Mortality and utilisation of *Sclerocarya birrea* subsp. *Caffra* between 2001 and 2008 in the Kruger National Park, South Africa

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Abstract

A resurvey of a sample of marula trees (n=474) in the Kruger National Park (KNP) originally documented in 2001, was conducted in 2008 to determine the response of this population segment to the conditions prevalent during that time. These included an increasing elephant population and changes to the KNP fire policy. The overall mortality rate was estimated to be 2.6% per annum, with the mortality rate for individuals >5 m in height being 3.7% per annum. The highest level of mortality was found in the 5–8 m height class (7.1% per annum), while the highest number of dead individuals occurred in the 11–15 m height class (25). In addition minimal recruitment into the seedling size class was observed (n=6). No growth of saplings less than 2 m in height to heights greater than 2 m was observed. Almost half the individuals that were heavily damaged in 2001 had died by 2008. Heavy elephant utilisation and tree mortality was concentrated in the Sabie thorn thickets ecozone on granites where marula density was highest. Utilisation levels on the surviving individuals throughout the sampled area had almost tripled between 2001 and 2008, with individuals between 5 and 8 m in height accumulating the most additional elephant utilisation. It was concluded that the sampled marula population was not sustaining itself under the conditions prevalent between 2001 and 2008. Since sampled trees >5 m in height were strongly biased towards the Sabie thorn thickets, any projections for the likely fate of marulas in terms of adult mortality would mainly apply to this ecozone. The spatial variability described in this study suggests that further sampling is needed to adequately represent trends elsewhere.
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1. Introduction

Concern over the loss of mature trees in the Kruger National Park (KNP) due to the accumulation of damage by elephants (*Loxodonta africana* subsp. *Africana*) and fire (Eckhardt et al., 2000), has prompted a host of studies on the keystone tree species in the park, including *Sclerocarya birrea* subsp. *caffra* (marula). Marula (Family Anacardiaceae) is a dioecious tree species and is often a community dominant (Witkowski and O'Connor, 1996; Schmidt et al., 2002; Shackleton et al., 2002), specifically in the southern landscapes of the KNP. It is heavily impacted by

elephants (Coetzee et al., 1979; Jacobs and Biggs, 2002b) and is one of the most ecologically important trees, as it provides food and shade (Hall et al., 2002). The leaves are browsed by mammalian herbivores and insects, the bark is stripped by elephants and the abundant crops of fruit are eaten by wild animals such as elephants, vervet monkeys (*Cercopithecus aethiops*) and chacma baboons (*Papio ursinus*) (Shackleton et al., 2002). The canopy provides habitat for various insect and bird species as well as parasitic plants (Dzerefos et al., 2003). In the KNP, marula trees are mostly restricted to the crests and midslopes on both the granite and basalt substrates (Coetzee et al., 1979; Jacobs, 2001). Marulas are resilient to most types of damage. They can resprout from the base or epicormically if toppled (i.e. pushed over; the roots can either remain in the soil or

the tree can be uprooted to varying degrees), or if the canopy is broken, or if the canopy is burnt by fire (Coetzee et al., 1979; Gadd, 2002; Jacobs and Biggs, 2002b). In addition they can regrow stripped bark, recovering the underlying wood relatively quickly (Coetzee et al., 1979; Jacobs and Biggs, 2002a). Hence it is expected that marulas are able to sustain relatively high levels of damage before adults die.

Jacobs and Biggs (2002a) reported that 7% of marula trees sampled within four landscapes in the KNP were found dead. In addition, Shannon et al. (2008) found that 10% of individuals of trees >5 m in height (all species) in the southern KNP were dead. However, such values tend to tell only part of the story about the mortality patterns in a population and the time period since death is unknown. Repeat sampling of marked individuals within a population enables the mortality rate and time interval encompassed to be estimated.

Understanding the effects of elephant impacts on a tree population requires investigation into the long-term responses of the population to these impacts. However, as elephant are only one of many possible influences on woody plant dynamics, our understanding of their actual effect is confounded by their interactions with other ecosystem drivers (Prins and Van der Jeugd, 1993; Ben-Shahar, 1996; Van de Koppel and Prins, 1998; Whyte et al., 1998; Higgins et al., 2000; Zeng and Neelin, 2000; Owen-Smith et al., 2006; Shannon et al., 2008). These drivers include fire, competition from the grass layer, rainfall, soil texture and nutrients, and other herbivores (Scholes and Walker, 1993; Scholes, 1997). In addition, there is little consensus over whether the dynamics of woody plants are mostly influenced by the interactive effects of these drivers while the tree is still in the seedling phase (Higgins et al., 2000) or whether this influence is greatest after the tree has established (Hoffmann, 1996). Jacobs and Biggs (2001) suggested that the previous fire management policy (before 2002; see below) within the KNP was preventing the marula population from recruiting to adult size classes, and further evidence indicated that elephants were targeting individuals between 2 and 8 m in height causing mortality in this size class (Jacobs and Biggs, 2002b). In contrast, Lewis (1987) and Haig (1999) attributed marula mortality to be mostly in the seedling phase due to browsing by impala (*Aepyceros melampus*), while Walker et al. (1986) suggested that recruitment of marula was highly episodic and hence limited by rainfall events.

The present study was undertaken to assess the response of a segment of the marula population in the KNP to the conditions prevailing between 2001 (first assessment, M. Hofmeyr, unpublished data) and 2008. This period was characterised by an increase in elephant density (0.75 elephant per km^2 to 1.13 elephants per km^2 between 1988 and 2008 (Shannon et al., 2008)) and followed a number of changes to the KNP fire policy. From 1954 to 1992 the fire policy required the triennial burning of controlled block burns during late winter. In 1994 this was changed to a *laissez faire* burning policy where only lightning induced fires were allowed to burn. In 2002 this policy was again altered to combine point ignitions with unplanned and lightning fires, aiming to burn an annual target area determined by rainfall and fuel conditions (Van Wilgen et al.,

2008). Rainfall in the study area was approximately 140% and 150% of the long-term average in 2004/2005 and 2005/2006 respectively, while in 2006/2007 and 2007/2008 the rainfall was approximately 65% and 85% of the long-term average respectively (N. Zambatis, unpublished data). It was expected that 1) the increasing elephant population would result in the accumulation of higher levels of damage to individual marula trees and in the loss of targeted size classes and 2) the changes in the fire policy would allow trees within the fire trap to reach a fire escape height of 2.75 m (Jacobs and Biggs, 2001), and hence recruit to the taller size classes.

2. Materials and methods

2.1. Study area

The study area was restricted to the central and southern parts of the KNP which is itself located in the lowveld regions of Limpopo and Mpumalanga provinces of South Africa and covers an area of approximately 19 000 km^2. The KNP is divided longitudinally into the eastern basalts and the western granites on a broad scale (Venter et al., 2003). The clay basaltic soils of the east are of a higher nutrient status than the sandy granitic soils of the west. Patches of gabbroic soils resulting from gabbro intrusions occur interspersed within the granitic soil landscape and are characterised by flat plains with black or red clay soils with a higher nutrient content than the granitic soils. The study area is classified into seven main ecozones according to Grant and Thomas (2006): Delagoa thorn thickets, Marula knobthorn savanna, Mixed bushwillow woodlands, Sabie thorn thickets, Gabbro thornveld, Pretoriuskop sourveld and Malelane mountain bushveld. The study area receives approximately 500–700 mm of rainfall per annum.

2.2. Sampling

In 2001 (July and August) and 2002 (March and August), 33 transects of approximately 1.25 km in length and 50 m wide (area=62 500 m^2) were laid out in the following ecozones: Delagoa thorn thickets (Ecca shales; 5 transects), Marula knob-thorn savanna (basalt; 9 transects), Mixed bushwillow woodlands (granite; 5 transects), Sabie thorn thickets (granite; 9 transects), and Gabbro thornveld (gabbro; 5 transects) based on the classification of Grant and Thomas (2006) (M. Hofmeyr, unpublished data). All trees less than 0.5 m in height were recorded within a 2 m belt transect nested in the middle of the larger transect. Each tree's location within the transect was recorded with a Global Positioning System (GPS) but not physically marked. The height and circumference at 30 cm above the ground or above the basal swelling were recorded (the basal circumference was recorded for seedlings, young trees and multi-stemmed individuals) and damage scores of 0 to 4 (least to most damage), as coded by Jacobs and Biggs (2002b) were assigned to each tree encountered within the transect. The scoring was assigned as follows: 0=no damage; 1=<50% bark removed from the stem circumference and/or secondary branches broken; 2=<50% bark removed and secondary branches broken or >50%
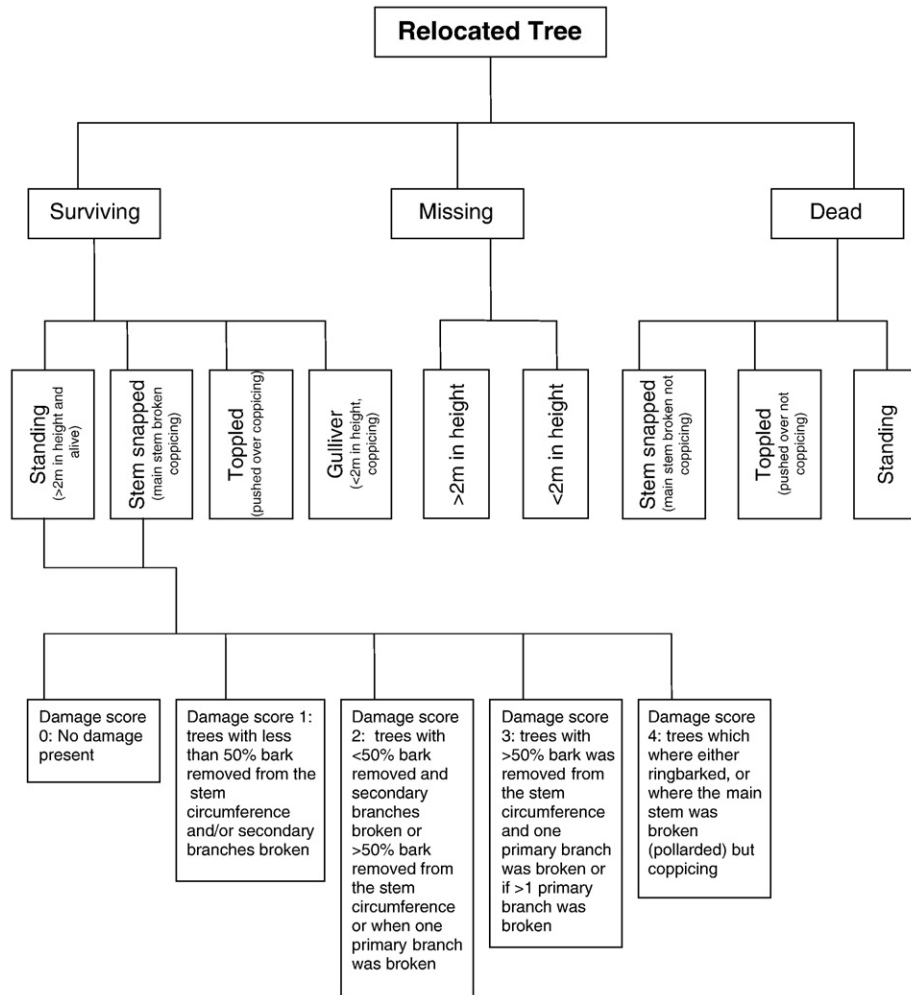
Relocated Tree

Fig. 1. Dendrogram detailing the categorisation of each relocated tree in 2008 to indicate the fate of the tree since it was first surveyed in 2001/2002 and the allocation of damage scores to surviving individuals.

bark removed from the stem circumference or when one primary branch was broken; 3=>50% bark was removed from the stem circumference and one primary branch was broken or if more than one primary branch was broken; 4=ringbarked, or where the main stem was snapped (stem snapped or pollarded) but coppicing.

In the winter of 2008 (June to August) 31 of these transects were resurveyed by relocating each tree recorded in the transect in 2001/2002 using its GPS location. Two transects in the Delagoa thorn thickets were not resurveyed due to a lack of accurate GPS locations. This translated into the relocation and reassessment of 474 trees that were classified as alive in 2001/2002. For the analyses it was assumed that all trees found in 2002 had existed in 2001 and no significant changes in height or damage had taken place within that year. Any individuals <2 m in height not originally recorded in 2001/2002 within an approximated 10 m wide transect nested in what was thought to be the middle of the larger transect were also recorded. The number of individuals found in this transect was divided by five to make the area comparable to the original size sampled in 2001/2002 (i.e. 2 m wide), and the number obtained was assumed to be indicative of the number of new recruits since 2001. This approach was followed (only for the estimation of new recruits)

since it was impossible to determine exactly where the nested transect had been placed in 2001/2002 due to a lack of transect markers. By increasing the size sampled five fold it was assumed that the entire transect sampled in 2001/2002 was covered in 2008. The height and circumference at breast height and/or the basal circumference for each tree was recorded. A photograph of each tree was taken for future records and the presence of fruit stones at the base of the tree (indicative of the tree being fruit producing and hence female) was noted. Tree height was used to classify the marulas into size classes which were comparable to other studies (Gadd, 2002; Jacobs and Biggs, 2002a) as follows: 1 (0–0.5 m), 2 (0.5–2 m), 3 (2–5 m), 4 (5–8 m), 5 (8–11 m), 6 (11–15 m) and 7 (>15 m). However, for broad based comparisons, the marulas were grouped into only three height classes: <2 m; 2–5 m; and >5 m. A further size class of 0 was used to group dead and toppled, surviving individuals for certain analyses.

Each tree found in 2001 was further classified into one of three broad categories (surviving, missing, and dead) to indicate its fate since 2001 (Fig. 1). The surviving category was further subdivided into four categories namely: 1) Standing trees=individuals >2 m in height that had not been toppled or stem snapped.
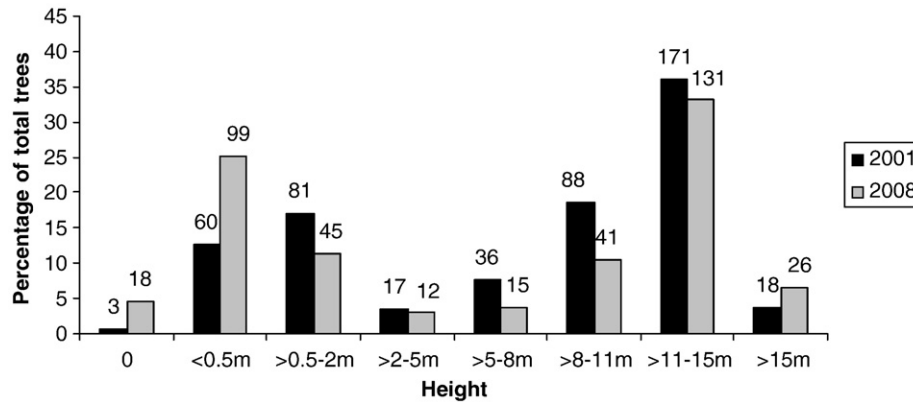
Fig. 2. Comparison of the distributions of the resurveyed marula individuals in the Kruger National Park between 2001 and 2008 within the eight size classes. Size class 0 represents all toppled individuals. (n_{2001}=474; n_{2008}=387). The values for 2008 exclude the new recruits and the dead and missing mature individuals. Numbers above the bar represent the number of trees in each height size class.

Trees that were bent over but where the canopy was higher than 2 m above the ground were also grouped into this category. 2) Stem snapped=trees with main stem broken (removing the entire canopy above the snapped area) but which were coppicing; 3) Toppled trees=trees that had been pushed over and were lying on the ground but were coppicing. Toppled trees were not classified as dead as done by Jacobs and Biggs (2002a) as many examples of toppled trees surviving even intense fires were found during the surveys. In addition at least two trees classified as dead in 2001 due to toppling were found to be still alive in 2008. Trees that were bent at 90°, but where the stem was not snapped clear off from the trunk, were also classified as toppled when the canopy was close enough to the ground to be affected by fire (<2 m); 4) Gullivers=individuals <2 m in height within the fire trap which were surviving due to basal coppicing from the rootstock after each fire event (following Bond and Van Wilgen, 1996). The missing category consisted of all individuals that could not be relocated in 2008. This category was further subdivided into two categories: <2 m and >2 m in height. Individuals <2 m in height may have been surviving undetected at or below the ground as a rootstock (due to fire topkill) during the dormant season when the

resurvey was conducted. For mortality analyses it was assumed that missing individuals >2 m in height were dead while individuals <2 m in height were alive in 2008. This was thought reasonable as it is unlikely that the taller trees would not have been found during the resurveys in 2008. Dead trees were further subdivided into 1) Stem snapped=main stem broken with no coppicing; 2) Standing=upright tree with bark coming off from the stem and no coppicing; and 3) Toppled=pushed over and no coppicing. The cause of mortality for toppled and stem snapped trees was assumed to be elephant damage, while for standing dead trees it was attributed to either ring-barking by elephants, natural senescence or boring insect activity (Jacobs and Biggs, 2002b). Damage scores were reassigned to each surviving mature and stem snapped tree for direct comparison with the 2001 data. Surviving toppled individuals were excluded from damage score analyses.

2.3. Statistical analysis

All statistical analyses were conducted in Statistica v.6. The significance level was set at $p < 0.05$. The number of individuals
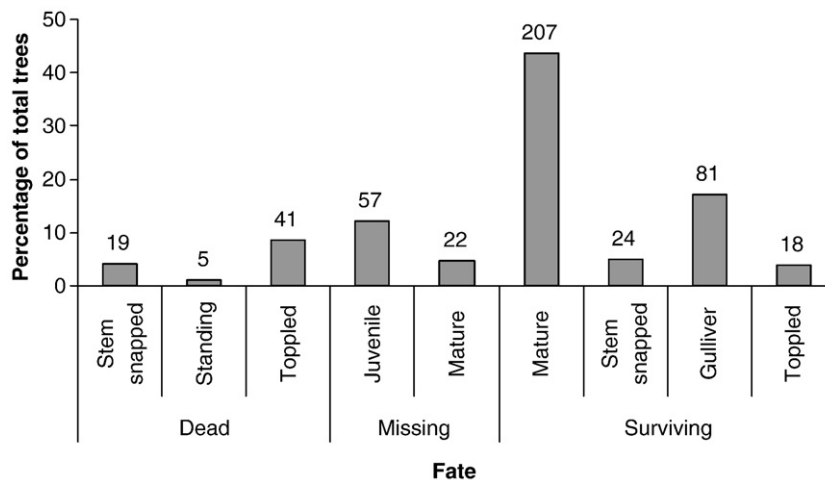

Fig. 3. Fate of the resurveyed marula trees in the Kruger National Park between 2001 and 2008 (n=474). Numbers above the bar represent the number of trees in each class.

Table 1
Annual mortality rates (%) of the height size classes of the sampled marulas in the Kruger National Park between 2001 and 2008.

	Height size classes						
	<0.5 m	>0.5–2 m	2–5 m	5–8 m	8–11 m	11–15 m	>15 m
Annual mortality assuming the missing individuals are alive (%)	0.0	0.0	0.8	6	3.4	2.1	1.6
Annual mortality assuming the missing individuals are dead (%)	8.1	4.1	3.4	7.1	4.9	2.6	2.4
Annual mortality assuming missing individuals <2 m in height are alive and missing individuals >2 m are dead (%)	0.0	0.0	3.4	7.1	4.9	2.6	2.4
Total standing individuals in 2001	60	81	17	36	88	171	18
Total standing individuals in 2008	42	45	12	15	41	131	26
Total dead in 2008	0	0	1	15	21	25	2
Total missing individuals	34	23	3	3	9	6	1
Total toppled alive individuals in 2008	0	1	5	1	4	5	0
Total stem snapped alive individuals in 2008	0	3	6	9	3	3	0

in each category was converted to percentages to describe the fate of the trees during the study period. A Chi-squared test was used to test for differences in the size class distribution of the sampled population in 2001 compared to the surviving population in 2008 and to determine whether more individuals were toppled, dead or stem snapped in the Sabie thorn thickets compared with the other ecozones. A Wilcoxon paired test was used to assess differences in damage scores between 2001 and 2008 as well as differences in damage scores for each size class between 2001 and 2008 for those individuals that survived to 2008 only.

3. Results

3.1. Overall analysis

3.1.1. Size distributions

The distribution of alive individuals within the eight size classes in 2001 was significantly different from those resurveyed in 2008 ($\chi^2_7 = 168.09$; $p \ll 0.001$; $n_{2001} = 474$; $n_{2008} = 387$) (Fig. 2) (2008 values exclude dead and missing mature individuals, and new recruits). This resulted mainly from the removal of individuals from size classes 3, 4, and 5 (2–11 m) into class 0 due to toppling and the complete removal by death. The distribution of the live standing individuals in 2008 (surviving mature, stem snapped and gullivers i.e. excluding size class 0, new recruits and missing

mature individuals i.e. toppled individuals removed) was also significantly different from that present in 2001 ($\chi^2_6 = 93.08$; $p \ll 0.001$, $n_{2001} = 471$, $n_{2008} = 369$).

3.1.2. Mortality

Of the 474 resurveyed marulas, 13.7% ($n = 65$) were conclusively dead in 2008 due to the presence of the dead tree, stump, bark or ash bed outline at the site where a tree was present in 2001 (Fig. 3). 27.8% of the missing individuals were >2 m in height while 72.2% were <2 m in height in 2001 (Fig. 3). Therefore, based on our assumption that the missing individuals <2 m were actually alive while those >2 m were dead, this translates into an overall mortality rate across all size classes of 2.6% per annum (range 1.9% to 4.3%). Individuals between 5 and 8 m in height had the highest annual mortality rate (7.1%) followed by individuals between 8 and 11 m in height (4.9%), while size class 7 (>15 m) had the lowest annual mortality rate (2.4%) (Table 1). Size classes 1 and 2 had an annual mortality rate of 8.1% and 4.1% respectively if missing individuals were assumed to be dead (Table 1). Individuals above 5 m in height had an annual mortality rate of 3.7%.

In 2001, 38.5% ($n = 25$) of the 65 dead trees found in 2008 had no damage and 21.5% ($n = 14$) had a damage score of 4 (Fig. 4). If the missing mature individuals are included as dead, 58.6% ($n = 17$) of the trees that had a score of 4 in 2001 were dead in 2008. The group with the highest percentage of dead individuals (30.8%)
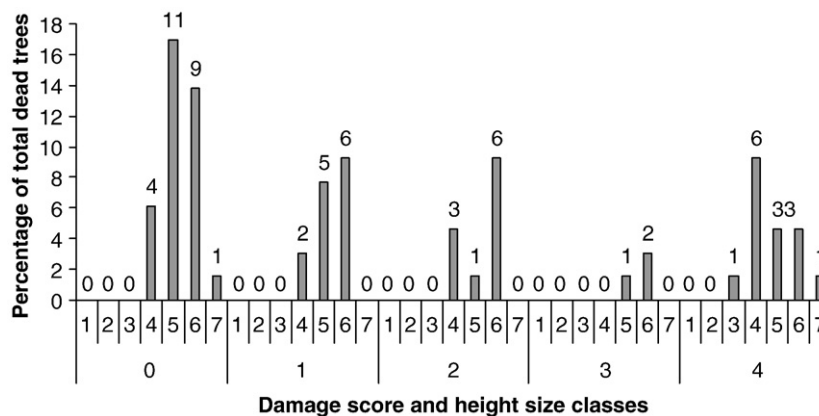

Fig. 4. Damage scores in 2001 and height size classes of all marula individuals that were found dead in the Kruger National Park in 2008 ($n = 65$). Size classes are as follow: 1 (0–0.5 m), 2 (0.5–2 m), 3 (2–5 m), 4 (5–8 m), 5 (8–11 m), 6 (11–15 m) and 7 (>15 m). Numbers above the bar represent the number of trees in each class.
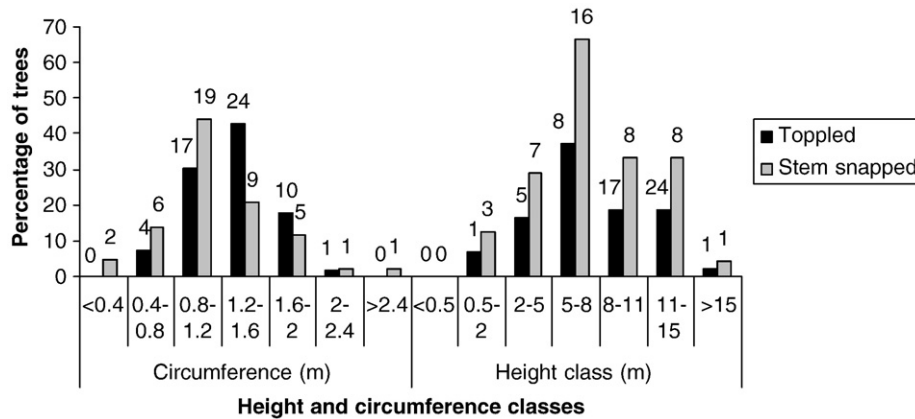
Fig. 5. Comparison of the height class distribution and circumference (*m*) in 2001 of the toppled and stem snapped marulas (dead and alive) in the Kruger National Park (*n*=99) in 2008. Numbers above the bar represent the number of trees in each class.

in 2008 was those between 8 and 15 m in height with a damage score of 0 in 2001 (Fig. 4).

63.1% (*n*=41) of the dead individuals had been toppled and 29.2% (*n*=19) had been stem snapped (Fig. 3). 69.5% of the toppled individuals (*n*=41) had died while only 44.2% (*n*=19) of the stem snapped individuals had died. The highest percentage of stem snapped individuals had a circumference at breast height (cbh) of between 0.8 and 1.2 m and were in size class 4 (5–8 m), while the highest percentage of toppled individuals had a cbh of 1.2 to 1.6 m and were also in size class 4 (5–8 m) (Fig. 5).

3.1.3. Survival

Of the surviving marulas, 62.7% (*n*=207) were standing individuals (>2 m in height) and 24.5% (*n*=81) were gullivers (Fig. 3). These gullivers showed an overall tendency to decrease in height since 2001 (43.2% had decreased in height by between 0 and 0.5 m), indicating that little recruitment to the higher size classes was occurring.

Damage levels in the surviving population in 2008 (excluding the gullivers and toppled individuals) were significantly higher than for the same trees in 2001 (*p*<<0.001; *n*=231) (Fig. 6). The greatest percentage increase was in damage score 2 which increased from 3.5% in 2001 to 39.0% in 2008. For individuals greater than 5 m in height the changes in damage levels per size class indicated that the smaller size classes (e.g. 5–8 m) had experienced most of

the additional damage compared to the larger size classes (e.g. >15 m) (Fig. 6). In size class 4 (5–8 m), the percentage of individuals with damage score 4 increased from 5.6% to 61.1%. In size class 5 (8–11 m), the percentage of individuals with damage score 4 increased from 0% to 13.8% and in size class 6 (11–15 m), it increased from 0.7% to 6.4%. The damage levels in size class 4 (5–8 m) were significantly higher in 2008 than in 2001 (*p*<<0.001; *n*=18). For size class 5 (8–11 m) the damage levels were also significantly higher in 2008 than in 2001 (*p*<<0.001; *n*=58). Similar results were found for size classes 6 (11–15 m) (*p*<<0.001; *n*=140) and 7 (>15 m) (*p*=0.005; *n*=15).

The reproductively active population of marulas was represented by 249 mature individuals (>5 m in height, and included stem snapped and toppled individuals as flowering was observed on individuals in both categories in the KNP). Fruit production was observed in 92 (37.0%) of these reproductively active marulas through the presence of fruit stones at the base of the tree. This represents a male:female sex ratio of 1.7:1.

3.2. Ecozone analysis

3.2.1. Size class analysis

Almost half of the sampled marulas occurred in the Sabie thorn thickets (*n*=226), while few represented the Delagoa thorn thickets (*n*=11) (Fig. 7a). The Sabie thorn thickets were dominated by
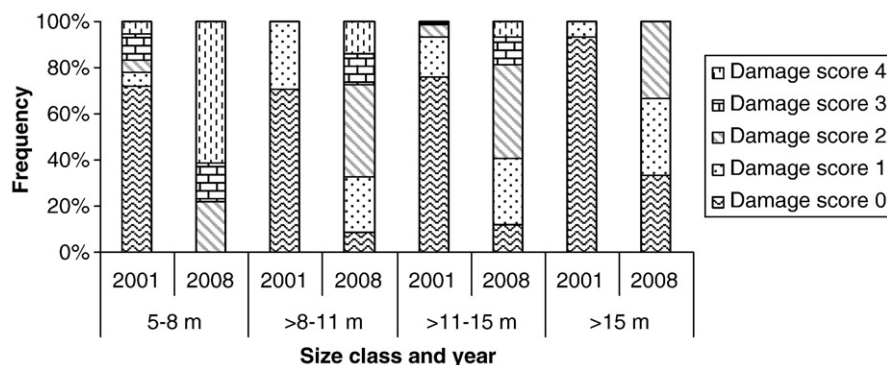

Fig. 6. Comparison of the damage scores assigned to each marula size class (heights) in 2001 and in 2008. For a description of the damage scores see Fig. 1.
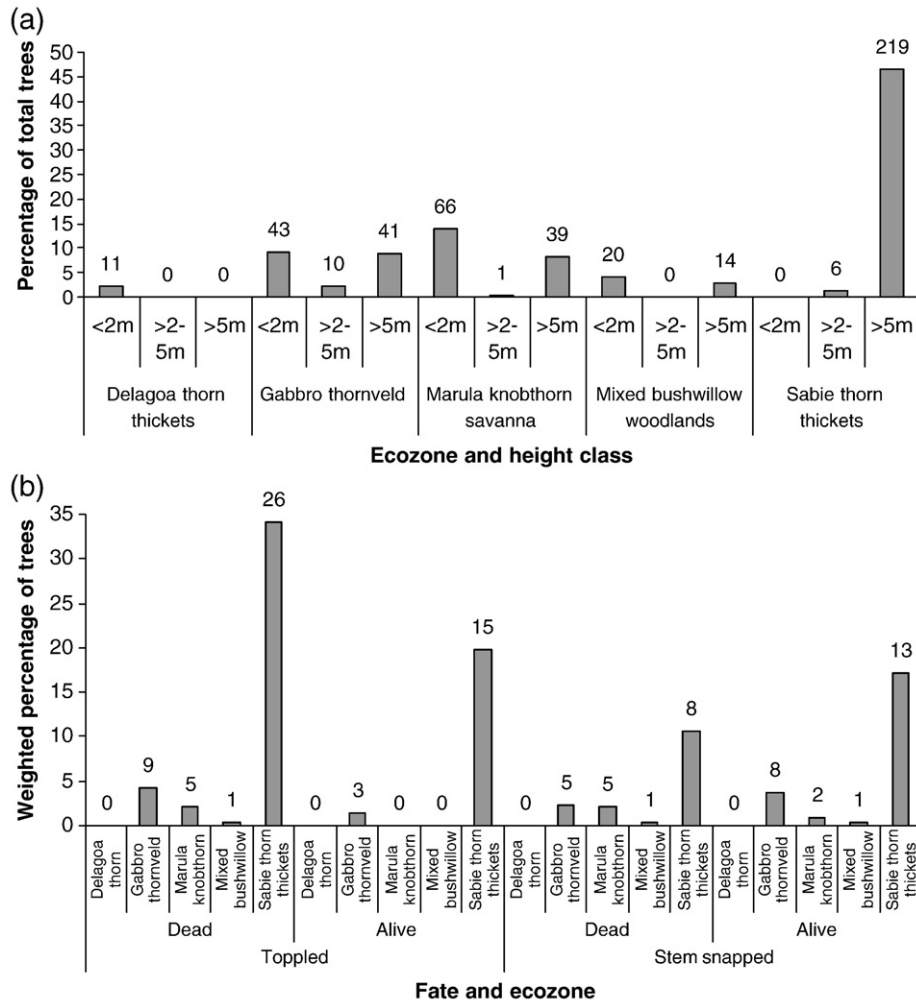
Fig. 7. a) Height class distributions of the sampled marulas in the five ecozones in 2001 in the Kruger National Park, (b) The weighted percentage of dead and surviving stem snapped and toppled marulas in 2008 in the five sampled ecozones in the Kruger National Park. Numbers above the bar represent the number of trees in each ecozone.

individuals > 5 m in height (96.9%), while the other ecozones were all dominated by individuals < 2 m in height (66.7%) (Fig. 7a). There is, therefore, wide spatial variability in demography that has not been adequately sampled by the population segment examined in this study. Therefore, this analysis will emphasise the patterns observed in the Sabie thorn thickets.

3.2.2. Mortality and new recruits

The Sabie thorn thickets, gabbro thornveld, marula knobthorn savanna and mixed bushwillow woodlands had annual mortality rates across all size classes of 3.6%, 2.4%, 1.5% and 0.8% respectively. 58.5% of the dead individuals occurred in the Sabie thorn thickets (n = 38). In the Sabie thorn thickets the highest mortality occurred in size class 5 (8–11 m; 40.4%).

The percentage of stem snapped individuals between 2001 and 2008 in the Sabie thorn thickets, gabbro thornveld, marula knobthorn savanna and mixed bushwillow woodlands was 9.3%, 13.8%, 6.6%, and 5.9%, respectively. The percentage of toppled individuals during the same time period in the Sabie thorn thickets, gabbro thornveld, marula knobthorn savanna and mixed bushwillow woodlands was 18.1%, 12.8%, 4.7% and 2.9%

respectively. Comparison of the toppled and stem snapped individuals, both dead and alive, in the Sabie thorn thickets indicated that there was a higher proportion of dead toppled than alive toppled individuals in 2008 (Fig. 7b). In contrast, there was a higher proportion of alive stem snapped individuals than dead ones in this ecozone. The number of toppled individuals in the Sabie thorn thickets was higher than expected compared to the other ecozones ($\chi^2_1 = 12.50; p = 0.0004$) while the number of stem snapped individuals was not ($\chi^2_1 = 0.014; p = 0.9065$).

Twenty nine individuals < 2 m in height which had not been identified in 2001 were found within the 10 m wide belt transects, translating into six new recruits since 2001. The new recruits occurred mainly in the Gabbro thornveld ecozone (44.8%, n = 13). However, most of these recruits (61.5%) occurred in the portion of the Gabbro thornveld ecozone near Satara. No new recruits occurred in the Sabie thorn thickets.

4. Discussion

The studied marula population decreased by 2.6% per annum since 2001. In the much smaller Pongola Nature Reserve,

elephants were killing marulas at a rate of 5.0% per annum (Duffy et al., 2002). These are the only published studies to date and to our knowledge which have produced an annual mortality rate for marula specifically. Population studies done by Jacobs and Biggs (2002a) in 2000 found the percentage of dead trees within transects placed in four landscape types in the KNP to be 7.0%, while Gadd (2002) found that 2.0% of the trees in private reserves on the boundary of the KNP in 1996 were dead. The population surveyed in this study consisted of only 1.8% dead trees in 2001, while in 2008 this had increased to 13.7%. These results indicate that mortality rates have increased since previous studies were conducted. Mortality was concentrated in individuals between 5 and 8 m in height. Since the prevalence of individuals between 2 and 5 m in the areas studied was already low in 2001 ($n=17$), the further loss of individuals between 5 and 8 m widened the gap between recruits <2 m in height and mature individuals >8 m in height between 2001 and 2008 (Fig. 2).

89.2% of the mature marula population sampled in 2008 showed some form of utilisation, compared to only 26.8% in 2001 (Fig. 6), indicating that the proportion of damaged trees has more than tripled. This value is also higher than figures presented by earlier studies. According to Gadd (2002), 62.1% of the marula trees sampled in the private reserves bordering the KNP in 1996 showed signs of utilisation. Jacobs and Biggs (2002b) found that almost half of the surveyed population over four different KNP landscapes suffered damage from elephant activity in 2000. Similarly, Shannon et al. (2008) found 75% of marulas sampled in the southern KNP were utilised in 2006. In the Waza National Park, Cameroon, only 14% of marulas had been utilised (Tchamba, 1995). Shannon et al. (2008) and Trollope et al. (1998) also found that marulas had a higher frequency of utilisation relative to other tree species in the KNP. This is important because marulas may show negative responses, despite their reported resilience (Coetzee et al., 1979; Gadd, 2002; Jacobs and Biggs, 2002b) to the elephant impact, long before other less utilised species do and hence could be used as an indicator species. For example, when setting thresholds of potential concern for elephant impacts on woody vegetation in the KNP. Utilisation appeared to be highest on individuals between 5 and 8 m in height. This indicates that this size class was being actively selected by elephants (even though their density was low compared to the taller size classes).

Appearance of new marulas into the seedling size class was very low. Only six new individuals were estimated to have established and survived to 2008. This could be attributed to dry years, wet season droughts or high inter-annual rainfall variability during the study period. However, according to the soil water model of Botha (2006), there was at least one year between 2001 and 2008 in the Satara area that would have been conducive to seedling establishment. Further detailed investigation into the rainfall patterns over the study period may, however, reveal inadequate rainfall conditions for recruitment. Annual recruitment of trees will vary by species and region but it has been calculated to be in the range of 1–4% for savannas (Duffy et al., 1999). Thus, tree mortality greater than 4% per year could eventually remove that tree population from an area (Duffy et al., 2002). A lower level of mortality of 2.6% per annum was found by this study. However, recruitment levels in

the sample area were below this mortality level (approximately 1.1% per annum). These values suggest a population decline over the study period.

More importantly, only one of the individuals in size classes 1 and 2 (<2 m) in 2001 had recruited to a higher size class by 2008. In contrast, 60.5% of marulas <2 m in height had decreased in height as a result of fire. Jacobs and Biggs (2001) reached similar conclusions for marulas in the KNP in 2000. This suggests that the fire policy during the study period continued to prevent the escape of these marulas from the fire trap.

Viljoen (1988) reported that, between 1944 and 1981, the number of large trees in the Satara section had decreased by 93.4%. This area corresponds closely to the marula knobthorn savanna sampled in this study. In 2001 only individuals less than 2 m in height were still dominant in this area and by 2008 none of these plants had grown above 2 m in height. In addition, mortality of the large trees sampled in this area between 2001 and 2008 was 10.5%. The results indicate that the large tree loss trend in this area has continued. However, there are a healthy number of recruits less than 2 m in height in this area which could, should conditions permit their escape, allow for the regeneration of a stable size class structure. In contrast, the 3.6% annual mortality of individuals >2 m in height within the Sabie thorn thickets, has resulted in the loss of 25.2% of the trees between 2001 and 2008. The additional lack of recruits in this ecozone does not bode well for the future of this population segment. Since sampled trees >5 m in height were strongly biased towards the Sabie thorn thickets, any projections for the likely fate of marulas in terms of adult mortality would mainly apply to this ecozone.

It has been suggested that a decline in large trees is not necessarily an indication of ecological decline but rather a natural regression to a state that was prevalent before herbivores were "wiped out" from the area in the late 1800s due to hunting and the rinderpest epidemic (Prins and Van der Jeugd, 1993; Van de Vijver et al., 1999; Skarpe et al., 2004; Shannon et al., 2008). If the present density of large trees is due to an episodic recruitment event in the late 1800s, it has been postulated that the ongoing loss of trees due to factors such as elephants would be overshadowed by mass large tree senescent mortality (Shannon et al., 2008). Episodic recruitment is most likely to occur either during the seedling establishment phase or during the phase where saplings are able to escape from the fire trap. Long-term suppression of both these phases may result in the absence of certain size classes. Walker et al. (1986) found evidence of episodic recruitment in a small marula population in the Nylsvley Nature Reserve. In contrast, Jacobs and Biggs (2002a) indicated that recruitment was taking place continuously in certain landscapes within the KNP. To further confound the issue, the present study shows evidence of no recruitment in some ecozones (e.g. Sabie thorn thickets), while continuous recruitment was found in others. Higher browsing pressure from impala in the Sabie thorn thicket ecozone could be causing the early death of emerging seedlings and hence the lack of recruiting individuals in this ecozone. We postulate that recruitment is prevented by suppression of marulas in size class 2 (0.5–2 m) by fire in areas with higher grass biomass (hence more frequent or intense fires (Van Wilgen and Scholes, 1997)), while recruitment is prevented through browser pressure on individuals

in size class 1 (<0.5 m) in areas with higher tree density and hence lower fire occurrence. Therefore, a number of different stages of vulnerability in the marula life history still need elucidation.

Overlaying these bottlenecks is the elephant impact, resulting in losses of >3.7% of adult trees per annum with some size classes experiencing 7.1% mortality. Annual mortality rates of 1% for Australian savannas (Andersen et al., 1998) and 5% for South African savannas (Shackleton, 1997) have been reported. Higgins et al. (2000) modelled that <5% annual adult mortality is required for tree persistence. In light of the low recruitment rates into the higher size classes and the lack of establishment into the seedling size class, this level of adult mortality is relatively high. Although marulas are able to recover substantially from damage through resprouting and bark regrowth, a high proportion is still succumbing to elephant utilisation. With both the recruitment bottleneck (either at the seedling stage due to browser pressure or at the Gulliver stage due to fire suppression) and elephant impact operating simultaneously, the marula population in the KNP may be under threat of significant reduction and possibly even local extirpation if the conditions prevalent between 2001 and 2008 continue. This is thought to have already occurred in the mopane dominated shrubveld on basalts in the northern parts of the KNP (Jacobs and Biggs, 2002a). Since marula is actively selected by elephant (Shannon et al., 2008), it may be the species of the greatest concern when examining elephant and large tree interactions and a decline in the population of this species could still be indicative of a general ecological decline, regardless of whether large tree loss is due to a regression back to a pre late 1800s state.

In addition to all the issues raised above, the surviving resurveyed marula population had a male skewed sex ratio (1.7:1), indicating a deviation from the 1:1 ratio of males to females expected for dioecious populations optimising pollination success through random distribution in the landscape (Bawa and Opler, 1977). Assuming that deviations from a 1:1 sex ratio are not due to greater production of either sex (Bawa and Opler, 1977) or differential niche utilisation by males and females, the deviations could be attributed to preferential elephant utilisation of one sex. Hemborg and Bond (2006) found that females were more utilised than males in the Hluhluwe-Umfolozi Park, KwaZulu-Natal, South Africa in 2000, while Gadd (2002) found no significant difference between the utilisation of fruiting and non-fruiting trees in the private reserves bounding the KNP in 1996. If preferential utilisation of females is occurring in the KNP it could result in the greater removal of females from the landscape than males, further exacerbating the mortality issue by reducing the number of fruit bearing individuals in the landscape.

5. Conclusions

Elephants accelerated the decline of mature trees through increased damage levels, while fire prevented recruitment into the mature size classes. Further investigation into the utilisation of seedlings and saplings by elephants and other herbivores, the growth rates of marulas and their growth responses to fire and browsing may improve our understanding of the effects of fire frequency and small browsers on the ability of marulas to escape the fire trap. Natural senescence of large trees also requires further investigation to determine natural age-related levels of mortality. In addition, wider spatial sampling is required to account for the spatial variability noted by this study. While some authors (Prins and Van der Jeugd, 1993; Van de Vijver et al., 1999; Skarpe et al., 2004; Shannon et al., 2008) suggest that the large tree decline is due to a large episodic recruitment event in the late 1800s, the levels of utilisation of marula and its mortality rate in the areas sampled in the KNP suggest that this species may be declining at a rapid rate locally and, therefore may be more vulnerable to elephant density increases than other tree species.

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