The impact of the African elephant on marula trees in the Kruger National Park

O.S. Jacobs* & R. Biggs

Centre for Wildlife Management, University of Pretoria, Pretoria, 0002 South Africa

Received 5 September 2000. Accepted 1 February 2002

Previous vegetation studies in the Kruger National Park have shown a dramatic decline in the density of large trees in four major vegetation units of the Park. An assessment of the damage status of *Sclerocarya birrea* (marula), identified as one of the most important tree species in the Kruger National Park, was conducted across three major landscapes of the Park. Previous studies indicated that marula were most utilized by elephants, resulting in weak regeneration and recruitment, with consequent changes to the population structure of the species. Furthermore, results indicated that the marula populations in two major landscapes of the Kruger National Park were threatened. The objective of this study was to generate a data set, which can be used in conjunction with future monitoring, to quantify the elephant damage to the marula population in the Kruger National Park. Results indicated that almost half the surveyed population suffered from damage due to elephant activity, predominantly in the form of bark stripping and felling. Felling resulted in a large proportion of marula trees being reduced to a height of less than five metres. Main stem breakage by elephant was the main cause of the 7% mortality observed in the marula population.

Key words: damage, population structure, savanna, utilization.

INTRODUCTION

Van Wyk & Fairall (1969) stated that the most important tree species in the Kruger National Park were *Combretum apiculatum, Terminalia sericea, Acacia nigrescens, Sclerocarya birrea* (marula) and *Colophospermum mopane,* which together constituted about 80% of the total tree population at that time. Concerns about the potential impact of elephants (*Loxodonta africana*) on marula in the Kruger National Park gave rise to an earlier research project (Coetzee, Engelbrecht, Joubert & Retief 1979), which indicated that the impact, at that time, did not constitute a threat to the marula population. However, Trollope, Trollope, Biggs, Pienaar & Potgieter (1998) recorded marked declines in the woody vegetation of the Kruger National Park between 1960 and 1989, and speculated that this could be the result of the drastic increase in elephant density in combination with the fixed triennial fire policy.

The severe impact that elephants have on marula populations has been documented in private protected areas in the South African Lowveld (Gadd 1997; Weaver 1995). Gadd (1997) found that marula was one of the trees most utilized by elephant and that recruitment and regeneration of these trees were very weak. Weaver (1995) found that the impact was particularly pronounced on marula and *Acacia nigrescens* in the Klaserie Private Nature Reserve, where marula were nearly five times as likely to suffer mortality by elephants in all habitat types as *Acacia nigrescens.* This is in accord with data suggesting preference in elephant diets for selected woody species (Coetzee *et al.* 1979).

Bark removal by elephants can kill woody plants directly or by increasing susceptibility to fire or infection by boring insects (Barnes 1980). Van Wyk & Fairall (1969) and Owen-Smith (1988) reported severe bark stripping of marula in the Kruger National Park. Gadd (1997) confirmed that this tree species was repeatedly the target of bark stripping. Old wood underneath healed areas may burn or rot, leaving an apparently healthy individual with a hollow trunk (Coetzee *et al.* 1979). Although the bark of the marula tree has a self-healing response (Lewis 1987), Coetzee *et al.* (1979) found that 26% of the scars did not manage to heal after five season's regrowth. This could possibly have a detrimental effect on trees over the long term. Some marula trees that have been partially uprooted or broken when pushed over

---

*To whom correspondence should be addressed.
E-mail: wfw.olga@intekom.co.za

may continue to grow, the broken ones coppicing from the remaining stump and new trunks emerging from the partially uprooted trees (Coetzee *et al.* 1979).

The feeding methods of elephants vary according to the size-classes of woody plants (Vancuylenberg 1977). In a study of *Acacia tortilis* at Lake Manyara, Tanzania, Mwalyosi (1987) reported that smaller trees were less susceptible to being killed by elephants than larger trees. Lewis (1987) and Gadd (1997) found stems smaller than 2 cm in diameter to be a minor part of the elephant's diet, while Pellew (1983) found that elephants did not eat or destroy stems less than 1 m in height. Since the lower canopy (below 2 m) is browsed by other mammals, it is often difficult to attribute the little damage present with any degree of certainty solely to elephant activity (Ishwaran 1983). In particular, Lewis (1987) and Gadd (1997) found marula seedlings to be consumed by other browsers, especially *Aepyceros melampus* (impala). Jachmann & Croes (1991) found the preferred feeding levels of elephants to be between 2 and 3 m, while Jachmann & Bell (1985) found that trees above this height were regularly pushed over. Guy (1976) suggested that the pushing over and uprooting of trees by elephants were more a social display than a feeding necessity, although, Coetzee *et al.* (1979) found that marula trees were utilized after being pushed over in the Kruger National Park. Coetzee *et al.* (1979) concluded that a zone of high elephant impact on vegetation extends to 10 m on either side of the road, followed by a zone of intermediate impact between 10 and 50 m and relatively low impact beyond 50 m from the road. Jacobs & Biggs (2002) found no significant differences in the density of marula seedlings (less than 2 m tall) between 30 and 50 m from the road.

The dramatic increase in elephant density in the Kruger National Park from 1100 in 1960 to over 8500 in 1970 (Whyte & Wood 1995) led to the implementation of a population control programme in 1976, with the aim of keeping the elephant population constant at about 7500 individuals (Hall-Martin 1992). In 1996 a moratorium was placed on elephant culling and the population has since increased to 8896 in 1998 (Whyte 2001). Concerns about the potential impact elephants have on marula trees in the Kruger National Park gave rise to a study of the population structure of the marula in four landscapes of the Kruger National Park. Results of this study showed the height structure of mature marula trees in the mixed *Combretum/ Terminalia sericea* woodland (Landscape 5) and *Sclerocarya birrea/Acacia nigrescens* savanna (Landscape 17) not to be significantly different, whereas a skewed height structure in the *Colophopermum mopane/Acacia nigrescens* savanna (Landscape 12) differed significantly from the other landscapes (Jacobs & Biggs 2002) (Fig. 1). Jacobs & Biggs (2002) suggested that the virtual disappearance of marula trees from the *Colophospermum mopane* shrubveld in the Kruger National Park could be attributed to increased elephant populations in combination with triennial fires. The objective of this study was therefore to generate a data set, which can be used in conjunction with future monitoring, to assess the role played by elephant in the observed population structure of the marula in the Kruger National Park, and hence contribute to the adaptive management strategy of the Park.

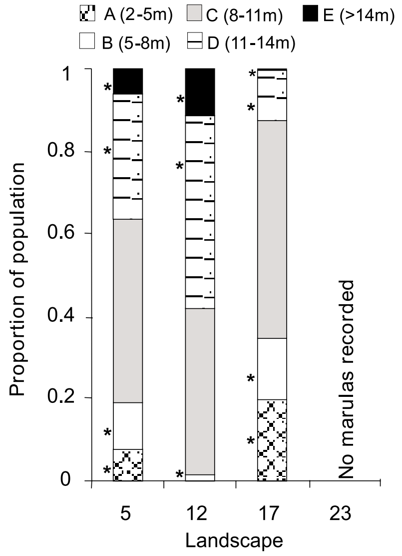

Fig. 1. Landscape differences in the population structure of *Sclerocarya birrea* in the Kruger National Park (Source: Jacobs & Biggs 2002). Landscape 5 = Mixed *Combretum/Terminalia sericea* woodland, Landscape 12 = *Colophospermum mopane/Acacia nigrescens* savanna, Landscape 17 = *Sclerocarya birrea/Acacia nigrescens* savanna, Landscape 23 = *Colophospermum mopane* shrubveld. *Indicates that this height class differs significantly between landscapes at $P < 0.05$.

STUDY AREA

The Kruger National Park encompasses an area of 18 998 km^2 and forms part of the Lowveld regions of Mpumalanga and the Northern Province, semi-arid regions of the southern temperate zone (Smuts 1975). The climate is subtropical with warm, wet summers and mild winters, seldom experiencing frost. In the Kruger National Park precipitation decreases from south to north, except for the area around Punda Maria, which is situated at a higher altitude (Gertenbach 1980). The pattern of rainfall over the past century has been characterized by extended wet and dry periods with cycles of about 10 years. This study was conducted in three major landscapes of the Kruger National Park as described by Gertenbach (1983): the mixed *Combretum/Terminalia sericea* woodland (Landscape 5) and *Colophospermum mopane/Acacia nigrescens* savanna (Landscape 12) on granite, and the *Sclerocarya birrea/ Acacia nigrescens* savanna (Landscape 17) on basalt.

Landscapes 5, 12 and 17 were exposed to the following fire frequencies and fire management practices prior to 1956 up to date (Van Wilgen, Biggs, O'Regan & Mare 2000):

- Prior to 1956: fire protection with limited burning to provide green grazing for wildlife;
- 1957 to 1991: prescribed burning of fixed management blocks on a triennial basis in spring;
- 1992 to present: Only lightning fires are allowed to burn, while all fires from human origin are suppressed.

METHODS

Data collection

In order to quantify the damage to a single tree species such as marula, it is necessary to record as many trees as possible in the study area that will be representative of the population in each landscape. Thus the survey transects were selected by stratified sampling of habitats, in such a way as to cover the major marula tree clumps in each of the landscapes. Thirty possible transects were mapped in each landscape of which 20 were selected at random to provide a good coverage of the marula tree population. The location of transects were restricted by the availability of vehicle tracks such as firebreaks. Each transect was 2 km long with a width of 50 m on either side of the road. Every mature marula (greater than 2 m in height) was examined and assigned to one of the following size classes: A = 2–5 m, B = 5–8 m, C = 8–11 m, D = 11–14 m and E > 14 m.

Dead trees were recorded as standing, uprooted or felled. Contrary to the method used by Okula & Sise (1986), uprooted trees with roots still in the soil were considered dead because of the high risk of subsequent destruction by fire. Trees, of which the main stem was broken and no coppicing had occurred, were classified as felled trees. Uprooted and felled trees were assumed to have died as a result of elephant damage. Causes of mortality for standing dead trees include death due to old age, boring insect activity and ring-barking by elephants.

Overall damage to living trees was ranked into five broad classes to determine areas of relatively uniform damage: N (nil), no damage; L (light), trees with light tusk marks and <50% bark removed from trunk circumference; or secondary and smaller branches broken; M (moderate), <50% bark removed from trunk circumference with secondary and smaller branches broken; or >50% bark removed from trunk circumference; or one primary branch broken; H (heavy), >50% bark removed from trunk circumference and primary branches broken; or with more than one primary branch broken; X (extremely heavy), ringbarked (100% bark removed from trunk circumference); or main stem broken and coppicing.

The agent of damage was recorded as being elephant or unknown. Unless damage could be positively attributed to elephants, it was classified as unknown damage. Elephant damage to bark is characterized by stripped bark and tusk markings on the exposed sapwood. Where broken branches were visible, but without elephant damage to the trunk, the damage was classified as unknown damage. Unknown damage could be due to other large mammalian browsers such as giraffe *(Giraffa camelopardelis*) or greater kudu (*Tragelaphus strepsiceros*), or to old age, wind, disease, lightning or frost (Ben-Shahar 1993).

Bark damage was recorded in three categories: bark removed from <50% of trunk circumference; bark removed from >50% of trunk circumference (but not ringbarked); ringbarked trees.

Damage in the form of broken branches and main stem breakages were recorded. Trees coppicing as a result of main stem breakages were recorded under elephant damage as it can be assumed that no other agents could have broken the main stems of mature marula trees. Main stem breakage could also result from wind after woodborers have inhabited and weakened a trunk previously damaged by elephants (debarking). Fire damage to trees was also noted, and could be recognized by scorch marks on dead branches or a peeled and dark bark surface (Coetzee 1983).

Table 1. Results for the stacked graphs in Fig. 2.

Parameter	A Dead trees	B Damage class	C Damage agent	D Bark damage
Composition across landscapes	Fire: NS Standing: NS Uprooted: NS	Light: $r^2 = 0.192$, $P = 0.004$ Moderate: NS High: NS Extreme: $r^2 = 0.271$, $P < 0.001$	$r^2 = 0.250$, $P = 0.003$	<50: NS 50–100: NS Ring: NS
Composition across height classes	–	Light: $r^2 = 0.685$, $P < 0.001$ Moderate: $r^2 = 0.337$, $P < 0.001$ High: $r^2 = 0.226$, $P = 0.002$ Extreme: $r^2 = 0.812$, $P < 0.001$	$r^2 = 0.299$, $P < 0.001$	<50: NS 50–100: NS Ring: NS
Composition across damage classes	–	–	$r^2 = 0.306$, $P < 0.001$	–

r^2 refers to proportion of total deviance explained by the model.
P-values adjusted for multiple testing according to the Bonferoni Theorem.

Data analysis

In order to correct for density differences, all data were analysed in the form of proportions and examined with binomial regression analysis. Overdispersion was corrected using the Williams procedure (Williams 1982). Proportions were calculated per transect, and except for the dead tree parameter which was examined as a proportion of the total sample, all parameters were examined as a proportion of the sample of living trees. Each parameter was analysed for composition across landscapes, height classes and damage classes. The *P*-values were adjusted for multiple testing according to the Bonferroni Theorem.

The fire parameter was not analysed as too few observations were recorded (only 23 living trees with fire scars were observed). In order to investigate the tree damage in relation to elephant densities, the annual elephant census results for the period 1985–1998 (Whyte 2000) were used to determine the mean elephant densities (elephants/km^2) in the three landscapes.

RESULTS

Table 1 and Figs 2 and 3 summarize the results of this study. The mean elephant densities per landscape for the period 1985–1998 were estimated as: Landscape 5 = 4.3 elephants/km^2; Landscape 12 = 5.7 elephants/ km^2; Landscape 17 = 2.6 elephants/km^2.

Dead trees

Approximately 7% of the sampled marula population in the Kruger National Park consisted of dead trees. Most of these trees had been felled. The proportion, as well as the nature of dead trees did not differ between marula populations in the different landscapes (Fig. 2A).

Living trees

Landscape differences

Approximately 70% of trees in Landscapes 12 and 17 showed signs of damage compared to only 25% in Landscape 5. However, most damage in Landscape 12 was light, whereas a high proportion of extreme damage was recorded in Landscapes 5 and 17 (Fig. 2B). A higher proportion of the damage in Landscape 12 was attributable to elephant (Fig. 2C). Landscape 12 showed mainly bark damage (Fig. 2D), whereas damage in Landscapes 5 and 17 also consisted of a significant proportion of broken branches and main stem breakages (coppicing trees) (Fig. 3A,B).

Height class differences

Damage to the shorter trees (class A) was significantly higher than the damage experienced by the taller trees (classes C, D & E). Trees in the 2–8 m classes showed a significantly higher proportion of extreme damage compared to the predominantly light damage throughout the 8–14 m classes (Fig. 2B). Almost 99% of the population sampled in class A (2–5 m) yielded extreme elephant damage, mostly due to main stem breakage. Of this sample, 78% trees were coppicing. The damage across all height classes was mainly ascribed to elephant impacts (Fig. 2C). Trees in the 8–14 m

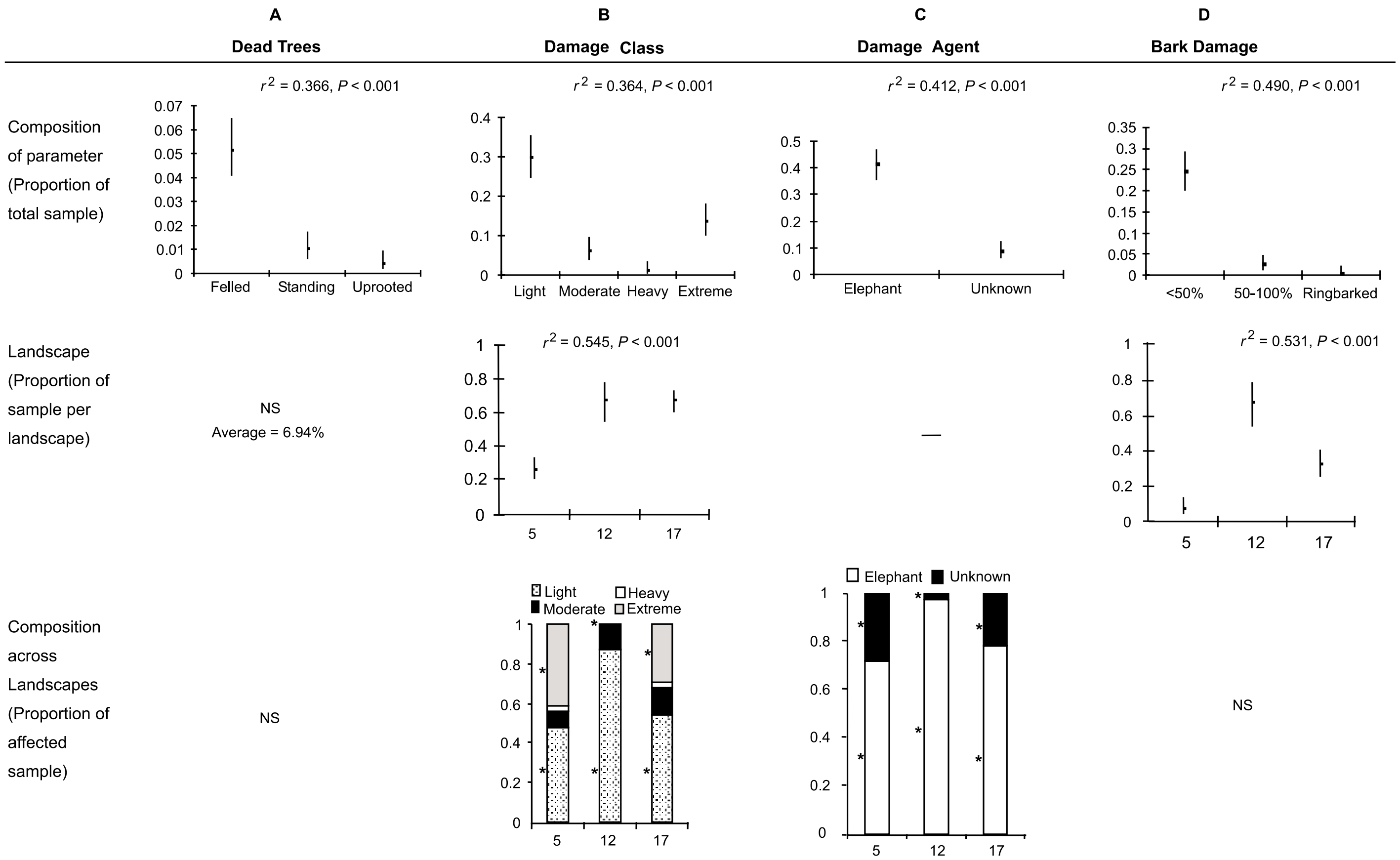

Fig. 2 continued on p. 18

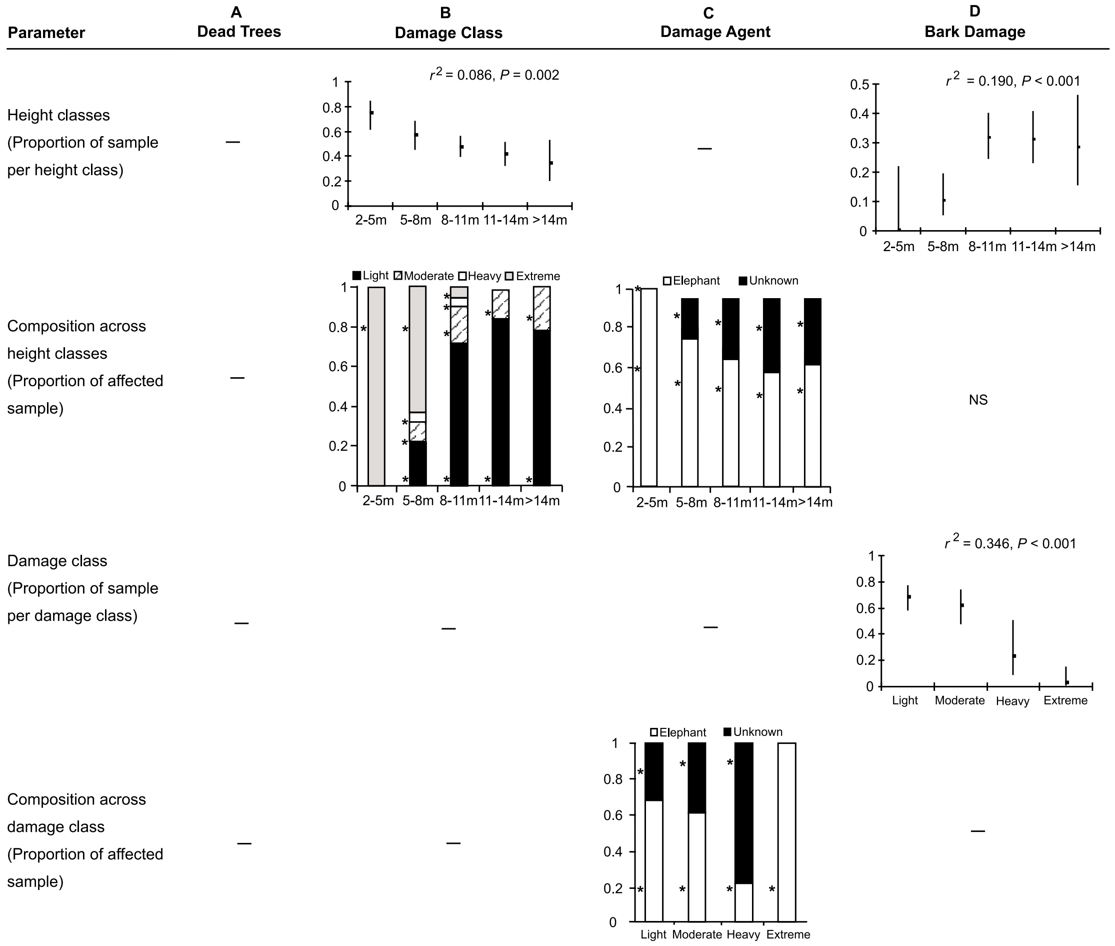

Fig. 2. Internal contrasts in proportion of dead trees, degrees of damage, agents responsible for damage and types of bark damage across landscapes, height and damage classes. Landscapes: 5 = mixed *Combretum/Terminalia sericea* woodland; 12 = *Colophospermum mopane/Acacia nigrescens* savanna; 17 = *Sclerocarya birrea/Acacia nigrescens* savanna. Damage classes: Light = tusk marks, <50% bark removed; Moderate = <50% bark removed, secondary and smaller branches broken; Heavy = >50% bark removed, primary branches broken; Extremely heavy = ringbarked or main stem broken. *Indicates that this damage class differs significantly between landscapes at $P < 0.05$.

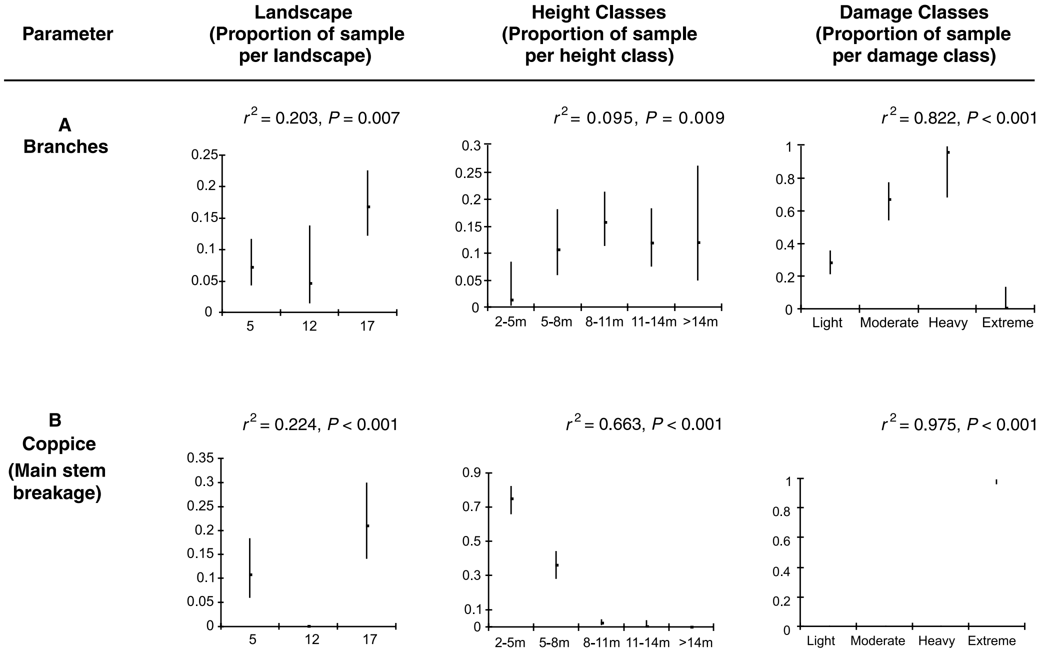

Fig. 3. Proportion of sample suffering branch and main stem breakage impact across landscapes, height and damage classes. Landscapes: 5 = mixed *Combretum/Terminalia sericea* woodland; 12 = *Colophospermum mopane/Acacia nigrescens* savanna; 17 = *Sclerocarya birrea/Acacia nigrescens* savanna. Damage classes: Light = tusk marks, <50% bark removed; Moderate = <50% bark removed, secondary and smaller branches broken; Heavy = >50% bark removed, primary branches broken; Extremely heavy = ringbarked or main stem broken.

height classes had predominantly bark damage (Fig. 2D) and broken branches, while damage to shorter trees consisted predominantly of main stem breakages resulting in coppicing (Fig. 3A,B). Bark damage to all height classes was predominantly light (<50% bark removed from trunk circumference) (Fig. 2D).

Damage class differences

Approximately 55% of the surveyed marula population had suffered damage of some kind, with about 15% of all recorded damage being extremely heavy. The greater proportion of damage was ascribed to elephants, except in the case of the high damage class where damage was mainly recorded as unknown. Elephant are the dominant agent causing extreme damage (Fig. 2C), mainly in the form of main stem breakages, resulting in trees coppicing (Fig. 3B). The largest proportion of heavy damage was recorded on trees between 5 and 11 m tall (Fig. 2B). Light and moderate damage (also ascribed to elephant impact) involved bark damage, whereas almost all heavily damaged trees had broken branches (Fig. 3A). Branch breakage appears to be a minor form of damage as only 10% of the surveyed population had broken branches.

DISCUSSION

This study provided an evaluation of the status of marula utilization by elephants in order to examine their role in shaping the current population structure in three major landscapes of the Kruger National Park.

Dead trees

Main stem breakage (felled trees) indicates that elephant damage is the main cause of mortality amongst the marula trees (taller than 2 m), supporting the findings of Gadd (1997). Mortality appears to be taking place uniformly across the landscapes.

Living trees

Structural changes

The significant proportion of the population that has suffered extreme elephant damage, which entails mainly broken main stems from which the marula trees would probably not be able to recover

(Barnes 1982), suggests that the population structure is changing towards the shrub category (below 3 m in height). The high percentage of coppicing trees in the 2–5 m category indicates that a number of bigger trees had suffered main stem breakage (and hence height reduction) as a result of severe browsing. Anderson & Walker (1974) found that elephant damage in the form of broken stems and branches could reduce the height structure of selected trees, and that severe reduction in height caused a proportion of trees previously not affected by fire, to be susceptible to fire impacts. Jacobs & Biggs (2001) found that the empirical fire escape height for marulas is between 2.5 and 3 m. This supports Jachmann & Croes (1991) who stated that elephant damage to mature trees which results in smaller, coppicing stems, increases the individuals' vulnerability to fire. They further found that the combined effects of foraging and fire resulted in the loss of a high percentage of woody stems. Although Haig (1999) found that mature trees are mostly resilient to elephant damage and that they coppice readily, it appears as though the interaction between elephant impact and fire might have a significant impact on the height structure of the marula population in the Kruger National Park.

Damage class differences

Heavy damage to trees in the 5–11 m height classes can be ascribed to branch breakage due to elephant, giraffe or wind. Branch breakage does not appear to be an important factor in marula mortality as relatively few trees suffer this form of damage and marula trees generally survive any branch breakage if less than 75% of damage occurs to an individual tree (Gadd 1997). Results further support Tchamba & Seme (1993) who found that ringbarking of trees, uprooting and bark stripping constitute a minor part of the elephants' feeding activity. Although bark stripping was found to be the main type of bark damage, a large proportion of the affected sample would probably recover due to the self-healing process (Coetzee *et al.* 1979). Trees, however, are susceptible to boring insects once the sapwood is exposed, and elephant damage to trees most probably contributed to the 1% mortality rate of dead but standing trees (Fig. 2A). Haig (1999) found that 35% of the marula population sampled with bark damage yielded borer infection, indicating that elephant impact due to bark damage is not as minimal as suggested by Coetzee *et al.* 1979).

Height class differences

The higher incidence of damage amongst shorter trees indicates that elephants select the smaller trees in preference to the larger ones, supporting Van Wyk & Fairall (1969) and Anderson & Walker (1974). The high level of extreme damage in class A (2–5 m) is probably because this class includes the preferred level of elephant feeding, estimated at between 2 and 3 m (Jachmann & Croes 1991). Jachmann & Bell (1985) found that trees, higher than the preferred feeding level, were pushed over or felled. This could explain the high proportion of extreme elephant damage in class B (5–8 m). The fact that trees taller than 8 m are not as severely impacted on by elephants as those less than 8 m supports Jachmann & Bell (1985), who found that trees taller than 7 m were more difficult to fell or uproot, depending on the root system. Van Wyk & Fairall (1969) found that marula trees were, in comparison with other trees with shallow root systems, less often completely uprooted and destroyed. The classes less than 8 m in height are therefore probably more uprooted and foraged upon, and this could explain the smaller proportion of trees below 8 m throughout the different landscapes as found by Jacobs & Biggs (2002).

Landscape differences

The significantly lower incidence of elephant damage in Landscape 5 as opposed to Landscape 12 (both on granite) may indicate that marulas in less diverse vegetation are more prone to suffer elephant damage. Landscape 12 is an open tree savanna dominated by mopane trees, where a study on the population structure of the marula (Jacobs & Biggs 2002) showed a highly skewed structure (Fig. 1). A higher elephant density may further exaggerate elephant impact in Landscape 12. The high elephant damage encountered in Landscape 17 (on basalt), however, may indicate that marulas are more selected for on the basalt substrata, independent of other available browse and elephant densities. It further appears as if the extent of elephant damage depends on the composition of the marula population structure. Jacobs & Biggs (2002) found the marula populations in Landscape 5 and 17 to have a good distribution of individuals throughout the different height classes (Fig. 1). It appears as though the higher proportion of extreme damage in Landscapes 5 and 17 corresponds to the higher proportions of small trees (2–5 m tall) encountered in these landscapes since it is clear that extreme damage dominates the 2–8 m height class.

The damage recorded in Landscape 12, however, might be an underestimation of the total elephant damage throughout this landscape, as Jacobs & Biggs (2002) suggested that the low vegetation diversity probably enhanced the impact on the 2–8 m classes, yielding a lack of immature marula trees. The significantly higher bark damage recorded in Landscape 12 could possibly also be ascribed to less diverse vegetation and hence browsing material in this landscape.

This supports Buechner & Dawkins (1961) who stated that access to an abundant supply and great variety of browse may alleviate the need, or desire for feeding on the bark of trees. Barnes (1982) found that bark was stripped in the late dry season, just before the trees started to produce leaves, and Guy (1976) suggested that more bark was eaten in the late dry season because of the increased translocation of water from the roots towards the new leaves.

Jacobs & Biggs (2002) further stated that Landscapes 5 and 17 appear to have healthy populations. However, results of this study indicated that more than 60% of the trees in classes A and B were suffering extreme elephant damage, and therefore the impact on marula populations in Landscapes 5 and 17 might cause a decline in the health of these populations.

CONCLUSION

The combined effects of elephants and fire are documented to result in the loss of woodlands (Laws, Parker & Johnstone 1975; Barnes 1983; Ben-Shahar 1996). Beuchner & Dawkins (1961) stated that all woody vegetation is undergoing a process of conversion to grassland under the combined influence of elephants and fire. Results of Trollope *et al.* (1998), who found a dramatic decrease in large tree densities, indicate that this might be happening in the Kruger National Park. This study highlighted the role played by elephant in this process with regards to the marula population in the Kruger National Park. More than half the marula trees sampled in this study are suffering elephant damage at present, with elephants being the main cause of the 7% mortality recorded. Marula individuals with bark damage are likely to be affected by fire damage to exposed tissues by the actions of animals gouging, peeling and ripping the bark while foraging and rubbing on the boles of the trees (Beuchner & Dawkins 1961). Bark damages also increase marula trees susceptibility to borer activity.

Elephants appeared to alter the structure of marula trees, resulting in a significant number of trees between 2 and 8 m in height coppicing, hence increasing the number of trees susceptible to fire and decreasing the number of trees in the 5–8 m height class. Anderson & Walker (1974) found that elephants move on to the next favoured species when food becomes less available, and the process will repeat itself. The amount of elephant damage in Landscape 12, reviewed in conjunction with the population structure, is of great concern as it appears that successful recruitment into the upper canopy is not occurring (Jacobs & Biggs 2002), while most of the older trees suffer bark damage, increasing their susceptibility to boring insects and fire. It further appears that the healthy population structure in Landscapes 5 and 17 (Jacobs & Biggs 2002) is threatened since the majority of the trees in the 2–5 m class appear to have been bigger trees which have suffered main stem breakage, and are now coppicing. These findings support Trollope *et al.* (1998) who stated that the changes in woody vegetation involve a change in structural diversity where the woody vegetation of the Kruger National Park is being transformed into a short woodland community interspersed with a low density of large trees.

Stewart & Veblen (1982) further stated that once a structure has become homogenous through the action of any single agent or combination of factors, the population is set to undergo a synchronous mortality. Clear thresholds of potential concern (TPCs) should therefore be formulated against which these structural changes can be measured in order to revise certain management practices where necessary to protect important tree species in the Kruger National Park in the light of current management objectives.

ACKNOWLEDGEMENTS

We would like to thank various section and field rangers of the Kruger National Park who assisted during the data collection period. A further word of gratitude goes to Rina Grant, George Bredenkamp, Terina Vermeulen and Naledi Wessels for their assistance, support and criticism

REFERENCES

ANDERSON, G.D. & WALKER, B.H. 1974. Vegetation composition and elephant damage in the Sengwa

Wildlife Research Area, Rhodesia. *J. Sth. Afr. Wildl. Mgmt. Ass.* 4(1): 1–14.

BARNES, R.F.W. 1980. The decline of the baobab tree in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 18: 243–252.

BARNES, R.F.W. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 20: 123–126.

BARNES, R.F.W. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *J. Appl. Ecol.* 20: 521–540.

BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biol. Conserv.* 65: 249–256.

BEN-SHAHAR, R. 1996. Woodland dynamics under the influence of elephants and fire in northern Botswana. *Vegetatio* 123: 153–163.

BEUCHNER, H.K. & DAWKINS, H.C. 1961. Vegetation changes induced by elephants and fire in the Murchison Falls National Park. *Ecology* 42(4): 752–766.

COETZEE, B.J. 1983. Phytosociology, vegetation structure and landscapes of the Central District, Kruger National Park, South Africa. *Diss. Bot.* 69: 1–456.

COETZEE, B.J., ENGELBRECHT A.H., JOUBERT S.C.J. & RETIEF, P.F. 1979. Elephant impact on *Sclerocarya caffra* trees in *Acacia nigrescens* tropical plains thornveld of the Kruger National Park. *Koedoe* 22: 39–60.

GADD, M. 1997. Factors influencing the impact of elephants on woody vegetation in private protected areas in South Africa's lowveld. M.Sc. thesis, University of the Witwatersrand, Johannesburg.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 23: 35–43.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26: 9–122.

GUY, P.R. 1976. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa Area, Rhodesia. *S. Afr. J. Wildl. Res.* 6: 55–64.

JACOBS, O.S. & BIGGS, R. 2001. The effect of different fire treatments on the population structure and density of the marula, *Sclerocarya birrea* (A.Rich.) subsp. *caffra* (Sond.) *kokwaro* (Kokwaro & Gillet 1980) in the Kruger National Park. *Afr. J. Ran. For. Sci.* 18: 13–23.

JACOBS, O.S. & BIGGS, R. 2002. The status and population structure of the marula in the Kruger National Park. *S. Afr. J. Wildl. Res*. 32(1): 1–12.

HAIG, A.W. 1999. The impact of impala and elephant on the demography and dynamics of *Sclerocarya birrea* subsp. *caffra* (marula) in the eastern lowveld of South Africa. B.Sc. (Hons.) Agriculture, School of Applied Environmental Sciences, University of Natal, Pietermaritzburg.

HALL-MARTIN, A.J. 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652–1992. *Koedoe* 35(1): 65–88.

ISHWARAN, N. 1983. Elephant and woody-plant relationship in Gal Oya, Sri Lanka. *Biol. Conserv.* 26: 255–270.

JACHMANN, H. & BELL, R.H.V. 1985. Utilisation by elephants of the *Brachystegia* woodlands of the Kasungu National Park. *Afr. J. Ecol.* 23: 245–258.

JACHMANN, H. & CROES, T. 1991. Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biol. Conserv.* 57: 13–24.

LAWS, R.M., I.S.C. PARKER & JOHNSTONE, R.C.B. 1975. Elephants and their habitats. Clarendon Press, Oxford.

LEWIS, D.M. 1987. Fruiting patterns, seed germination, and distribution of *Sclerocarya caffra* in an elephant-inhabited woodland. *Biotropica* 19(1): 50–56.

MWALYOSI, R.B.B. 1987. Decline of *Acacia tortilis* in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.* 25: 51–53.

OKULA, J.P. & SISE, W.R. 1986. Effects of elephant browsing on *Acacia seyal* in Waza National Park, Cameroon. *Afr. J. Ecol.* 24: 1–6.

OWEN-SMITH, R.N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press. Cambridge, U.K.

PELLEW, R.A.P. 1983. The impact of elephant, giraffe and fire upon *Acacia tortilis* woodlands of the Serengeti. *Afr. J. Ecol.* 21: 41–74.

SMUTS, G.L. 1975. Reproduction and population characteristics of elephants in the Kruger National Park. *J. Sth. Afr. Wildl. Mgmt. Ass.* 5(1): 1–10.

STEWART, G.H. & VEBLEN, T.T. 1982. Regeneration pattern in southern rata (*Metrosideros umbellate*) and kamahi (*Weimannia racemosa*) forest in central Westland, New Zealand. *N.Z.J. Botany.* 20.

TCHAMBA, M.N & SEME, P. M. 1993. Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *Afr. J. Ecol.* 31: 184–193.

TROLLOPE, W.S.W., TROLLOPE, L.A., BIGGS, H.C., PIENAAR, D. & POTGIETER, A.L.F. 1998. Long term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe* 41(2): 103–112.

VANCUYLENBERG, B.W.B. 1977. Feeding behaviour of the Asiatic elephant in southeast Sri Lanka in relation to conservation. *Biol. Conserv.* 12: 33–54.

VAN WILGEN, B.W, BIGGS, H.C, O'REGAN, S.P. & MARE, N. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *S. Afr. J. Sci.* 96: 167–178.

VAN WYK, P. & FAIRALL, N. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* 9: 57–95.

WEAVER, S.M. 1995. Habitat utilisation by selected herbivores in the Klaserie Private Nature Reserve, South Africa. M.Sc. thesis, University of Pretoria, Pretoria.

WHYTE, I.J. & WOOD, C.A. 1995. Census results for elephant and buffalo in the Kruger National Park in 1995. Scientific Report 14/95. National Parks Board, Skukuza.

WHYTE, I.J. 2000. Census results for elephant and buffalo in the Kruger National Park for the years 1977 to 2000. Scientific Report 4/00. National Parks Board, Skukuza.

WHYTE, I.J. 2001. Conservation management of the Kruger National Park Elephant population. Ph.D. thesis, University of Pretoria, Pretoria.

WILLIAMS, D.A. 1982. Extra-binomial variation in logistic linear models. *Appl. Stat.* 31: 144–148.