Diversity, population structure and regeneration patterns of *Faidherbia albida* vegetation community in the Zambezi Heartland area

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Abstract: The objectives of this study were: (i) to establish the diversity and population structure of *Faidherbia albida* community, and (ii) to determine major environmental factors that influence recruitment and regeneration of *F. albida* in the Zambezi Heartland area. *F. albida* woodland community constitutes an important habitat in Lower Zambezi (Chongwe) National Park, Zambia and Mana Pools National Park, Zimbabwe which forms the Zambezi Heartland. Data on woody vegetation and environmental variables were collected in 2005 from 25 sample plots distributed across the study area using a stratified random design. A total of 38 tree species were recorded with Mana Pools National Park ($H' = 1.3$) having a higher species diversity compared to the Lower Zambezi National Park ($H' = 0.8$). *F. albida* tree density was significantly higher in Lower Zambezi National Park than in the adjacent Mana Pools National Park ($P < 0.05$). The size class distribution of stems of *F. albida* exhibited roughly a negative exponential or "inverse *J*" curve, however, with Lower Zambezi National Park having a higher recruitment of seedling compared to Mana Pools National Park. The lower *F. albida* tree density and regeneration capacity in Mana Pools National Park may be attributed to increased herbivore pressure, changes in river flooding regime that followed the river impoundment at Kariba Dam, and also variation in soil composition.

Key words: Elephant, herbivory, protected area, savanna.

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Introduction

Several reasons have been proposed for the reduced regeneration and recruitment of woodlands in the savanna ecosystem. Suppression of regeneration by large herbivores, such as the elephant (*Loxodonta africana* Blum), is considered to be the primary factor (Baumgartner *et al.* 2015; Gandiwa *et al.* 2011; Kupika *et al.* 2014; O'Connor *et al.* 2007; Staub *et al.* 2013; Styles & Skinner 2000). Other factors include seed predation, disease and fire, soil, latitudinal gradient, climate variables and their interactive effects (Barthelemy *et al.* 2015; Bond 2008; Roques *et al.* 2001; Sarker *et al.* 2014; Smith *et al.* 2013). Amounts of seed rain, dispersal mechanisms, processes related to
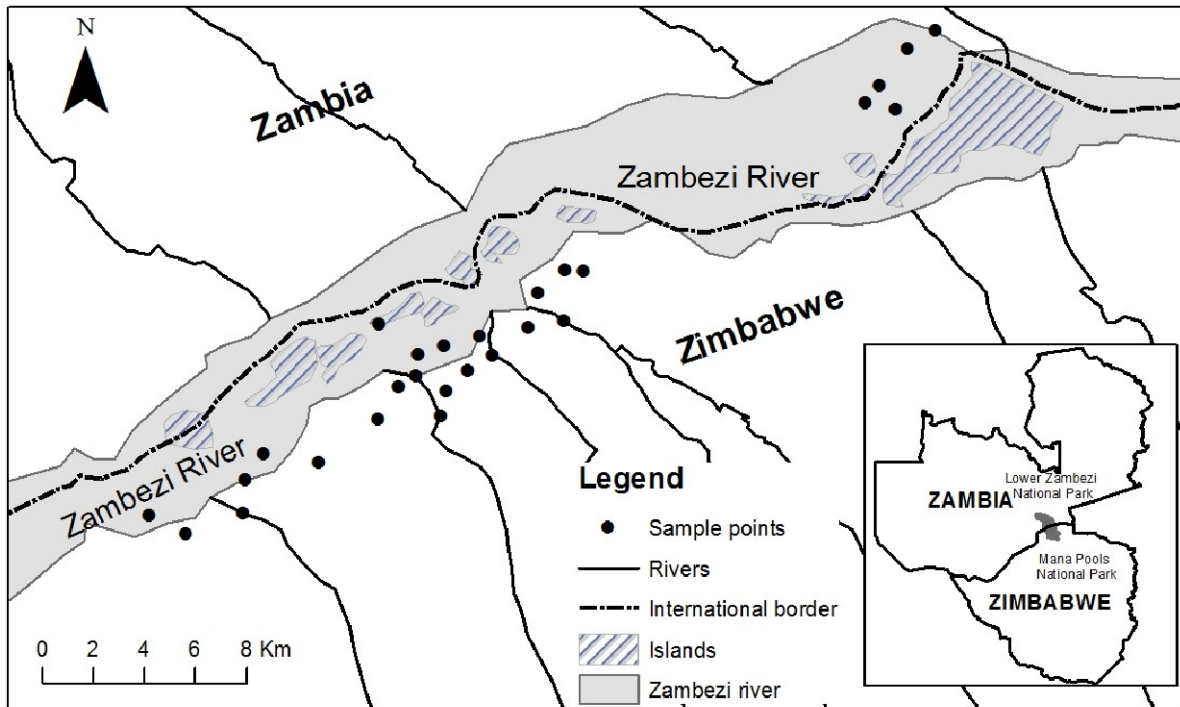
Fig. 1. Location of Lower Zambezi National Park (Chongwe National Park) and Mana Pools National Park in the Zambezi Heartland area.

seed dormancy (Tybirk *et al.* 1992) as well as inter- and intra-specific competition (Brown *et al.* 1998; Harrington 1991) are also contributing factors.

The Zambezi Heartland system has been subjected to a series of large-scale river control through construction of dams, e.g., Kariba Dam between Zambia and Zimbabwe. The dams have segmented the natural hydro-biological system with undoubted impact on biota (Gope *et al.* 2015). Riparian vegetation has been most affected in many places, aggravating erosion (Dunham 1990). Quantitative data on flood-related mechanisms critical to growth and regeneration of plants in the floodplain are, however, limited (but see Gope *et al.* 2015). The Zambezi Heartland system is entirely situated within semi-arid savanna, and is, therefore, potentially prone to water stress during low rainfall years. Effects of altered hydrology are likely to be reflected in performance of long-lived (> 150 years) key components of the riparian community, such as the pioneer *F. albida* which is a widespread species across Africa (Sileshi *et al.* 2014). The species colonizes newly created substrates (Dunham 1989). Conditions of the riparian zone may, therefore, be evaluated through mortality, dieback and population structure of *F. albida*.

The present study offers an opportunity to evaluate changes in condition of an area by comparing vegetation status within and outside a protected area. This study will contribute in understanding the flood-related mechanisms critical to the growth and regeneration of floodplain woodlands in Africa. Understanding the dynamics of species and ecosystems will help to predict and minimize the possible consequences of human activities as well as enhance the management of natural resources. Presently, there appears to be some decline in *F. albida* and *Milletia* spp. in Mana Pools National Park (Ncube *et al.* 2013; Ndoro 2013).

Various reasons have been proposed for the reduced regeneration and recruitment of various tree species in savanna ecosystems. These include the suppression of regeneration by large herbivores such as elephants (Dunham 1989; Styles & Skinner 2000), seed predation by insects (Mason 2000), disease and fire (Belsky 1984). Interactive effects among some of these factors in limiting regeneration and recruitment have also been highlighted (Roques *et al.* 2001). The amount of annual seed rain, dispersal mechanisms, processes related to seed dormancy (Tybirk *et al.* 1992) as well as inter- and intra-specific competition (Brown *et al.*

1998) are some important factors in the population dynamics of plant species. It appears, therefore, that there is interplay among some of the above factors in influencing the regeneration and recruitment patterns of *F. albida* in the Zambezi heartland area.

F. albida provides shade to large mammals in the hot season, mainly due to its unusual phenology that sheds leaves during the wet season and turning green during the dry season (Sileshi *et al.* 2014). Thus, this study aimed at enhancing our knowledge on the present status on *F. albida* vegetation in the Zambezi Heartland area. Specifically, the objectives of the present study were twofold: (i) to establish the diversity and population structure of *F. albida* community, and (ii) to determine major environmental factors that influence the recruitment and regeneration of *F. albida* in the Zambezi Heartland area.

Materials and Methods

Study area

The study area is represented by the Lower Zambezi National Park (Chongwe National Park) on the Zambian side (15° 07' - 15° 44' S and 29° 10' - 30° 10' E) and Mana Pools National Park on the Zimbabwean side (15° 40'-16° 20' S and 29° 08' - 29° 45' E; altitude 360 m a.s.l.) (Fig. 1). The spatial extent of the two protected areas is the Lower Zambezi National Park (4,092 km²) and Mana Pools National Park (2,196 km²). Lower Zambezi National Park and Mana Pools National Park are both downstream of Kariba Dam. Soils covering much of the southern section of the valley floor (i.e., occupied by mopane [*Colophospermum mopane*] vegetation) are derived from Karoo sandstones. The surface horizons are mainly fine or medium grained acidic sandy loams. The study area has a semi-arid climate, with rainfall (annual range 600 - 800 mm) usually confined to the period November to March. Major vegetation communities include: riparian vegetation on the alluvial areas alongside the larger rivers which support *F. albida* woodland, mopane woodland, *Combretum imberbe / Terminalia prunioides*, *Diospyros kirkii* wooded grassland, and *Colophospermum mopane / Kirkia acuminata / Terminalia prunioides* woodland on ridges among other species.

During the dry months of May to October, the Mana Pools National Park attracts a high density of big game into the riparian woodlands, which include elephant, hippopotamus (*Hippopotamus amphibious*, L), buffalo (*Syncerus caffer*, Sparrman), greater kudu (*Tragelaphus strepsiceros*, Pallas), eland (*Taurotragus oryx*, Pallas), zebra (*Equus quagga*, Gray), lion (*Panthera leo*, L), leopard (*Panthera pardus*, L), impala (*Aepyceros melampus*, Lichenstein), waterbuck (*Kobus ellipsiprymnus*, Ogilby), warthog (*Phacochoerus aethiopicus*, Pallas), baboon groups (*Papio ursinus*, Kerr), vervet monkey groups (*Cercopithecus aethiops*, L). The study area's once healthy rhinoceros population was decimated by poaching and this led to their translocation to safer areas where they previously existed. A detailed description of the study area is provided by Ndoro (2013).

Study design

The study was based on a completely randomized design with three sampling levels. The area was divided into three sampling levels based on herbivory intensity as follows: "High herbivory" referred to Mana Pools National Park outside the enclosure. "Moderate herbivory" referred to the Zambian Lower Zambezi (Chongwe) National Park opposite the Mana Pools Area across the Zambezi River, and "No herbivory" to an enclosure that excludes large herbivores, and located in the Mana Pools area. The three areas were treated as sampling sites from which random sampling points were drawn. There were nineteen replications in the Mana Pools area outside the enclosure, five in the Lower Zambezi National Park (Chongwe National Park) and one in the Mana Pools enclosure.

The sampling points were located randomly into units of apparently homogenous vegetation on the basis of tonal differences on the aerial photographs at a scale 1:25 000. An outline of the boundaries of each vegetation units was made on acetate sheets placed on top of the prints. Positions of sampling points were selected by super-imposing a grid system on the marked areas, and random number tables were used to generate points on grid intercepts.

As the study was intended primarily to assess structure and composition of *F. albida*, woodlands, 18 of the 25 points were deliberately located in the *F. albida* dominated woodland. The remaining seven were sited on mixed *F. albida* woodland. Points which fell in areas with tall *Vetiveria nigritana* Benth grass, were moved to nearest and accessible zones. None of the sampling points was, however, located closer than 30 m from a route to avoid possible effects on the vegetation. Geogra-

phical Positioning System (GPS, Garmin 92 GPS, UK) was used to indicate exact location of each sampling point. Sample plot size was determined using the nested quadrat technique (Mueller-Dombois & Ellenberg 1974). The assessment showed that a 15,000 m² (100 m × 150 m) sample plot captured at least 15 individuals *F. albida* plants. Rectangular plots were preferred as they proved easier to mark, and these were marked with the located sampling point marking the centre of a plot.

Data Collection

Woody vegetation

Data were collected between March and April in 2005 after a reconnaissance trip carried out in February of the same year. This was considered the best time of year for botanical field research in Southern Africa (Walker 1976).Tree species were identified in the field in 100 m × 150 m sampling plots. Samples were collected for those species that could not be identified in the field or whose identification needed confirmation at the National Herbarium, Harare, Zimbabwe. For all *F. albida* plants of a basal diameter greater than 2 cm, the following were recorded: (i) basal stem circumference by using a Sterling Fiberglass Measuring Tape (Australia), (ii) number of trees, and (iii) seedlings in sampling plot. In the case of multistemmed trees, where more than one trunk appeared to emerge from the same root stock and circumference for each trunk were recorded, but the whole was regarded as a single individual for computation purposes (Krebs 1972).

Edaphic Variables

Three sub-samples of soil were excavated by a soil augur from three random positions, to a depth of 20 cm from each of the 25 sampling points [20 cm (length) × 20 cm (width) × 20 cm (depth)]. These were made into composite samples approximating ± 2 kg each following Soedarson & Kuswata (1991). Soil colour was determined in accordance with the Musell Color Company chart (2000). Soil physical (% clay, % silt, % sand) and chemical (pH, Ca, Mg, K, Na, N, P) analysis was carried out according to the methods of Anderson & Ingram (1993).

Particle size distribution was determined on a single 100 g (sandy soil) or 50 g (clay soil) by the Bouyoucos (1936) hydrometer method. pH was determined on a single sub-sample with a glass electrode pH meter on a 1:5 suspension of soil in 0.01 M calcium chloride solution (15 g soil: 75 ml $CaCl_2$). Soil nitrogen was determined titrimetrically on the NH_4^+ released by modification of the Conway micro-diffusion method as described by Bremner (1965).

Phosphorus was determined calorimetrically on the leachate obtained from 4 g soil according to the method of Saunder & Metelerkamp (1962). Extractable bases (K, Ca and Mg) were determined on the filtered leachate: K and Na were determined by flame photometry, and Ca and Mg by atomic absorption spectrometry. A value for total extractable bases was obtained by summation of the four cations.

Data analysis

Data were summarised per plot for tree density, diversity and basal area following methods outlined by Gandiwa & Kativu (2009). The Shannon-Weiner diversity index (H') (Magurran 1988) was used to determine tree species diversity. Species diversity was compared between sites using one-way analysis of variance (ANOVA) since a Shapiro-Wilk test showed that data were normally distributed. Differences in the density of *F. albida* trees were determined using the Chi-Square test. Canonical Correspondence Analysis (CCA) using CANOCO, version 4.0, Netherlands (ter Braak 1995) was used to explore species-environment relationships. The following nine explanatory variables were explored: (a) % clay; (b) % silt; (c) % sand; (d) % K; (e) % Na; (f) % Ca; (g) pH; (h) ppmP; and (i) ppmN. Neither transformation of species data, nor down weighting of rare species was used. The significance of correspondence between floristic and environmental variables was tested with the Monte Carlo permutation test available in CANOCO. Relations were considered significant at $P < 0.05$ throughout the analysis.

Results

Species composition and abundance

A total of 38 tree species were recorded in the 25 sampling. The enclosure plot had the highest species diversity ($H' = 2.9$) followed by Mana Pools National Park ($H' = 1.3$) and lastly, Lower Zambezi National Park ($H' = 0.8$). Only five species were common to all sampling, namely, *Dichrostachys cinerea, F. albida, Gardenia volkensii, Kigelia africana* and *Trichilia emetica*. Two shrub species,

Diospyros sinensis and *Croton megalobotrys,* frequently occurred. The Lower Zambezi National Park had a significantly higher density of *F. albida* followed by Mana Pools National Park, whereas the enclosure had the least ($\chi^2 = 28$, df = 2, $P < 0.0001$; Table 1).

Table 1. Density of *F. albida* trees per hectare in the three study sites.

| Site	Total area sample m^{-2}	Total number of *F. albida*	Density ha^{-1}
Mana Pools National Park	285,000	395	14
Lower Zambezi National Park	75,000	299	40
Enclosure	60,000	49	8

Size class distribution

The size class distribution of stems of *F. albida* exhibited roughly a negative exponential or "inverse *J*" curve. The smallest size-class (< 0.01 m²) represented seedlings recorded for the three sites (Fig. 2). This size class showed the highest percentage (68 %) of individuals when considered for the whole study area. This indicates that *F. albida* is an *r*-strategist which is characteristic of pioneer species. A majority of the seedlings were found in drying pans. *F. albida* seedlings appeared to form clumps in the middle of former marshy areas, leaving the edges of the pans empty of any seedlings. Much fewer seedlings of the species were recorded in the Mana Pools area (334) than in the Lower Zambezi National Park (1,121).
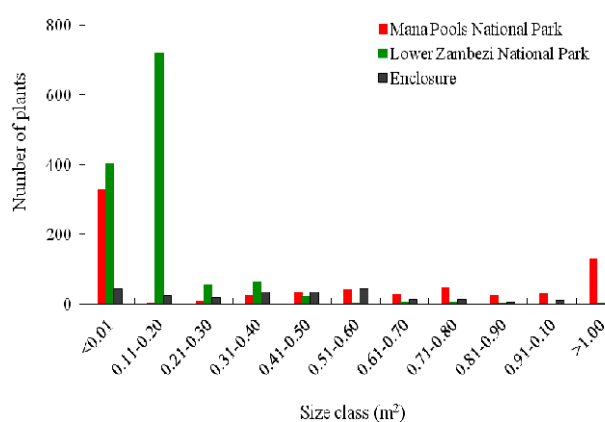
Fig. 2. Basal diameter size class distribution of *F. albida* for the three sites in the Zambezi Heartland area.

Vegetation environment relationships

There was a significant influence of edaphic variables along the first canonical axis ($F = 4.25$; $P < 0.05$). A test of the canonical axes was also significant ($F = 1.90$; $P < 0.05$). The first axis accounted for much of the variation (55.0 %). The second axis accounted for a further 28.1 % of the variation (Fig. 3). Axes 3 and 4 accounted for 32.0 % of the remainder of the variation. Total inertia (total variance in the species data/sum of all unconstrained eigenvalues) was 2.4. The edaphic variables explained 36.6 % of the residual inertia. Out of the ten edaphic variables, only four (sand, Ca, Mg and pH) contributed significantly to the total variance of the floristic data (Table 2). Accordingly, a significant correlation ($F = 3.91$; $P < 0.05$) was found between the first species axis and the first environmental axis (0.9). Of the cumulative variation explained by the first three axes, Axis 1 accounted for 23.3 % variation, Axis 2 accounted for 35.2 % variation and Axis 3 accounted for 42.5 %. The overall test showed that the effect of edaphic variables on species distribution was significant ($P < 0.05$).
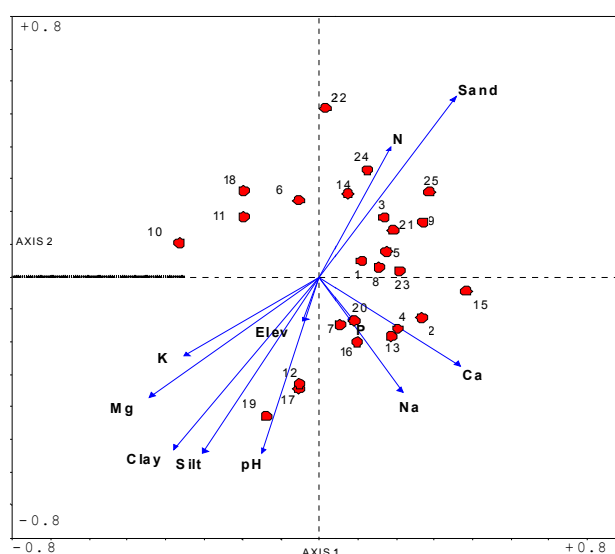
Fig. 3. Plot-environment biplot from Canonical Correspondence Analysis. Notes: numbers 1 to 25 represent the sampling plots and in bold are the measured soil variables.

Discussion

Our results suggest that *F. albida* has an unstable population structure within the Mana Pools National Park. This contrasts the situation

Table 2. A summary of the significance of the effects of environmental variables on species.

Soil variable	*F*-ratio	*P*-value
Clay	0.74	0.66
Silt	2.11	0.03
Sand	2.13	0.08
pH	1.93	0.05
Na	0.62	0.72
K	0.86	0.56
Mg	2.95	0.15
Ca	2.28	0.01
P	1.38	0.21
N	2.37	0.03
Elevation	2.58	0.13

in the Lower Zambezi National Park which has distinct lower and mid-size class individuals. The situation in Mana Pools National Park reflects minimal recruitment and, therefore, decline of *F. albida* species. Moreover, differences in floristic composition were recorded across the study area. The diversity of *Acacia* in Mana Pools was low. For example, no *Acacia tortilis* was encountered in the sampling plots of Mana Pools National Park, except the enclosure. A study for similar ecosystems (Traoré *et al.* 2007) showed that the low diversity of *F. albida* is mainly influenced by environmental factors in eastern Burkina Faso. Elephant herbivory is a possible factor influencing regeneration, diversity and recruitment of *F. albida* in Mana Pools National Park as also reported by Ndoro *et al.* (2015, 2016). Seedlings hardly graduate to the sapling stage. The absence of saplings indicates substantial herbivore pressure on young age classes. This has also been reported in studies conducted elsewhere (Birkett 2002; Gandiwa *et al.* 2011; Kupika *et al.* 2014; Mapaure & Mhlanga 2000).

All adult *F. albida* trees observed in Mana Pools National Park had elephant scars. Density estimate for Mana Pools National Park in 2003 was 1.96 elephants km^{-2} and was higher than that of Lower Zambezi National Park (0.37 elephants km^{-2}) (Dunham 2003). Thus, elephant density is a possible factor to explain the higher tree mortality in Mana Pools National Park especially during the dry season when large numbers of ungulates concentrates in relatively small areas near water points (Ndava 2005) as also recorded in Gonarezhou National Park (Gandiwa *et al.* 2012). Moreover, small herbivores such as the impala

may possibly hamper woodland regeneration during herbivore population peaks (Moe *et al.* 2009; O'Kane *et al.* 2014).

Dunham (1991) and du Toit (1982) reported that the study area was increasingly becoming drier since the last flooding in 1957 prior to damming. The closure of the Kariba Dam floodgates in 1959 caused an immediate drop in water level (Dunham 1994). Since 1981, rainfall throughout southern Africa has been low and water flow into Kariba Dam was too low to require floodgates to be opened. The decrease in subterranean water reserves in the study area would probably be detrimental to woody riparian species, particularly *F. albida*. The decrease in old *F. albida* trees in Mana Pools National Park could possibly be linked to plant water stress induced by lowered water table due to channel abandonment (Gope *et al.* 2015). Roots of juvenile *F. albida* trees are able to follow the receding ground water table for some time. By the time trees mature, they are not able to tap from the receding water table. Thus, spatially heterogeneous and temporally stochastic regeneration events, together with occasional tree mortality caused by channel abandonment, create the complex pattern of coarse-grained woodland patches presently observed in Mana Pools National Park floodplain (Dunham 1991). Elsewhere, water stress resulting from river impoundment or abstraction has been implicated in mortality of *F. albida* in the Kuiseb River, Namibia (Theron *et al.* 1980).

Soils showed a clear dichotomy as regards nitrogen content. Some soil samples recorded no nitrogen at all, yet close to 50 % of the soil samples recorded nitrogen content of 2 - 32 ppm. Such nitrogen values are far much lower than the average (0.2 % - 0.5 %) recorded for the savannah (Brook 1983). This indicates that soils in the floodplain are generally nitrogen deficient. The highest nitrogen content (32 ppm) that was recorded in Lower Zambezi National Park perhaps results from high water table on that part of the study area. The samples recorded potassium levels ranging between 0.13 % and 0.40 %. These low values indicate absence of recent flooding in the Zambezi Heartland. These results indicate that floods largely control differences in *F. albida* associations within the Zambezi Heartland. Floods are responsible for increasing potassium supply through groundwater input as groundwater is poor in phosphate (3 - 34 ppm), but rich in calcium (0.86 - 10.32 %), which is a sink for potassium. Phosphorus deficiency is a major factor limiting

the establishment of most nitrogen fixing trees in many soils of degraded lands throughout tropical Africa (Barnes 2001), and this could be the case with the Zambezi Heartland. Phosphorus increases in the dry season. Sufficient amounts of phosphorus have been found to increase nodulation and nitrogen fixation. Higher levels (above 3.0 mol m^{-3}) of phosphorus, however, reduce plant growth, nodulation and nitrogen fixation (Barnes 2001). This could explain why the sampling plots with higher amounts of phosphorus had lower amounts of nitrogen and those with sufficient phosphorus had higher nitrogen content.

The observed seedling level for the study sites indicates that *F. albida* has high regeneration capacity characteristic of pioneer species. Moisture stress, however, limits seedling emergence and establishment, while trampling and browsing activities prevent recruitment (Ndibalema *et al.* 2014). River damming was the primary initiator of woodland change, and large herbivores now inhibit recovery. Large parklands of *F. albida* in Mana Pools National Park are fast declining, and are being replaced by other species. Smaller units of the tree species now remain. These are likely to be of significance in future population reorganisation as they act as seed banks.

Conclusion

This study has highlighted the striking extent to which different areas of woodland in relatively close proximity and of similar composition differ in structure and species composition. The short life span of *F. albida* tree species indicates that the *F. albida* woodlands of the Mana Pools National Park may shortly transform, especially under present conditions of low recruitment. Given an increase in elephant density near surface water sources, especially in the dry season, managers are faced with the choice between intervention to protect the declining *F. albida* woodlands or non-intervention to allow for succession but change in woodland composition. The present transformation of the *F. albida* woodland may not be attributed to effects of dam impoundment alone, but other factors related to herbivory and drought.

Acknowledgements

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