was calculated as an average annual rate:

$$\text{mortality} = 1 - (1 - \text{mortality}_i)^{1/\text{years}}$$

where, 'mortality_i' refers to the overall mortality rate reported for the O'Connor (2010) study or this study, and 'years' is the number of years of the respective study period. This approach assumes that declines in population sizes were exponential.

2.4. Causes of mortality

The importance of the various factors potentially responsible for tree mortality were assessed using survival analysis (Pyke and Thompson, 1986). For water stress resulting from water abstraction, a categorical variable was created indicating whether an individual was within 80 m of the nearest well. This was preferable to using 'distance to well' as a continuous variable, as the majority of the trees were too far from the wellfield to have been affected, and these would have obscured any effect on those located close to a well. The distance between wells was approximately 60 m, and it is likely that their placement was designed to prevent overlap of zones of water table drawdown. It was therefore assumed that abstraction would not have much effect on water availability for individuals located more than this distance from a well, but a threshold of 80 m was used to allow for edge effects, and to create more balanced sample sizes. Using a lower or higher threshold (60 m or 100 m) did not alter the results qualitatively.

For water stress resulting from low rainfall, daily rainfall data were obtained from a rain gauge located approximately 2.8 km from the site. Four rainfall metrics were used: annual rainfall for the hydrological year (September to August) ending in the year of sampling, annual rainfall for the previous hydrological year, the sum of the current and previous year, and the sum of the previous two years.

For measures of water stress resulting from low river flows, river flow data were obtained from the South African Department of Water Affairs and Sanitation for the nearest gauging station (Beit Bridge). This is located approximately 68 km downstream of the site, but as no perennial or seasonal rivers enter the Limpopo over this stretch, it is likely to provide a good estimate of inter-annual variation in flow at the study site. Flow data consisted of monthly total discharge, which was summed from September to August to create the same metrics used for rainfall (total flow of the hydrological year prior to sampling, the previous year, the sum of current and previous year and the sum of the previous two years). Inundation was estimated using a categorical variable to indicate if flooding had occurred in the year of sampling. Two similar variables were created to test for lag effects of inundation: the occurrence of flooding in the previous year, and the number of years in which floods occurred within the past 2 years. Inundation was evident from high water marks observed in 2014, 2021 and 2022, and based on the river flow data for these years it was assumed that this also occurred in 2013 and 2017. For an additional measure of water stress resulting from low river flows, the distance of an individual to the river channel was calculated for each individual, on the assumption that an individual further from the river would receive less water via the hyporheic pathway belowground or via inundation. This variable was calculated

relative to floodplain width, i.e. the percentage of the distance from the river channel to the edge of the forest, measured along a line perpendicular to the direction of the channel.

To assess impacts of elephant damage, the cumulative percentage of the circumferences of each main stem debarked was calculated for each individual each year. A cumulative measure was used as multiple years of partial debarking might have the same deleterious effect as a single year of complete debarking (ringbarking). Elephant can also kill large trees by pushing them over or pollarding primary stems but as this was only recorded for a few individuals it was not included in the statistical analysis.

The potential impact of infestation by climbing plants was included as the maximum percentage of the tree canopy estimated to be covered by climbers in any year.

Finally, to test for age-related mortality, it was assumed that size is a reasonable surrogate for age and thus the effect of age would be revealed by lower survival of individuals that were larger at the start of the study. Tree ring analysis on *F. albida* in a natural floodplain habitat (Gope et al 2015) shows a fairly linear relationship between age and stem diameter, making this assumption reasonable for this species at least. The basal area of all primary stems in 2011 was used as the measure of size.

Parametric survival models were fitted using the flexsurv package in R (Jackson, 2016) which allows for the inclusion of time-varying covariates in parametric survival models. This provided a means to compare the effects of all the potential drivers of mortality, including time-varying covariates which varied from year to year (the rain, river flow, debarking and climber infestation variables) with those that were fixed over the duration of the study (distance to nearest well, distance to river channel and initial size). Parametric models were used rather than Cox proportional hazard models as there were many 'ties' in the data because many individuals died in the same year. Separate models were fit for each species, and a Weibull distribution of errors was found to provide the best fit to the baseline survival rate (based on both lowest AIC and visual inspection of survival plots). This is consistent with the increasing hazard rate evident in Fig. 2. Due to the large number of covariates, and correlations amongst them, separate univariate models were fit for each covariate for each species, and the best fit compared on the basis of AIC and the confidence intervals of the co-efficient for the covariate. To test for the effect of specific variables of interest, a second term was included with the best univariate model, and only retained if it had a lower AIC.

2.5. Stable isotope analysis

To determine differences in sources of water used by the focal species, stable oxygen and hydrogen isotopes were analyzed from trees, rainfall, soils at 5 cm and 50 cm depth, the river, and groundwater samples collected from wells within the study site. Tree stem samples were collected from a subset of the tagged trees, using a stratified random sampling design along transects perpendicular to the river. Stem samples (1–2 cm diameter) were collected on three occasions at the end of the wet season (12 March 2012, 13 March 2013 and 2 April 2014) and two occasions at end of the dry season (3 October 2013 and 23 October 2014). Soil, river, and well samples were only collected during the March 2013, March 2014, and October 2014 sampling. Rainfall samples were taken from the manual raingauge from November 2012 to November 2014, and stored at 2 °C.

After collection, samples were placed in Exetainer vials (Labco, Lampeter, UK) for transport and storage. Plant and soil samples were frozen prior to water extraction using cryogenic distillation. Extraction occurred using an open manifold system, and water samples were analyzed using a Picarro L1102-l CRDS analyzer (Picarro, Santa Clara, California, USA) at the Stable Isotope Mass Spectrometry Laboratory at Kansas State University. ChemCorrect software was used to identify any samples flagged for organic contaminants. If samples were flagged, they were removed from subsequent analysis (less than 5% of all samples).

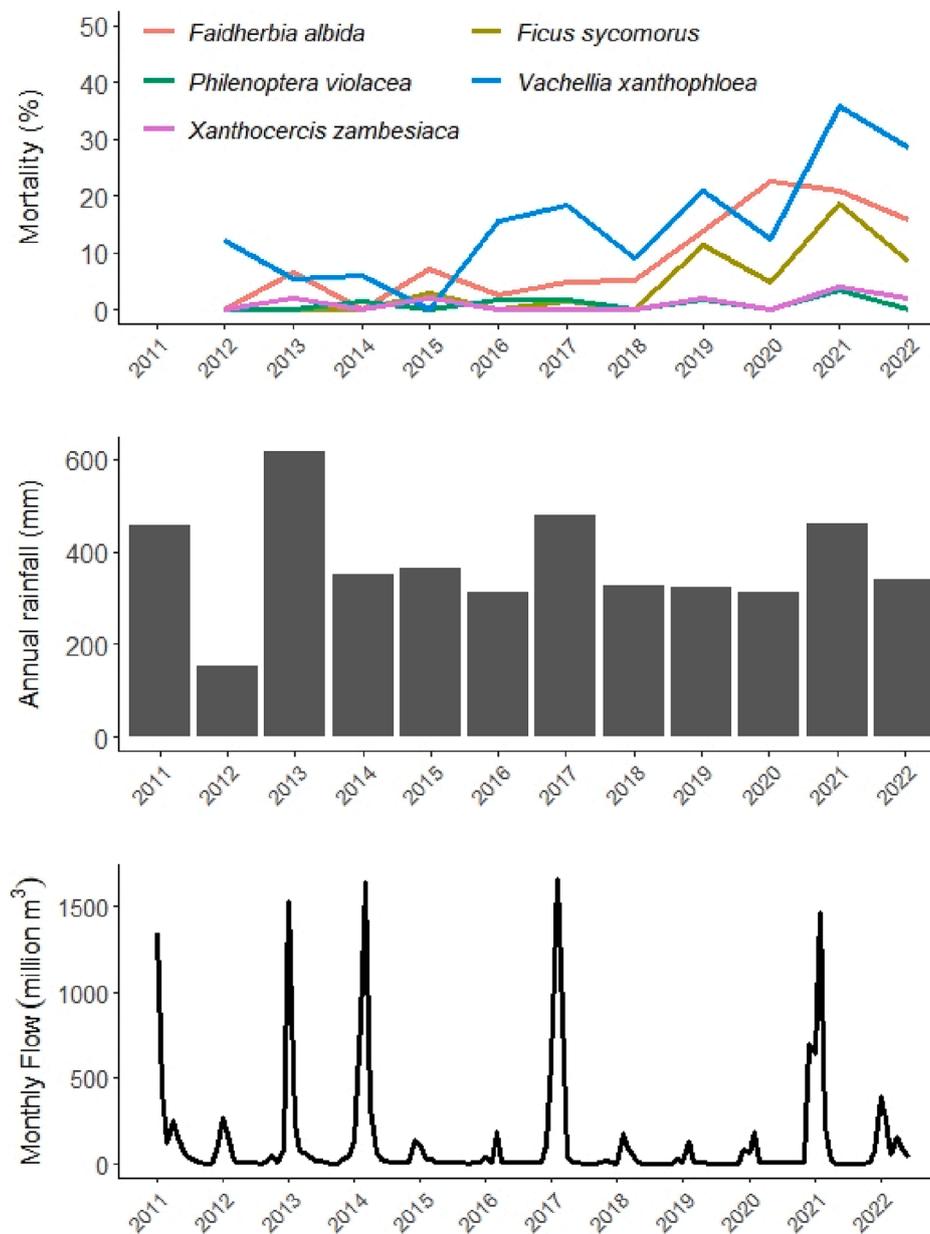


Fig. 2. Annual mortality rates for the five dominant floodplain species at the Greefswald site, Mapungubwe National Park (A), annual rainfall (B) and river flow (monthly volumes) of the Limpopo River measured downstream of the site (C).

The stable isotopic ratios of water samples ($\delta^{18}\text{O}$ and δD) were reported as deviations from international standards GISP, SLAP, V-SMOW (Coplen 1995). Samples were calibrated to in-house standards and expressed using δ notation in parts per thousand (‰):

$$\delta = \left[\left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} \right) - 1 \right] * 1000$$

where R is the absolute ratio of the rare to common isotope, respectively. Analytical uncertainty was 0.2‰ and 1.5‰ (for $\delta^{18}\text{O}$ and δD) of the calibrated value of the standards.

The SIAR isotopic mixing model was used to establish proportional contributions of multiple water sources for the water isotopic signature within the tree species measured here (Parnell et al. 2010). Mixing-model analyses were performed per species, but only for the March 2013, April 2014, and October 2014 sampling periods as these were the only times when water sources were measured. Measured water sources used in the mixing model analysis included river water, the alluvial aquifer (i.e. well samples), and soil water from 5 cm and 50 cm depths.

The rainy season in 2013 was particularly wet, and rainfall from this period likely recharged soils to their maximum water-holding capacity. The largest rainfall events were most likely to infiltrate to the deepest soil layers (deeper than 50 cm). This ‘deep soil water’ was approximated using the mean isotopic signature of rain events over 30 mm in size. For the March 2013 sampling date, rainfall events on 15th, 16th and 21st January and 5th February 2013 were used to estimate the signature of ‘deep soil water’ (Figure S2, S3). For the April 2014 and October 2014 sampling dates, this included the aforementioned large rainfall events in 2013 as well as those on 4th April, and 21st and 30th November 2013, and 3rd March 2014.

For analysis during each sampling period, three water sources with unique stable isotope signatures were selected for inclusion in the mixing model. For the analyses in March 2013, the unique sources considered in the model included river water, and 5 cm and 50 cm soil moisture. For the analyses in April and October 2014, the sources considered included river water, 50 cm soil, and ‘deep soil water’. As signatures for river water overlapped with those for the alluvial aquifer,

the two sources were not distinct (Figure S4).

3. Results

3.1. Mortality

The annualized mortality rate from 2011 to 2022 was greater than from 1990 to 2005 for four of the five species, and was particularly high for *V. xanthophloea* and *F. albida* (Table 1). Mean annual mortality rates for 2011 to 2022 were similar to the annualized rates calculated from the overall mortality from 2011 and 2022, indicating that the annualized rate provided a reasonable surrogate for comparing mortality between the two studies. Mortality resulting from trees falling over or being washed away during floods was less frequent over the past decade despite numerous high flows. While canopy dieback was lower for three of the five species, infestation by climbers and debarking by elephant were higher for all (Table 1).

For the two species with relatively low mortality (*P. violacea* and *X. zambesiaca*), too few individuals died to allow for statistical testing of the potential causes of mortality, and no covariates provided an improved fit compared to the baseline survival model. For *F. albida*, *F. sycomorus* and *V. xanthophloea* measures of the temporal variation in water availability were the best predictors of survival (Fig. 2, Table 2). Rainfall of the hydrological year preceding the year of death was the best predictor for *F. albida* and *F. sycomorus*, while the metric incorporating a greater lag - the sum of rainfall of the previous year and the year prior to that - provided the best fit for *V. xanthophloea*. Although models with the various river flow variables never provided the best fit, some were close: the number of floods in the two preceding years had a positive effect on the survival of *F. sycomorus*, as did the total flow of the preceding year for *V. xanthophloea*. Combinations of rain and flow variables did not provide any improvement on the above models, most likely due to correlation of rainfall and river flow ($r = 0.63$, p less than 0.05).

While the measures of previous rainfall were the best univariate predictors of survival, these relationships showed a large amount of variance (Fig. 3) suggesting that additional factors contributed to mortality. However, multivariate models provided little improvement on the univariate rainfall-related models (Table 1). For *F. albida*, the combined effect of previous rainfall and infestation by climbers provided a considerably better fit, but the effect of climbers was in the opposite direction than expected - individuals with greater canopy infestation tended to survive longer. For *F. sycomorus*, cumulative debarking by elephant improved the model fit, but again in the opposite direction to

that expected - trees with higher levels of debarking had longer survival times. For *V. xanthophloea*, the combined effect of prior rainfall and distance from the river channel provided only a slightly better fit than prior rainfall alone, and the effect of proximity to river was not statistically greater than zero.

Proximity to a well was not a good predictor of survival for any of the high mortality species (Table 2). The samples for this categorical variable were however unbalanced, with approximately twice as many individuals located further than 80 m from a well than closer, and sample sizes within the zone assumed to be impacted by abstraction may not have been sufficient to detect an effect at the time scale of this study.

While elephant damage was recorded for the majority of trees, it was mostly not severe and usually did not lead to mortality within the study period. Of the total sample of 275 individuals, 210 had some degree of debarking, but only 38 had more than 50% of the circumference of their trunk(s) debarked in any year. Twenty-seven of these trees did subsequently die, but for 9 the cause was bank erosion. Therefore, at most 20% of mortality (18 of the 88 individuals that died from causes other than floods) may have been due to debarking. *Faidherbia albida* suffered the most severe debarking. It was the only species for which 100% of the stem circumference was removed from an individual in a single year, and eight individuals were completely ringbarked during the study period. These eight all died - one was washed away but the others may well have died from the debarking. Debarking was therefore likely to have been the cause of 26% of the *F. albida* mortality (7 of the 27 individuals that died from causes other than floods).

While infestation by climbers apparently increased the survival of *F. albida*, it had little effect on the survival of *V. xanthophloea* and *F. sycomorus* (Table 2). Across the three species, the maximum level of infestation recorded for individuals that had died by 2022 was lower than that recorded for those that had survived (median of 29% versus 37%).

Size had little effect on survival and the 2011 size of individuals which died during the study period was no larger than those which survived: mean \pm sd of basal area (m^2) were 0.99 ± 0.57 versus 1.3 ± 0.88 for *F. albida*, 3.0 ± 3.8 versus 4.0 ± 3.6 for *F. sycomorus*, and 0.45 ± 0.29 versus 0.56 ± 0.40 for *V. xanthophloea*.

3.2. Plant water use

When plotted against the meteoric water line, species-specific xylem-water $\delta^{18}O$ and δD signatures showed considerable variation across the five sampling periods, as well as substantial differences between species

Table 1

Mortality, dieback, and the percentage of sampled trees with climber infestations and debarking, for the five dominant riparian tree species of Greefswald section, Mapungubwe National Park, for the periods 1990 to 2005 and 2011 to 2022. n = number of tagged individuals at the start of each study period. "Mortality annualized" is the estimated annual % mortality assuming a fixed annual rate (see text for calculation). "Mortality, mean annual" is the mean of the 11 years of annual % mortality rate data, which were only available for 2011 to 2022. "Killed by flood" is the percentage of dead individuals that died as a result of bank erosion. Values for 1990 to 2005 from O'Connor (2010).

Species	n		% mortality		Mortality annualized		Mean annual mortality	Killed by flood		Median dieback (%)		Trees with climbers (%)		Trees debarked (%)	
	1990 - 2005	2011 - 2022	1990 - 2005	2011 - 2022	1990 - 2005	2011 - 2022	2011 - 2022	1990 - 2005	2011 - 2022	2005	2022	2005	2022	2005	2022
<i>Faidherbia albida</i>	60	47	37	67	3.0	9.6	8.5	18	3.5	18	30	58	74	18	88
<i>Ficus sycomorus</i>	89	73	25	29	1.9	3.1	4.2	73	7.0	38	25	31	66	94	97
<i>Philenoptera violacea</i>	63	62	11	11	0.8	1.0	0.98	0	0	5.0	23	21	57	0	22
<i>Vachellia xanthophloea</i>	59	41	56	83	5.3	14.9	16	0	1.4	38	28	19	26	92	100
<i>Xanthocercis zambesiaca</i>	47	52	6.4	10	0.4	0.9	0.99	67	0.7	28	15	16	56	18	83

Table 2

AIC values and lower and upper limits of the 95% confidence intervals ('L95%' and 'U95%') for each covariate used in the parametric survival models. 'Baseline' is for a model without covariates. Values in bold show models with a lower AIC than the baseline model and for which the 95% confidence interval for the covariate coefficient did not overlap zero. A Weibull distribution was used for all models.

	<i>Faidherbia albida</i>			<i>Ficus sycomorus</i>			<i>Vachellia xanthophloea</i>		
	AIC	L95%	U95%	AIC	L95%	U95%	AIC	L95%	U95%
Baseline	186.2			153.4			199.3		
Univariate models									
Rainfall	187.5	-0.0024	0.00088	155.4	-0.0015	0.0014	201	-0.0013	0.0024
Rainfall previous year	173.9	0.0018	0.0049	143.5	0.0009	0.0049	198.5	-0.00028	0.0031
Sum of current and previous years rainfall	180.6	0.00038	0.0046	147	0.00037	0.0029	195.3	0.0003	0.0048
Sum of previous and 2 years previous rainfall	179.8	0.00054	0.0049	155.1	-0.001	0.0017	188.9	0.0012	0.0059
River flow	did not converge			did not converge			201.3	-0.0001	0.000087
River flow previous year	185.5	0.000066	0.00014	did not converge			197.5	0.000093	0.00024
Flood	187.5	-0.16	0.41	152	0.018	0.32	201.1	-0.42	0.28
Flood previous year	186.5	-0.13	0.56	148	0.02	0.61	196	0.0019	1
Floods in previous 2 years	186	-0.062	0.37	147.5	0.048	0.26	199.7	-0.11	0.45
Proximity to borehole*	186.8	-0.62	0.05	151			201.2	-0.77	0.42
Distance from channel	185.7	-0.01	0.0012	154.4	-0.0029	0.0085	195.6	-0.021	-0.00024
Cumulative Debarking	188.2	-0.0029	0.003	141.4	0.0027	0.0077	201.1	-0.011	0.0069
Creepers	172.2	0.0034	0.032	145.3	0.0019	0.016	198.2	-0.005	0.028
Size	186.3	-0.065	0.33	153.8	-0.013	0.056	201.1	-0.62	0.41
Multivariate models									
Rainfall of previous year + Creepers	159.8	0.0019	0.0053						
		0.0027	0.026						
Sum of previous and 2 years previous rainfall + Distance from channel							186.0	0.001	0.0057
								-0.022	0.00064
Rainfall of previous year + Cumulative Debarking				130.9	0.00044	0.0045			
					0.0024	0.0069			

for any one sampling period (MWL; Figure S5). The highest inter-specific variability occurred for the two samples collected at the end of the dry season (October). *Vachellia xanthophloea* had the most variable values, with high variability among individuals within a sampling period, as well as dissimilar isotopic signatures across all sampling periods. *Faidherbia albida* was the only species with a distinct seasonal pattern, with heavier isotopic signatures in March / April and lighter isotopic signatures in October.

Estimates of proportional source-water use varied by species and time period (Fig. 4). In March 2013, 50 cm soil moisture was the dominant water source for all species, although *F. albida* was also sourcing a substantial amount of 5 cm soil moisture (32%), and river or aquifer water (16%). Water from the 50 cm soil moisture source was most likely derived from infiltration from exceptionally large rainfall events that occurred over the previous 2 months (Figure S2, S3). In April 2014, at the end of a relatively drier wet season, the three species with high mortality had mixed reliance on all three water sources and the mixing model estimates had considerable overlap in proportional water use (Fig. 4). In contrast, *P. violacea* and *X. zambesiaca* had a mean reliance (of 87% or more) on soil moisture deeper than 50 cm. By October

2014, when soil water availability was likely to be lower, *F. albida* and *X. zambesiaca* continued to exhibit strong reliance on this deep soil moisture, while the other species utilized relatively more river or alluvial water, with mixed reliance on all water-sources and overlap in mixing model predictions.

4. Discussion

High mortality rates of large adult trees in the largest floodplain of MNP persisted over the past decade, exceeding those of the two preceding decades. The two species which suffered the greatest mortality between 1990 and 2005 had exceptionally high rates in this study, and less than ten *V. xanthophloea* remain in the study area. If these rates continue, both species are likely to be lost from the site within the next 30 years.

Water stress during dry years again emerged as a primary cause of mortality. Despite multiple flooding events from 2011 to 2022, bank erosion during floods was far less important than before, and no longer the primary cause of mortality for *F. sycomorus* and of much less importance for *F. albida* and *X. zambesiaca*. This reflects the

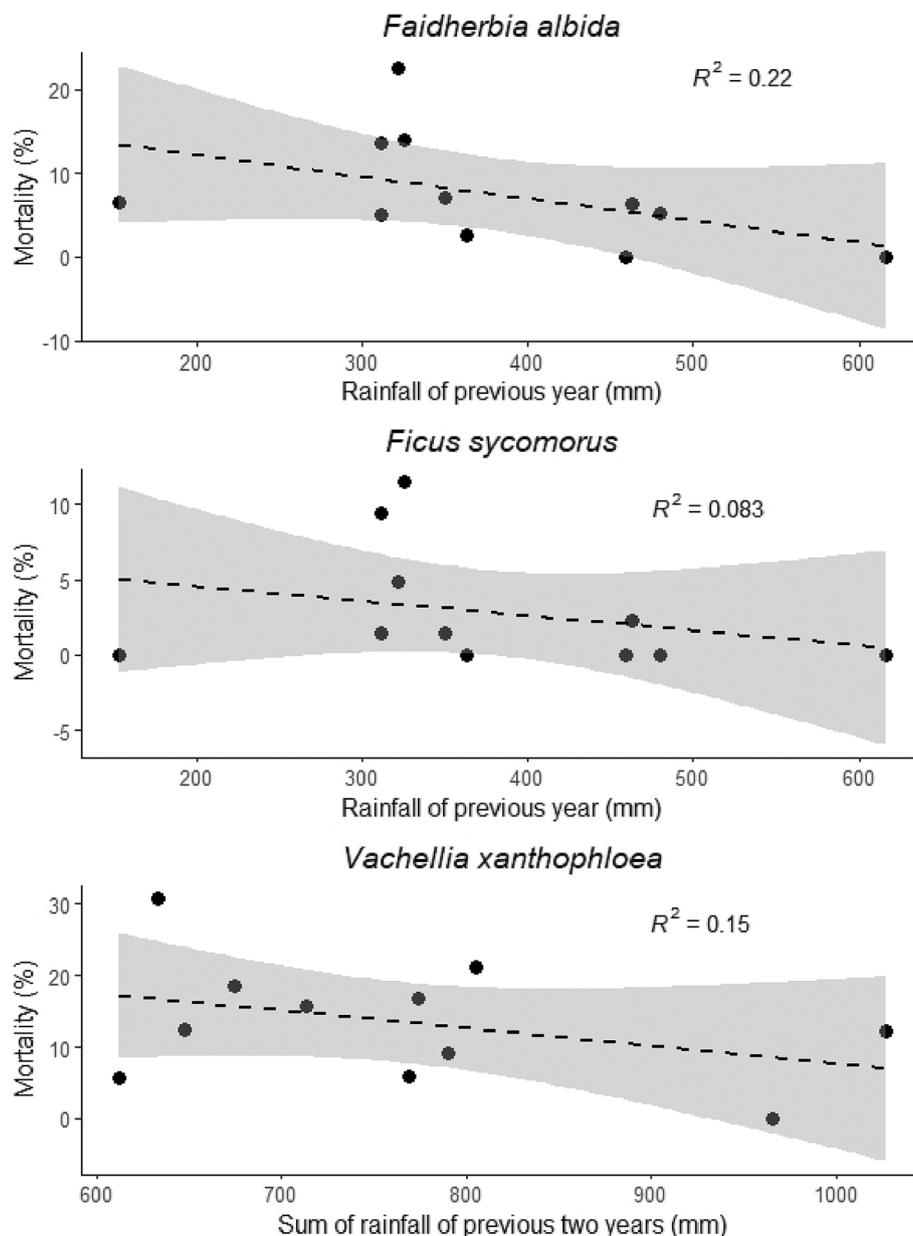


Fig. 3. Linear relationships between annual mortality and the best predictor of survival from the survival analysis, for the three species with the highest mortality (2011 to 2022).

extraordinary impact of the 2000 flood, when peak flows exceeded any in recorded history and when so many of the riparian trees in the original sample were lost.

For those individuals not lost to floods, low rainfall was found to be the most important determinant of inter-annual variation in mortality. The lagged effect of rainfall may indicate the importance of water storage in the alluvial soil, with soil water only reaching critically low levels a year or more after a dry year. Alternatively, it could reflect a degree of water and / or carbohydrate storage in the trees, which may have been able to survive for a year or two after soil water levels reached critically low levels. The source water isotopic analysis supported the importance of rainfall, as it showed that soil water derived from rainfall - rather than the river - was the primary source of water for the focal species. It is counter-intuitive that large riparian trees with potentially deep roots would not be utilizing substantial amounts of hyporheic or alluvial water. Furthermore, *F. albida* has been shown to utilize primarily groundwater in a terrestrial environment, although substantial use of deep soil water did occur at certain times (Roupsard et al. 1999).

However, similar results - of riparian trees utilizing primarily rain water - have been found for a number of other studies (Bowling et al., 2017; Costelloe et al., 2008; Engel et al., 2022), and this pattern may simply indicate that the deep alluvial sediments at the site are able to store sufficient rain water to maintain large trees (at least at their current density). Another plausible explanation is that the alterations of the flow regime of the Limpopo river over the past half century (Mwenge Kahinda et al., 2016), and continued abstraction from the alluvial aquifer at the study site, have lowered the alluvial water table to the extent that adult trees have had to switch from using river-derived water to rainfall-derived soil water. Incision of the macro channel during the 2000 flood may have also lowered the alluvial water table through reduced hyporheic flows from the river to the alluvial aquifer (Webb and Leake, 2006). More recent floods may have exacerbated this process resulting in further water stress, but a long-term, retrospective analysis of water table heights is needed to test this idea.

The correlation of annual rainfall and river flow made it difficult to statistically distinguish their effects. It is possible that some of the effect

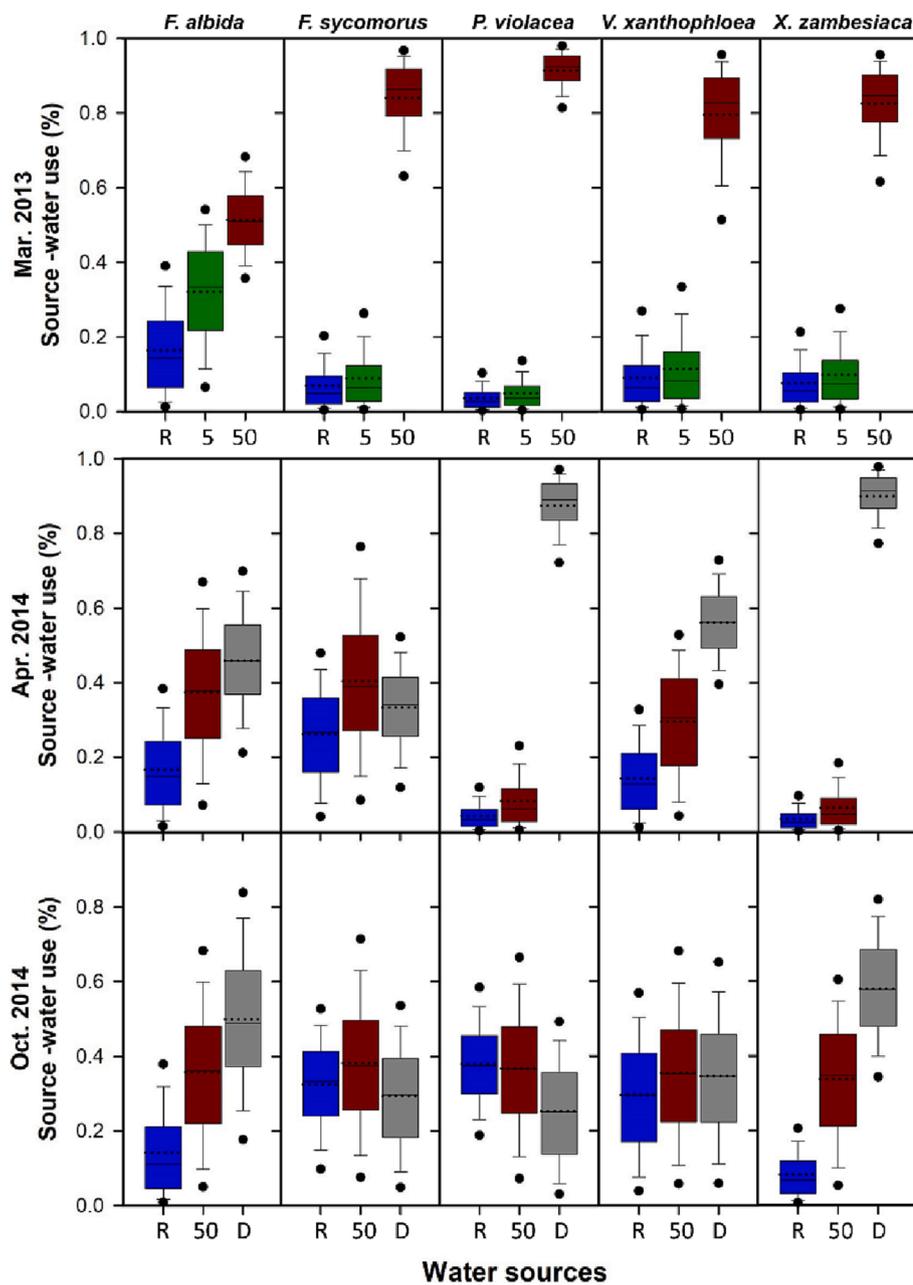


Fig. 4. Source-water use by species for samples collected in March 2013, April 2014, and October 2014. For March 2013, potential water sources include river water (R), and water from 5 cm and 50 cm soil depths. For April and October 2014, potential water sources include river water (R), 50 cm soil water, and rainwater infiltrated to beyond 50 cm depth (D). Boxplots show mean (dashed line) and median (solid line) values along with the 25th and 75th percentiles. Whiskers on boxplots describe the 10th and 90th percentiles, while 5th and 95th percentiles are shown as point outliers.

of rainfall found in the survival analysis was partly an effect of low river flows, which has been found to be a cause of mortality in many other studies of floodplain forest trees in arid environments (Catelotti et al., 2015; Douglas et al., 2016; Keram et al., 2021; Rood and Mahoney, 1990; Wen et al., 2009). This may be why so much of the inter-annual variation in mortality was not accounted for by the rainfall variables alone. The isotopic analysis did show that river water was used by the trees at times, with river-derived water accounting for around 30% of water use for *F. sycomorus* and *V. xanthophloea* at the end of the dry season. It is therefore likely that the development of chronic water stress over the past decade was the result of both low rainfall and low river flows.

The lack of a statistical effect of water abstraction in this study contradicts O'Connor (2010) who found higher mortality for the section of forest in which the wells are located. The results regarding abstraction must however be interpreted in the context of the current density and distribution of riparian trees, and the specific time span of this study. It is possible that the majority of the individual located nearest to the wells

(and therefore most affected by abstraction) had already died before the start of this study. Furthermore, surviving individuals located near to the wells may have lost their root connections with the alluvial aquifer and became more dependent on rain-derived soil water, as a result of continuous draw-downs of the water table over the past four decades.

Despite the widespread and regular damage to the studied trees by elephants, our study did not support elephants as the main cause of mortality. Debarking was only likely to have caused mortality if ring-barking occurred, and was responsible for at most a quarter of the trees that died from non-flood causes. This is consistent with losses in the 1990 to 2005 period, when elephant impacts were absent, as well as the plethora of studies documenting riparian tree declines at sites where elephants do not occur. While many studies have identified elephant as the cause of the losses of riparian trees at African sites, these have not directly tested alternate explanations such as water stress. At least one other has found no deaths despite widespread elephant damage (Gope et al. 2015, for large *F. albida*). It appears that riparian trees species as large as those in this study are able to survive regular elephant damage

and access to sufficient water is their primary vulnerability.

While water stress, and to a lesser degree floods and elephant, have caused drastic declines of three of the original dominants of the Greefswald riparian forest, two species persisted largely unaffected. *Philenoptera violacea* and *X. zambesiaca* maintained low rates of mortality and relatively low levels of canopy dieback even though they most likely experience lower levels of water availability (they utilized primarily soil water, and were mostly located towards the outer edge of the riparian zone where alluvial aquifer access is lower). This suggests these species are more tolerant of water stress, which is consistent with their broader distribution including non-riparian habitats. It may also indicate intolerance of the more frequent and deeper inundation that would occur closer to the river channel. *Philenoptera violacea* and *X. zambesiaca* also suffered far less debarking from elephant – none were ringbarked and the few that died during the study period showed no signs that elephant were responsible. The convoluted and often multi-stemmed trunks of adult *X. zambesiaca* make it difficult for elephant to ringbark them, and elephants are apparently averse to the bark of *P. violacea*. These two species are apparently far better adapted to the current ecohydrological conditions of the site than the others studied, and therefore good candidates for restoration initiatives.

4.1. Implications for management

More detailed ecohydrological research - including monitoring of soil water dynamics and water table heights, more frequent isotopic analyses, and analysis of a longer history of rainfall and river flow data - would be required for more definitive conclusions regarding the causes of the loss of the MNP riparian forest trees over the past thirty years. While such research would advance our understanding of riparian ecosystems, and inform the management of stands of riparian forest that still occur within the region, results would be of little value to the management of MNP. This study clearly shows that the current hydrological regime at the site cannot support populations of at least three of the five dominant riparian trees, and is consistent with high rates of mortality of riparian trees along other reaches of the Limpopo River, both inside and outside of MNP (unpublished data). As extreme floods and droughts are likely to become more frequent as global climate change intensifies, it is likely the remaining individuals of these species will be lost from the region within a few decades, and that mortality of the others will increase (an increase which may have already started in the past few years – Fig. 2). As rainfall and the flows of the Limpopo River are well beyond the control of park managers, no new research results or associated management interventions are likely to save the remaining large trees of sensitive species. Furthermore, efforts to reduce the impact of elephants would be futile if the majority of these trees die in the next drought.

While the futility of attempting to restore the riparian forests of the past century is a key implication of this study for management, it leads to the question of what the appropriate management objectives for the riparian zone within the park should be. The combination of more extreme droughts, lower river flows, elephant impacts and browsing by meso-herbivores may preclude the occurrence of any large riparian trees in future, as has been suggested for other large rivers in the region (Skarpe et al., 2004). Dense swards of grass now occur amongst the riparian trees at the site and the site could transition to a fire-driven grassland, which do occur elsewhere along large African rivers (Hughes, 1988). Alternatively, given the substantial contribution to biodiversity that tall trees confer, as well as potential carbon sequestration benefits, managers could attempt to establish a novel riparian tree community using other species. These would need to be species capable of growing tall and exploiting the large reserves of water in the alluvial soil and aquifer, but also tolerant of regular water stress and elephant browsing. Which species are likely to meet these requirements, and what ecological and hydrological conditions are needed for their recruitment and growth? *Philenoptera violacea* and *X. zambesiaca* may be

well suited to create a new forest over much of the study site, but their recruitment over the past decade has been limited (while a substantial number of juveniles of *P. violacea* and a few of other species were observed, these were all heavily browsed by elephants). These species may also not be tolerant of the degree of inundation that occurs over much of the current floodplain, while the on-going abstraction from the alluvial aquifer could preclude the establishment of any species from a substantial part of the floodplain (Shafroth et al., 2000). The shrubs and short trees of *C. megalobotrys* that have replaced stands of riparian forest indicate that this species is capable of recruiting under the current ecohydrological conditions across most of the floodplain, but it is not known whether some of these will grow into tall trees or be permanently stunted by water stress and elephant browsing. A number of tall trees that are common in the riparian zone of other rivers in the region, such as *Combretum imberbe* Wawra and *Diospyros mespiliformis* Hochst. ex A. DC., could also form tall stands at the site but are currently absent from the site for unknown reasons. Future management of this narrow stretch of riparian woodland of disproportionately high biodiversity value could therefore benefit from an increased understanding of the dispersal and establishment of all the common riparian trees of the region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank SANParks staff, particularly Steven Khosa, for providing access to the study site, historical rainfall data and assistance in the field. SAEON funded the fieldwork component with funds from the National Research Foundation of South Africa, and SAEON research assistants collected much of the annual tree status data, particularly Patrick Ndlovu and Mightyman Mashele. The Physiological Ecology Laboratory at Kansas State University funded the isotopic analysis. Anonymous reviewers for constructive comments that improved the paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121264>.

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