MANAGEMENT

The impact of fire and elephants on a mixed woodland in Liwonde National Park, Malawi: the results of a thirty-seven year study

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Abstract

Shortly after Liwonde National Park was gazetted in 1973, the influence of fire and elephant foraging was expected to be the priority management consideration. A number of permanent woodland plots were established, including a 200×10 m belt transect in open mixed woodland. All woody plants >1.5 m high were individually followed individually over the 37-year study. Declines in canopy tree numbers (58%) and species losses (7 of 19) were gradual throughout the period. Mean physical characteristics such as height, stem basal area and canopy cover were either stable (height) or increased slowly through the first three sample periods, with notable gains in the last 16 years. In spite of the substantial decline in the number of individuals, growth of the surviving larger trees compensated for these losses until 2014. During the first 21 years, upper canopy tree loss through fire remained stable at 0.8 trees/year. Over the last 16 years mean annual fire losses was 1.1 trees/year with five trees lost in 2015. Elephant damage through 'pushovers' remained very low at 0.3 trees/year up to 1999. With increasing elephant numbers this increased to 1.1 trees/year, reaching 5.0 trees/year in 2015. All pushovers were ultimately killed by fire. Elephant foraging had a strong synergistic effect on fire mortality. Tree species remain in the shrub layer as rootstock or fire suffrutices. With continued burning to ground level each year these will gradually die out. Damage and mortality at this intensity will eventually reduce this woodland to tall dense grassland with scattered large trees.

Résumé

Peu de temps après la démarcation officielle du Parc national de Liwonde en 1973, il était évident que l'influence de l'incendie et du fourrage par les éléphants seraient des préoccupations prioritaires de gestion. Plusieurs terrains ayant des forêts claires permanentes ont été établis, y compris un transect de ceinture de 200×10 m dans une forêt claire mixte ouverte. Toutes les plantes ligneuses d'une hauteur >1,5m ont été individuellement suivies au cours de l'étude de 37 ans. La baisse du nombre d'arbres de canopée (58%) et la perte d'espèces (7 sur 19) ont été progressives tout au long de la période. Les caractéristiques physiques moyennes telles que la hauteur, la surface basale de la tige et la couverture de la canopée étaient soit stables (hauteur), soit augmentaient lentement au cours des trois premières périodes d'échantillonnage, avec des gains remarquables au cours des 16 dernières années. Malgré le déclin substantiel du nombre d'individus, la croissance des arbres plus grands survivants a compensé ces pertes jusqu'en 2014. Au cours des 21 premières années, la perte des arbres de canopée supérieure par l'incendie est restée stable à 0,8 arbres/an. Au cours des 16 dernières années, les pertes annuelles moyennes dues aux incendies étaient de 1,1 arbres par an avec cinq arbres perdus en 2015. Les dégâts causés par le terrassement des éléphants sont restés très faibles à 0,3 arbres/an jusqu'en 1999. Avec un nombre croissant d'éléphants, cela a augmenté à 1,1 arbres par an, atteignant 5,0 arbres par an en 2015. Tous les arbres terrassés ont finalement été brûlés par les incendies. L'activité de fourrage par les éléphants a eu un effet synergique fort sur la mortalité due à l'incendie. Les espèces d'arbres restent dans la couche d'arbustes en tant que porte-greffe ou sous arbrisseaux des incendies. Après avoir continué de brûler au niveau du sol chaque année, ils vont graduellement disparaître. Les dégâts et la mortalité à cette intensité finiront par réduire cette forêt claire à de hauts herbages denses avec de grands arbres dispersés.

Introduction

Liwonde National Park (NP) is a relatively small protected area (540 km^2) situated in Malawi's section of the Great East African Rift Valley, just south of Lake Malawi and Lake Malombe (Fig. 1). Elephants, which historically roamed freely throughout this valley, are now restricted to thee conservation areas, Liwonde NP and Mangochi Forest Reserve in the north and Majete Wildlife Reserve in the south. Management of Liwonde has generally remained weak due to inadequate funding, limited technical ability and conservation being undervalued by Government. However, management has been successful in protecting the Park's elephant population. The elephant population, which stood at 200 in 1977, was expected to reach 800 by 2015 (Bhima 1998). Recent counts have shown this forecast to be correct (Research Office, Liwonde NP, pers. comm.). At 1.47 elephant/km^2, this density is more than twice as high as in Kruger NP (0.68/km^2 in 2010), where the landscape is similar to that at Liwonde (Pienaar 2012).

Liwonde is principally a landscape of mopane woodlands (74%), which are distributed throughout the Park in various complexes. However, there are also areas of other vegetation, including marshes, floodplains, dry forest/thickets, riverine forest/thickets, tall-grass tree savanna and mixed (undifferentiated) woodlands on several rocky hills and their piedmonts . The flora of Liwonde is surprisingly rich with more than 1030 species. Dudley (1994) describes the vegetation in detail.

Late season fires regularly affect all vegetation types in the Park. Their effect on vegetation varies. Mopane woodlands are seldom seriously damaged by fire as canopy cover is sometimes more than 50% and grass cover is normally poor (Thompson, 1960). Fire penetrates into riverine and dry forest vegetation due to elephants destroying the mopane–forest interface. Fire has greatest effect on the more open vegetation types such as the tall-grass tree savanna along the western flowing perennial rivers and the mixed woodlands of the hills and their piedmonts. For both types there is higher grass biomass.

Study site

The study site was chosen near Naifulu Hills located next to the eastern boundary of the park (Fig. 1A). The species mix found in the transect closely matched the '*Combretum* woodland' studied by Robertson (1984) and this woodland was used for comparison. I have simply called it 'mixed woodland'. Sometimes the term *chipya* is used to describe this type of woodland, which is capable of surviving intense annual burning.

Over the duration of the study, the plot in the piedmont area of Naifulu Hill (gradient 2–6%) contained a mixture of 34 species of trees. Medium-sized species (6–8 m high) included *Combretum* spp., *Terminalia* spp. and *Diospyros* spp.); large species (10–18 m) included *Pseudolachnostylus maprouniefolia, Xeroderris sthulmanni, Burkea africana* and *Acacia* spp.) (for a full list, see the Appendix). The rocky hill slopes above were much richer, with over 45 species recorded along a transect to the summit. The level plain (gradient 0.4%) to the west was covered by mopane woodland. Here, soils are deep, compact, sandy loam to sandy clay on a sandy clay subsoil (Mitchell and Ntokhota 1974).

The shrub layer included a large number of woody root and fire suffrutices embedded in a matrix of dense high grass (1.5–2.5 m high). Grass genera included *Panicum, Heteropogon, Bothriochloa* and *Setaria*, with tall *Hyparrhenia* being dominant. Basal area of the clumps was less than 20% with canopy cover 80–90%. Grass biomass was not measured but was undoubtedly more than 200 g/m^2. Robertson (1984) recorded similar values (basal area, canopy cover and biomass of grass) at Kusungu National Park.

Fires originate either directly or indirectly through the activities of the dense rural population just east of the boundary. Human presence is clearly evident from the well-worn paths that can be observed winding through the Naifulu Hills. Information from scouts and other field personnel and personal observation all

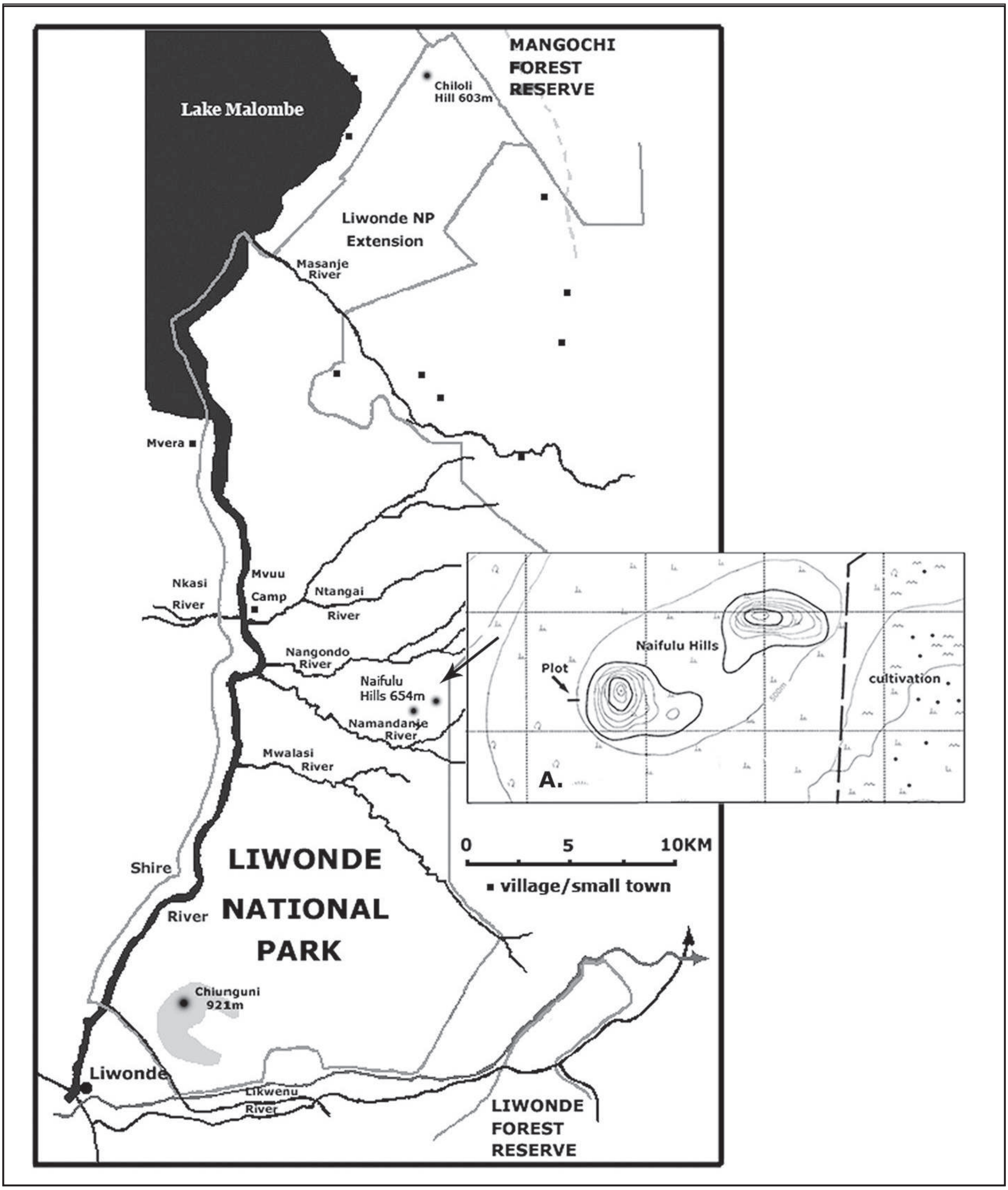

Figure 1. Liwonde National Park showing principal hills and rivers, boundaries and associated villages and small towns. **A**. Inset shows detailed plot settling at Naifulu Hills and cultivation and houses near eastern boundary (scale: 1 square=1 km^2)

indicate that these areas are subject to intense annual late-season fires.

My initial objective was to investigate the influence of fire on this woodland community over an extended time period. The location of the site seemed suitable for this study. Over time, as the elephant population increased, their activities extended into the interior of the Park. In response to this new development, the objective of the study was expanded to include the effect of elephant browsing and its interaction with fire.

Materials and methods

The 10×200 m transect was established west of Naifulu Hills' southern peak. The eastern end of the transect included 30–40 m of the rocky base of the hillside, and it extended westward along the gently sloping piedmont, ending well inside the boundaries of the *Combretum* woodland. The four corners and two mid points were marked by 50 cm painted angle iron stakes. In later years these points were re-established using a Garmin GPS.

The transect was divided up into twenty 10×10 m quadrats, with the first quadrat at its western end. All woody species ≥1.5 m high were identified, tagged, located using an xy-coordinate system and measured. Dead trees, where they could be identified and located, were also recorded but only for basal area. The principal measurements taken were height (HT), basal area and canopy size. Height was measured to the nearest 0.25 m using a Suunto inclinometer with a range finder. Basal area was determined by calipers to the nearest 0.5 cm from two perpendicular basal diameter readings. Two measurements (sometimes three) were required due to the irregular shape of many plant stems. Particular care was taken to note the basal diameter of the coppicing shoots and whether they originated from a single original stem or were themselves all basal. Canopy was measured directly by a marked board where plants were under 4 m in height. Taller trees were measured using a tape laid on the ground. In both cases, two perpendicular measurements were made, one along the length of the plot, the other along its width. Values were rounded to the nearest 0.5 m. Any canopy shape irregularities were noted in the field and each canopy was drawn on graph paper (mm^2) in correct proportionate shape as observed. Canopy areas were determined from these drawings.

Other aspects such as form and browse damage were assessed using an index system subdivided into age categories at assumed time of occurrence (≤1 year, >1 but ≤5 years, >5 years). The indices values are defined as follows:

Form: 0=basal stem unbranched below 2m; 1=branched between 0.5 and 2m; 2=branched below 0.5m

Browse damage: 0=plant unbrowsed; 1=some twigs and leaves browsed and/or minor bark stripping (≤0.5 m); 2=at least one main stem or branch broken and/or bark stripping (≤ 1. 0m); 3=two or three, but not all stem branches broken and/or severe bark stripping (≥1 m); 4=all major stems broken off, tree coppiced; 5=pushed over, alive; 6=killed

A second special enumeration was made of the woody plants within the shrub layer (<1.5 m). For each quadrat, a count was made of each species and their average height and basal area and total percentage cover were estimated, the estimate based on the measurements of a proportion of the plants present in each quadrat.

Additional detailed notes were made on the area and height of cover by woody plants intercepting all plot boundary lines, including those plants growing outside the plot.

The first survey was carried out in August 1979. Three further full surveys were undertaken in October 1991, August 1999 and July 2014. A fourth partial survey was done in April 1992, when only the shrub layer vegetation was assessed. A further partial survey (damage assessment only) was done in August 2015. Grass fires had occurred along the transect before the surveys carried out in 1991, 2014 and 2015.

Results and discussion

Canopy layers

Results are expressed in three vegetation levels: upper canopy (HT ≥ 3.0m), lower canopy (1.5 ≤ HT < 3.0 m) and shrub layer (HT < 1.5 m). While somewhat artificial, these categories provide an acceptable framework for analysis. Trollope et al. (1998) considered trees >3.0 m generally resistant (but not immune) to fire in Kruger NP. In this study trees above 6.0 m showed damage to crown via leaf and twig burn (fire index 1–2). Trees between 3.0 and 6.0 m showed limb charring with smaller structural branches killed (fire index 2–3).

However, trees under 3.0 m, the tallest crowns extending no more than 0.5–1.5 m above the grass canopy, were subject to more serious fire damage, including some individuals that lost some or all of their main branches to ground level (fire index 3–4). Of the 32 individually marked plants in 1979 with heights between 1.0 and 3.0 m, only seven were ever recorded as being taller than 1.5 m over the 37-year study. Only three individuals were able to 'escape' into the upper canopy. The rest, over time, declined to the shrub layer. Combining the marked and the simply counted plants of the shrub layer (a total of 283), no more than four were ever recorded taller than 1.5 m during this study.

The lower canopy is mostly a transitional stage, mainly of trees in decline from the upper canopy, the majority actually ending in the shrub layer. The lower canopy is effectively a fire-induced layer, the 3.0 m height acting as a barrier preventing replacement of trees lost in the upper canopy. The 1.5 m boundary of the shrub layer acts in a similar way. Once in the shrub layer, plants almost never leave.

Numbers

In 1979, 71 living upper canopy trees were marked and measured in the plot (Table 1). In addition, there was clear evidence of 14 more individuals, dead and most likely killed by fire. One, killed only earlier in the year, was standing, fully intact, measurable and identifiable. The remaining 13 existed only as stumps (1.0–1.5 m high), trees probably killed by fire, perhaps three or four years prior to this study. Using the living trees as reference and the basal areas of the stumps, their canopies and heights were estimated.

If the evidence of these 13 trees is accepted, the initial number of trees in the upper canopy was at least 85 (425/ha), perhaps as recently as 1972. By 2015, only 32 (160/ha) of the original 85 upper canopy trees remained, a decline of 61%. Over the course of the study, 49 individuals died while four others remained alive in the shrub layer. During the study a further four trees entered the upper canopy via growth from the lower canopy and shrub layer. Of the four, three remained in 2015. The other individual was no longer present in 2014 and probably killed by fire.

At the present rate of loss, few of the upper canopy trees will be present in 20 years. The three new additions to the upper canopy during the study period were of no real consequence.

The number of individuals in the lower canopy layers varied between 9 (45/ha) and 30 (150/ha). Numbers in the shrub layer varied between 267 (1,335/ha) and 413 (2,065/ha). No trend was discernable over the period with respect to numbers of individuals in these two strata.

Species

By 2015, eight of the 19 original tree species in the upper canopy were no longer present (Table 1). The weaker lower canopy contained only eight species originally (Table 2). Over the length of this study, this number varied between four and ten, with a total of 16 species recorded. Only two individuals of the original species listed in 1979 were present in 2014. The shrub layer included 33 mixed woodland species and contained all species found in the canopy layers. The species varied between the sample years but 21 were present in at least three of the four sampling periods. A further 10 species were found in two of the three years while 3 were found only once.

The upper canopy was initially not particularly species-rich, although the number approached the average of 23 species found by Robertson (1984) in her 10×50 m *Combretum* transects. However, the more stable shrub layer contained an additional 13 potential canopy species. This indicates that under more favourable conditions the upper canopy might have contained a greater number of species and perhaps numbers nearer to those found on the adjacent Naifulu Hill slopes. Robertson (1984) and White (1976) noted the importance of the shrub layer rootstock and fire suffrutices for the potential replacement of lost canopy species. Even with full protection, final reversion to woodland following a fire takes a long time. However the resulting woodland is likely to differ considerably in terms of both species and structure if potential canopy species are lost from the shrub layer (Robertson, 1984). The present poverty of species in the upper canopy may be the result of a long history of repetitive hot fires, as seven species were lost during the 37 years of this study.

Species survival and spatial pattern

In the upper canopy, four species occurring in numbers greater than two in 1979 showed significant declines: *Terminalia sericea* (100% decline), *Combretum adenogonium* (74%), *Terminalia stenostachya* (50%) and *Pericopsis maprouniefolia* (30%). The whole of the

Table 1. Evolution of the upper canopy in a mixed woodland transect in Liwonde NP, Malawi, from ca. 1972 to 2015

	~ 1972[1]	1979	1991	1999	2014	2015[2]
Number of tree species	19[3]	19	16	15	12	11
Number of living trees	85	71	56	49	40	35[4]
Mean tree height	6.6	6.7	6.9	7.2	7.7	7.6
Height of tallest tree (m)	17.5	18.0	13.3	12.8	12.6	12.6
Mean tree basal area (cm^2)	308	341	376	456	673	670
Total tree basal area (cm^2)	26,197	24,531	20,690	22,352	26,934	23,442
Net canopy cover (%)	37.8	35.5	29.6	32.5	41.1	36.7

[1]Values prior to 1979 include estimated structural characteristics of 14 dead trees. The heights and canopies of 13 of these were estimated based on basal areas of intact stumps and comparison made against trees in the plot with similar basal areas. The other dead tree was still standing and intact physically and identifiable.
[2]In 2015 only a damage assessment was made. Visual examination did not indicate any noticeable changes in height, basal area or canopy size in remaining trees since previous sampling date. Therefore, the 2014 figures were used for these trees.
[3]The 13 tree stumps are assumed to be of species observed to be present in 1979. Associated species, i.e. species not growing in the plot but with canopy overhanging it (see Appendix), are included in species number and canopy cover values.
[4]Since 1979, four trees were added to the canopy from the shrub layer (HT ≤ 1.5m): one new species (lost in 1999); one returned species and two species already present in the upper canopy. The last three remained in 2015, growing normally.

Table 2. Evolution of the lower canopy in a mixed woodland transect in Liwonde NP, Malawi, from ca. 1979 to 2015

	1979	1991[1]	1999	2014[1]
Number of tree species	8	4	10	6
Number of living trees	13	9	30	10
Mean tree basal area (cm^2)	180	83	103	52
Total tree basal area (cm^2)	2,342	666	3,093	567
Net canopy cover (%)	1.14	0.58	1.6	1.01

[1]Sampled one month after dry season fire. Values lower than expected due to fire loss of many coppice shoots of previous year.

decline of the last of these species occurred between 2014 and 2015 (Table 3). These four species represented 32 of the 39 trees lost in the upper canopy since 1979. Losses also varied according the location of the trees in the plot. Quadrats 17–20 at the rocky base of the hill had no loss of upper canopy trees, while *Combretum* and *Terminalia* species had 75% of their losses in quadrats 1–8.

Grass cover showed a similar pattern of variation. The rather thin growth and low height (1.0–1.5 m) of grass on the hillside became dense 2.0–2.5 m growth on the lower piedmont. The hottest and most intense fires likely occurred in quadrats 1–8. Also elephants do not enter into steeper rocky areas. No 'pushovers' were ever recorded in the quadrats 17–20. This location appeared to provide better security for all upper canopy species.

At the time of the initial survey in 1979, *Combretum* spp. and *Terminalia* spp. were most common in quadrats 1–8 in the upper canopy. A similar pattern was found in the distribution of the five most common species in the shrub layer. *C. adenogonium* was most common in quadrats 1–8, declining to very low numbers in quadrats 17–20. Similarly, *T. sericea* was mostly present in quadrats 5–8, declining to small numbers in quadrats 17–20. The other three species gradually increased in numbers from west to east along the full transect, with maximum numbers found in quadrats 17–20. Although *Combretum* spp. and *Terminalia* spp. can be found on the higher slopes of Naifulu Hills, they are not common there. This suggests that in addition to the influence of fire and elephants, soil factors may have affected the distribution of these two upper canopy species.

For the lower canopy there were too few individuals in any sampling year to look for pattern in loss of numbers. Individuals moved in and out of this layer and the individual plants present in 2014 were not identical to the plants recorded in 1979. Species survival for the shrub layer was not assessed. However, for the three sampling periods 1979–1999, quadrats 1–4 always had the fewest species or numbers while quadrats 17–20 always presented the highest values.

Species dominance

While basal area and canopy cover is often used by plant ecologists to evaluate dominance, in calculating it here I have also taken account of frequency and number. The dominance value for each species is determined by the average of the relative value (%) of each of these four variables. Sometime this value is called the species' 'importance value'.

Table 4 summarizes the dominance of the top four species in the upper canopy over the study period. Their dominance was considerable, although the trend was generally downward, 65 to 59%. The dominance of the two most dominant species remained stable (43–48%). While the dominance of the third and fourth placed species also remained stable (16–19%), the species were different in 2015.

The four most numerous and frequent tree species dominated at the start of the study, and their rankings were in line with these numbers. Although she measured dominance differently, Robertson (1984) also found that her *Combretum* plots were strongly dominated by three or more species. However, as mortality affected the canopy species of my Naifulu Hills transect differently, dominance rankings changed. The taller more massive trees became more dominant, with their larger basal areas and canopies compensating for their lower numbers and frequency.

C. adenogonium ultimately gave way to *P. maprouniefolia* and changed from being overwhelmingly dominant in 1979 to 2nd rank from 1999 onwards, while two other trees, *Crossopteryx febrifuga* and *P. angolensis*, moved into 3rd and 4th place, respectively. These two species occurred infrequently and achieved dominance due to their size alone. In 2015, the upper canopy continued to be strongly dominated by only four species. However, the total dominance of the top four species declined somewhat in 2015, with dominance more equally shared among the top four species in later surveys as structures of the upper canopy was altered by mortality and growth.

Dominance was not evaluated in the lower canopy and the shrub layer.

Physical characteristics: upper canopy

Tree height: Mean height, after initial stability, showed a small increase (Table 1). However, the height of the largest individual decreased from 18 m in 1979 to 12.6 m in 2015.

Table 5 summarizes the 'growth' of the original 71 living trees since 1979. Only 27% (18/71) could be considered to be growing normally (mean height increases >25%) or weakly (>10%); 11% grew marginally or showed decline, while 14%showed serious decreases in height of up to 25%. The remainder disappeared into the lower canopy (3%) or shrub layer (4%), or died (39%).

Table 3. Number of individuals of four principal tree species present in the upper canopy of a mixed woodland transect in Liwonde NP, Malawi in 1979 (first value) and 2015 (second value). Q=quadrat number.

Species	Q01–Q04	Q05–Q08	Q09–Q12	Q13–Q16	Q17–Q20	Q01–Q20
Combretum adenogonium[1]	4/18	2/3	0/3	1/5	1/1	8/30[1]
Terminalia sericea[1]	0/0	0/3	0/0	0/0	0/0	0/3
T. stenostachya	0/0	0/1	0/1	1/3	3/3	4/8
Pericopsis maprouniefolia	0/0	1/2	2/2	3/5	1/1	7/10
Total	**4/18**	**3/9**	**2/6**	**5/14**	**5/5**	**19/51**

[1]Two C. adenogonium and one T. sericea were still alive in the shrub layer as of 2014.

Table 4. Dominance values (%, left columns) and rank (right columns) of the top four ranked tree species in the upper canopy of a mixed woodland transect in Liwonde NP, Malawi in surveys carried out between 1979 and 2015.

Species	**1979**		**1991**		**1999**		**2015**	
Combretum adenogonium	31	1	25	1	21	2	18	2
Pericopsis maprouniefolia	17	2	23	2	24	1	25	1
Terminalia stenostachya	10	3	9	3	11	3	-	-
Diplorhynchus condylocarpon	6	4	-	-	-	-	-	-
Crossopteryx febrifuga	-	-	7	4	8	4	10	3
Pericopsis angolensis	-	-	-	-	-	-	9	4
Total dominance value for top four species	**65**		**64**		**63**		**59**	

Considering the length of this study one might have expected a large gain in height on all but the largest trees of the upper canopy. Coates Palgraves (2002) gives upper height values for all species in this study, with 10 m being the typical height of mature trees. For example, *C. adenogonium* and *T. sericea*, whose heights averaged 5.1 and 5.8 m, respectively, in 1979, could have been expected to approach 8–10m in 37 years in the absence of fire and elephants. Similar remarks apply to other species such as *C. febrifuga, Diplorhynchus condylocarpon, P. maprouniefolia, P. angolensis*, and *T. stenostachya*. In an area of better soils and slightly greater annual rainfall, Robertson's (1984) ten tallest trees averaged 12.5 m in her mature 0.05 ha *Combretum* plots. For our Naifulu Hills transect (0.2 ha) only two individuals ever reached this height over the 37 years of the study.

Tree basal area: Mean tree basal area increased by a total of 117% over the study period (Table 1). Total basal area, after an initial decline, regained its losses until ultimately declining by 10% between 2014 and 2015.

While the smaller trees, being more vulnerable to fire, were disproportionately lost over the years, the remaining larger trees continued to grow. Thus, there was a positive trend in mean basal area, which was small for the first 12 years but had increased significantly by 2014.

The pattern for total basal area is more difficult to explain. The greatest loss of trees (15, 1.25/year). occurred during the earliest sampling interval of 12 years. Over the next two sampling intervals of 8 and 15 years there were losses of 7 (0.88/year) and 9 (0.60/year) respectively, i.e. at rates much lower than during the first 12 years. From 1991, when the rate of tree loss slowed, the growth of the remaining more fire-resistant larger trees tended to more than offset basal area losses. Only in the transitional years 2014–15, when elephant had a major negative impact, did all basal area measurements decline. Even at its highest point in 2014, total basal area at 13.5 m^2/ha was less than the

Table 5. Changes in height of the 71 living upper canopy trees between one survey and the next, in survey of a mixed woodland transect in Liwonde NP, Malawi carried out from 1979–2014.

Species	**1979-1991**	**1991-1999**	**1999-2014**	**1979-2014**
Height increase >25% ('normal')	12	7	6	11
Height increase >10% ('weak')	7	7	10	8
Height change ±10% (little change or no growth)	19	26	8	8
Height decrease >10% (noticeable decline)	13	8	8	3
Height decrease <25% (serious decline)	4	0	5	7
Height decrease to <3.0m (lost to upper canopy)	2	4	2	2
Height decrease to <1.5m (lost to shrub layer)	6	4	4	4
Dead	8	7	13	28
Total trees evaluated over the period	**71**	**63**	**56**	**71**

15 m^2/ha found by Robertson (1984) in undisturbed *Combretum* woodland.

Net canopy cover: Net upper canopy cover, defined as total individual tree canopy cover minus overlapping canopies, was estimated at 37.8% in 1972 but had declined to 29.6% (by 21%) by the time of the 1991 survey (Table 1). Cover in 1999 increased to 32.5%, peaking in 2014 at 41.1% before declining sharply in 2015 to 36.7%.

Canopy cover followed a similar pattern to total basal area, probably for the same reasons. Declining tree mortality rates over the last 24 years allowed total canopy to recover. Again, the increased presence of elephants reversed these gains in 2015.

With annual rainfall >500mm and no edaphic limitations, a near closed canopy might be expected if fire and elephant were only minor influences (Walter 1971; Werger & Coetzee 1978).

Physical characteristics: lower canopy and shrub layer

The evolution of physical characteristics in the lower canopy followed a slightly different pattern, compared to the upper canopy. In summary there was no change in height, a strong decline in mean basal area (71%) and total basal area (76%), with net canopy cover being small and variable (0.58–1.60%) (Table 2). This supports the idea that this layer is a transition layer containing trees in decline.

For the shrub layer, only basal area and net canopy cover are relevant. Of the three inter-survey periods under examination, 1992–1999 was rather unusual. For both basal area and canopy cover, there was little change between 1979 (basal area: 5,832cm^2, 22cm^2/plant; cover: 1.48%) and 1992 (basal area: 5,851cm^2, 17cm^2/plant; cover: 1.12%). In 1999 the basal area values had increased to 12,989cm^2 and 40cm^2/plant, while cover was 1.25%. These figures highlight the capacity of woody plants in the shrub layer to persist in spite of intense annual fires.

Mortality factors

Table 6 summarizes the fire and browse indices of the trees in the upper canopy over the study period. The fire damage index averaged between 2.86 and 3.79. Any average over 3 suggests a fire impact causing serious damage to trees. Serious browse damage is clear when elephant push over trees or break off the main stem near the ground. 2014–2015 was a bad year for browse damage. However, more minor browse damage is difficult to separate from moderate fire damage when looking back in time.

The cause of tree death over the early years was principally due to fire, deaths being rather constant at slightly less than one tree/year over 1979–2015. As I was not able to account for the cause of all deaths over this period, this figure should be considered a conservative one.

With grass biomass over 200 g/m^2, late dry season bush fires will be hot (2,000 kJ/s/m) (Trollope & Potgieter 1983). Bell (1981) records temperatures of this level killing stems >5 cm diameter. However, cumulative hot fires may kill large standing trees (Trapnell 1959), as confirmed by this study, which found evidence of trees up to 5 m high being killed by fire. Commonly, trees 7–10 m high showed evidence of crown pruning by fire, i.e. death of ends of small branches, even in the upper part of the canopy. While naturally resistant to fire, many of the largest trees showed large fire scars reaching the xylem tissue (fire index 3). Eventually, repeated burning will kill these trees.

Table 6. Mean fire and browse indices and numbers of tree losses in the upper canopy due to fire and elephant damage in 1979–2015. Indices and numbers cover the period since the previous sample. Numbers of living trees at time of each sample are also shown, with values in brackets indicating percentage survival since 1972.

	1972	1979	1991	1999	2014	2015
Mean fire index	-	3.09	2.86	3.16	3.40	3.79
Mean browse index	-	0.00	0.54	0.10	1.45	1.77
Canopy trees pushed over by elephant (certain/maybe)[1]	-	0	5	1	10/2	5
Canopy trees killed by fire (certain/ maybe)	-	14	2	6	8/3	6
Number of living trees at end of previous sampling period[2]	85[3]	71 (84%)	63 (74%)	56 (66%)	43 (51%)	36 (42%)

[1]13 of the 25 trees pushed over by elephant were killed by subsequent fires

[2]Not all of these trees remained within the upper canopy level

[3]Estimated numbers based on dead stumps found in 1979

Trollope et al. (1998) considered the impact of the interaction of elephants and fire on the vegetation of Kruger NP to be greater than that of elephants alone. Woodland blocks fully protected from fire for 44 years but open to elephants developed a closed canopy. Adjacent blocks subjected to fire at frequencies of 1–3 years and open to elephants remained open woodland. In exclosures in more arid environments (with lower grass biomass?), fire alone had significantly less effect on vegetation than when combined with elephants. Moncrieff et al. (2008), also working in Kruger, found that bark removal from large *Acacia nigrescens* trees by elephants increased their vulnerability to fire, leading to greater damage and subsequent death. Dublin et al. (1990) also discussed this interaction, proposing two stable situations: high tree density with low elephant density and low tree density with high elephant density. Other states they considered unstable. The first state needs fire to initiate the movement to the second state. Eventually a stage is reached where elephant can maintain the situation without fire.

This synergistic effect between fire and elephants was also apparent at Naifulu. Trees pushed over by elephants in the wet season (but still alive) did not usually survive the subsequent dry-season bush fires (i.e. in 2014–15). While pushed-over trees may survive many years if conditions are favourable (Dudley, unpublished data), the combination of elephant damage and hot fire is nearly always fatal.

As a consequence of the natural, but very large increase in the elephant population in Liwonde, the elephants now forage to the extreme Park boundaries, and the remote Naifulu Hills area is no exception. Their impact in 2014–15 was very severe. However, elephant avoid foraging on rocky hillsides and elephants damage was not observed in quadrats 17–20. Throughout the study no upper canopy trees were pushed over in these quadrats or seen to be otherwise damaged by elephants. In addition, grass biomass was noticeably lower (though unmeasured) in these same quadrats. Not surprisingly, the three new trees added to the upper canopy during the study also occurred here.

There is always a random element with regard to individual tree survival in any one year due to the chance of fire frequency and intensity or elephant presence on a spot basis. Variations in rainfall amount and pattern, grass biomass and species and fire occurrence as well as elephant movements during the intervening years between samples are also important factors, but this information was not available.

Conclusions

If one accepts that the history of the Naifulu Hills woodland plot monitored in this study reflects the situation throughout areas of the Park where similar woodland conditions occur, then this vegetation is in serious decline. While growth of the largest trees may compensate for losses of smaller individuals for an extended time, the presence of elephants greatly changes the woodland dynamics. The loss of the largest trees reduces the structural complexity of the woodland, while plant species diversity is modified and ultimately lowered. Finally, these areas may be transformed into high, dense grasslands with widely scattered tall trees. For many years, most tree species will still be represented within the shrub layer, with coppicing each year to 1.0–1.5 m, but many will gradually die out over time.

Large trees have important roles to play in woodland ecosystems, affecting nutrient, water and light availability for understory vegetation as well as providing shade and roosts for various bird and mammal species (Belsky 1994; Ludwig et al. 2004). Maintenance of diverse green woodland would require serious fire management strategies and a considerable reduction in elephant numbers, both difficult propositions. A reduction to 300–350 elephants (0.56–0.65 ind./km^2) would put the number well within an acceptable range (Dudley 2016). This would help preserve not only this vegetation type but also several others in the Park now in decline. The management of fire with a regime of early, late and no burn options would also be an obvious help. But fire management needs to consider timing and methodology carefully as noted by Trollope et al. (1998). Both these 'solutions' are expensive and difficult. However, African Parks' assumption of full management of the Park in September 2015 gives hope that such solutions may be forthcoming.

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Appendix: List of tree species found in the transect over 36 years of study. Nomenclature after Coates Palgraves, 2002.

Species	**Upper canopy**	**Lower canopy**	**Shrub layer**
Acacia goetzei	*	*	*
Annona senegalensis		*	*
Bauhinia petersiana			*
Bridelia cathartica			*
Burkea africana	*	*	*
Seena petersiana		*	*
Catunaregam obovata			*
Combretum adenogonium	*	*	*
Combretum apiculatum	AS		*
Combretum collinum	*		*
Combretum zeyheri	*	*	*
Crossopteryx febrifuga	*	*	*
Cussonia arborea			*
Dalbergia boehmii	*		*
Dalbergiella nyasae	*	*	*
Dichrostachys cinerea			*
Diospyros kirkii			*
Diplorhynchus condylocarpon	*	*	*
Flacourtia indica			*
Hymenocardia acida	*	*	*
Lannea discolor			*
Pavetta cataractarum			*
Pericopsis angolensis	*	*	*
Philenoptera bussei			*
Philenoptera violacea	*		*
Piliostigma thonningii		*	*
Pseudolachnostylis maprouneifolia	*	*	*
Pterocarpus angolensis			*
Sterculia quinqueloba	*		*
Sterospermum kunthianum	*	*	*
Strychnos spinosa	*		*
Terminalia sericea	*	*	*
Terminalia stenostachya	*	*	*
Xeroderris stuhlmannii	AS		

AS = Associated species. Species not growing in the plot but with canopy overhanging it.