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THE STATUS AND POPULATION STRUCTURE OF THE MARULA (*SCLEROCARYA BIRREA* SUBSP. *CAFFRA)* IN THE KRUGER NATIONAL PARK

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Abstract

The South African National Parks expressed the need to implement autecological studies on specific rare indicator keystone plant species to determine habitat requirements and sensitivity to disturbances. *Sclerocarya birrea* subsp. *caffra* (marula) are one of the preferred tree species that are particularly selected for by elephant and whose current damaged condition and disappearance in a mature state in the Kruger National Park are causing serious concern. The density of marula trees and the current population structure of this tree species were examined in four major landscapes of the Kruger National Park. Results indicate that the marula population in the *Colophospermum mopane* shrubveld has become virtually extinct, while the *Colophospermum mopane/Acacia nigrescens* savanna has a markedly unstable population with a lack of immature trees. The marula populations in the southern landscapes (mixed *Combretum/Terminalia sericea* woodland and *Sclerocarya birrea/Acacia nigrescens* savanna) appear to be healthy. The population structures on the different sub-strata (granite and basalt) differed significantly. Results of this study further indicate that diversity of vegetation plays an important role in determining herbivory pressure, and consequently in influencing the marula population structure.

Keywords: basalt, density, granite, herbivory, key species

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Introduction

The South African National Parks expressed the need to implement autecological studies on specific rare indicator keystone plant species to determine habitat requirements and sensitivity to disturbances (Freitag & Biggs 1998). Preferred tree species that are particularly selected for by elephant and whose current damaged condition and reduction of mature trees are causing serious concern in the Kruger National Park are *Adansonia digitata* (baobab), marula, *Acacia nigrescens* (knobthorn), *Combretum imberbe* (leadwood) and *Pterocarpus angolensis* (kiaat) (Trollope, Trollope, Biggs, Pienaar & Potgieter 1998).

The marula tree is a member of the Anacardiaceae and is found throughout the eastern, low altitude regions of southern Africa. The marula has a warm-temperate to tropical distribution and is frost sensitive (Coetzee, Engelbrecht, Joubert & Retief 1979). It is a medium-sized tree up to 10 m in height, but may reach 15 m under favourable conditions (Palgrave 1983). Flowers have separate sexes on different trees. From March to June, large fruits up to 3.5 cm in diameter and approximately 42 g in weight, ripen and fall to the ground with as many as 8000 fruits per tree (Lewis 1987). The marula tree is rated as one of the most highly valued indigenous trees as they provide valuable food and shade and is a favourite food plant of the elephant (Coates Palgrave 1977). Their leaves are browsed by game, the bark stripped by elephants and the abundant crops of fruit, which are high in vitamin C, are eaten by game animals, monkeys and baboons (Pooley 1993).

Various studies showed marula tree populations to be highly clumped (Walker, Stone, Henderson & Vernede 1986; Lewis 1987; Gadd 1997). Lewis (1987) studied a population of marula trees in the Luangwa Valley, Zambia, and correlated the spatial distribution and highly aggregated pattern of this sample population with physical soil characteristics. The majority of this population (75%) was found on well-drained sandy soils (Lewis 1987). In the Kruger National Park, the marula tree occurs widely but clumped on sandy granitic soils, mostly on the crests, midslopes and dolerite intrusions where the soils are shallow. On the drier clayey basaltic soils, the tree populations decrease as soil forms with high clay contents become more dominant, and are largely restricted to crests and midslopes of moister climates with an annual rainfall exceeding 500 mm (Coetzee *et* *al.* 1979). This is in accord with Lewis (1987) who found the tree population decreased with increased clay content. The granitic landscapes in the Kruger National Park are therefore more suitable for the establishment of the marula tree population.

Previous studies on the population characteristics of the marula in other nature reserves suggested that the population structure of this tree species is not atypical for that of southern African trees. Walker *et al.* (1986), Lewis (1987) and Gadd (1997) found markedly unstable population structures with no immature trees and little or no evidence of successful regeneration and recruitment. Walker *et al.* (1986) concluded that the successful regeneration of the marula is highly episodic, while Lewis (1987) suggested that population regulation of the marula may be controlled by seedling browsers other than elephants. Lewis (1987) noted severe browsing on seedlings by *Aepyceros melampus* (impala), and Haig (1999) also attributed marula seedling mortality to impala browsing pressure. O.S. Jacobs & R. Biggs (In prep. 2000) found marula seedlings up to a height of 1.5 m to be highly susceptible to fire. They suggested that the fixed triennial winter burns in the Kruger National Park between 1954 and 1992 have hampered the establishment and development of marula seedlings into the upper canopy.

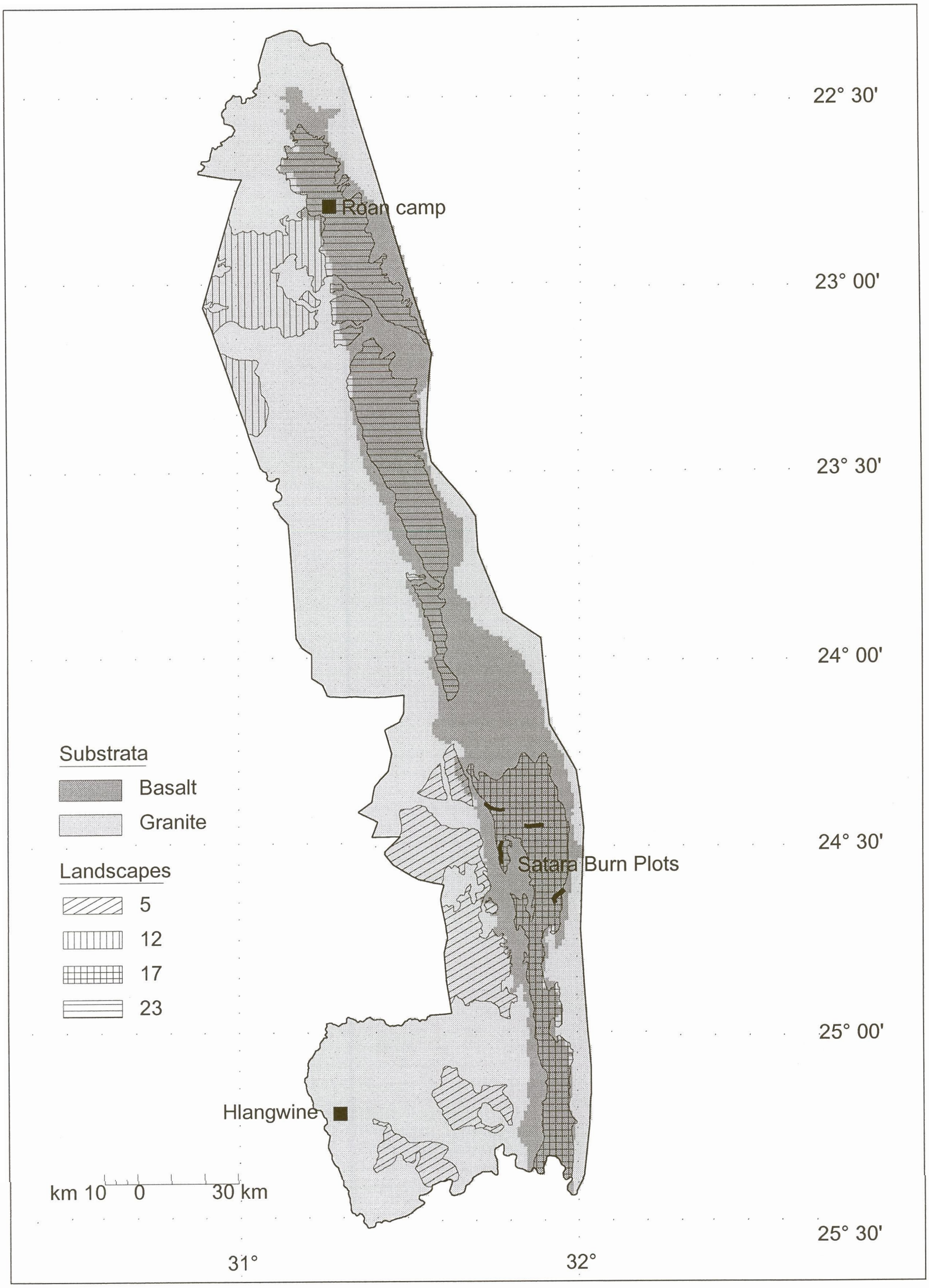
Trollope *et al.* (1998) investigated four major landscape units, as described by Gertenbach (1983), for long term changes in the woody vegetation of the Kruger National Park. Results of this study indicated moderate declines in the density of large trees in the mixed *Combretum/Terminalia sericea* woodland and the *Colophospermum mopane/Acacia nigrescens* savanna, whereas moderate to marked declines occurred in the *Sclerocarya birrea/Acacia nigrescens* savanna and *Colophospermum mopane* shrubveld during the period 1960 to 1989. Viljoen (1988) conducted a preliminary survey on changes in the density of large trees in the *Sclerocarya birrea/Acacia nigrescens* savanna landscape of the Kruger National Park by using aerial photographs. The results showed that during the period 1944 to 1981 (37 years) the number of large trees decreased by 93.4% in the Satara area. A similar trend, but not as marked a decline, was noted in the Lower Sabie area where during the period 1940 to 1977 (37 years) the large trees decreased by 49.6%. In both cases the major decline in the tree density occurred after the Kruger National Park experienced a highly significant increase in elephant densities and fire frequency during the period

1960 to 1986/89 (Trollope *et al.* 1998). The number of elephants increased from 1100 in 1960 to over 8500 in 1970, while a rotational triennial burning programme was implemented between 1954 and 1992 in the different management blocks.

The objectives of this study were to examine the current population structure of the marula in the Kruger National Park, to examine the regeneration and recruitment of marula seedlings and to compare the population structure of the marula trees in the different landscapes and hence the different sub-strata.

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 characterised by extended wet and dry periods with cycles of about 10 years. This study was conducted in four major landscapes of the Kruger National Park as described by Gertenbach (1983), i.e. the mixed *Combretum/Terminalia sericea* woodland (Landscape 5), the *Colophospermum mopane/Acacia nigrescens* savanna (Landscape 12), the *Sclerocarya birrea/Acacia nigrescens* savanna (Landscape 17) and the *Colophospermum mopane* shrubveld (Landscape 23) (Figure 8). Table 4 is a summary of the main characteristics of these landscapes. When examining the rainfall pattern of the four landscapes as described by the CCWR (Dent, Lynch & Shulze 1989), Landscape 5 yields a higher annual rainfall than the rest of the landscapes. The annual rainfall in Landscape 5 varies between 500 and 800 mm as opposed to 350 and 700 mm in the other landscapes.



Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 8. Location of Landscapes 5, 12, 17 and 23 and the roan enclosure within the Kruger National Park on the different substrata (granite and basalt).

Table 4

The main characteristics of the four major landscapes (Landscapes 5, 12, 17 and 23) of the Kruger National Park (Gertenbach 1983).

Aspects	**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)
Size	1587 km^2	1042 km^2	1411 km^2	1993 km^2
Geology	Granite	Granite and gneiss	Basalt	Basalt
Dominant soils	Sandy	Sandy	Clay	Clay
Soil clay Content	6 – 15%	15% and more	15% to 35%	20% to 50%
Rainfall (annual mean)	500 to 800 mm	500 to 600 mm	550 to 600 mm	450 to 500 mm
Vegetation diversity	Dense bush savanna Open tree savanna Dense riverine vegetation	Open tree savanna dominated by mopane trees	Dense bush savanna Open tree savanna Grassland Dense riverine vegetation	Mopane dominated shrubveld Other species rare
Impala Densities/km^2 (1983 – 1997)	215	118	171	115
Elephant densities/km^2 (1985 - 1997)	4.3	5.7	2.7	2.6

The N'waxitshumbe roan antelope enclosure was used as a control site for the population structure of the marula, as this area has been protected from browsing since 1967. It comprises 309 ha and is located in Landscape 23 on basalt, in the northern arid savanna near Shingwedzi. The N'waxitshumbe enclosure was erected in true roan habitat and consists of mopane woodland savanna, grassland savanna and *Sclerocarya birrea/Acacia nigrescens* savanna (Joubert 1970). This enclosure (which is divided into four blocks) has not been subjected to a fixed burning program, and the different blocks were burned on a random basis throughout the years with a mean fire return period of between 2 and 3 years. The burning programme within the camp was therefore not much different from the triennial fire regime throughout all the landscapes of the Kruger National Park. The dominant woody species inside the enclosure are *Colophospermum mopane*, *Ormocarpum trichocarpum* and *Dalbergia melanoxylon*. The animal population within the enclosure consists mainly of about 30 roan antelope (*Hippotragus equinis*), while smaller animals such as steenbok (*Raphicerus campestrus*) also occur. The diet of the roan antelope consists primarily of grass, although they occasionally browse green leaves and young shoots of shrubs and favoured trees (*Dalbergia melanoxylon* and *Lonchocarpus capassa*) during excessive dry periods (Joubert 1970). No comparable exclosure sites occur in Landscapes 5 or 12 on the granitic soils or in Landscape 17 on basalt.

Methods

Data collection

To examine the population structure of a single tree species such as the 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 structural composition of the marula tree population. The location of transects were restricted by the availability of vehicle tracks such as firebreaks.

Each road transect was 2 km long with a width of 50 m on either side of the road. Every living mature marula tree (>2 m in height) was examined, and the girth at breast height (GBH) and maximum canopy height were recorded. Trees coppicing from broken trunks were also recorded. Individuals in the lower canopy (<2 m) were sampled on 16 smaller belt transects (5 x 100 m) delineated and surveyed on foot within each road transect. These lower canopy transects were delineated parallel to the road at 30 and 50 m, placed at 500 m intervals from the beginning of the 2 km transects. Figure 9a shows the sampling scheme. Incidental sightings of all marulas in the lower canopy were also recorded on the way to and between the 30 and 50 m transects. The height class and stem status (single or multi-stemmed) of each individual in the lower canopy were recorded.

A road transect of 1.5 km was surveyed inside the roan enclosure, and sampling of mature marula trees was conducted in the same way as for the road transects conducted across the landscapes. For sampling of marula trees in the lower canopy of the roan enclosure, 12 belt transects of 100 m x 5 m were conducted in each of the four burn blocks, where these belt transects did not overlap with the road transect. Because only one road transect could be placed inside the roan enclosure, mature trees in the smaller belt transects were also recorded. Along the fire-break roads that surround the roan enclosure, three belt transects of varying sizes and one road transect were conducted (Figure 9b). The height, crown diameter and stem status of the individuals in the lower canopy inside and adjacent to the roan enclosure were measured.

Mature trees were defined as woody plants with a height exceeding 2 m and with one or a few definite trunks branching above ground level (Edwards 1983). Individuals <0.25 m were regarded as new seedlings (seedlings from the last growth season) (Ben-Shahar 1996). Small individuals were assigned to the following height classes: A=<0.25 m; B=0.25–1 m; C=1-2 m. Trees were assigned to the following height classes: D=2–5 m; E=5-8 m; F=8–11 m; G=11–14 m and H=>14 m.

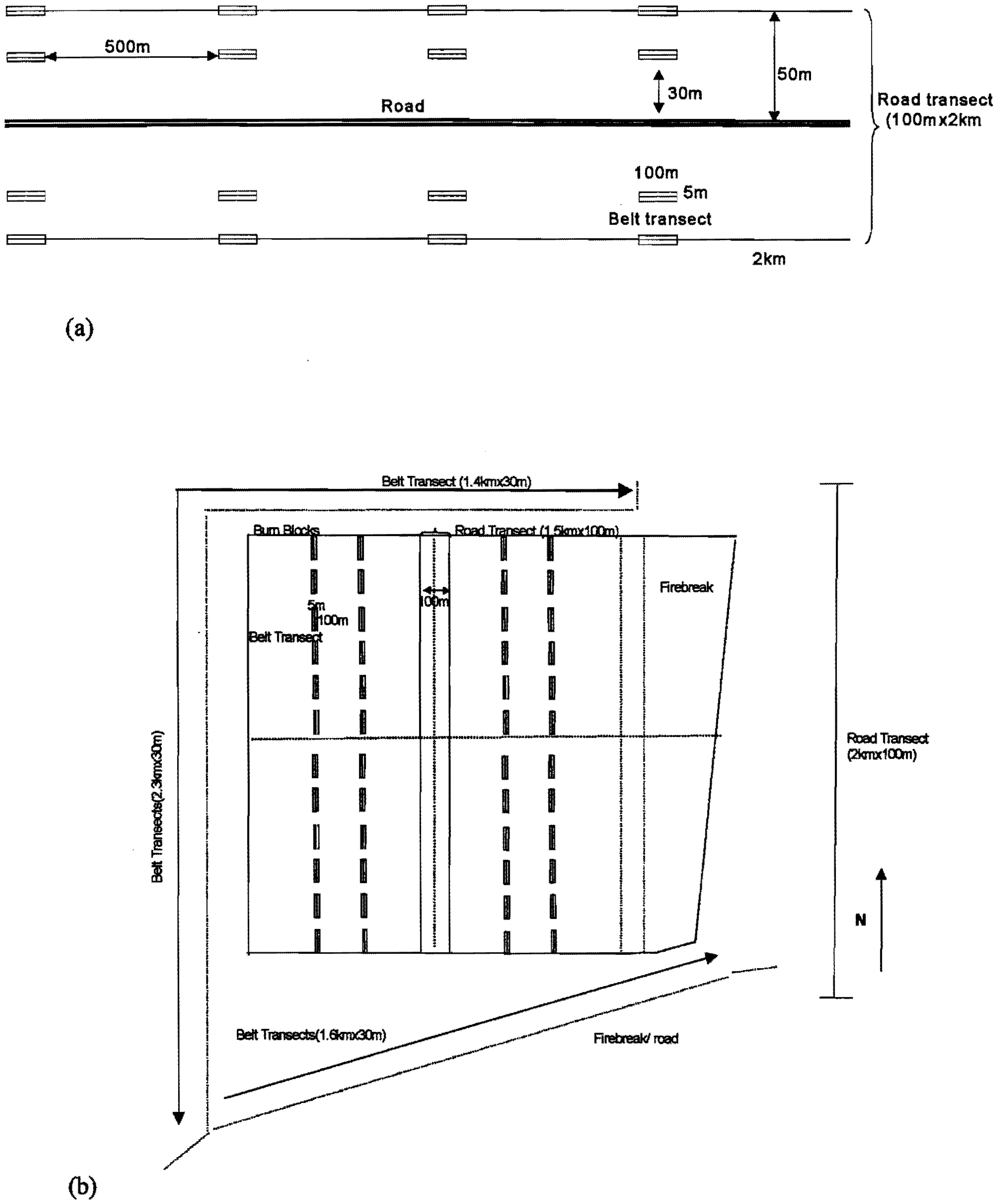


Figure 9. Sampling scheme used in (a) Landscapes 5,12,17 and 23 and (b) the roan enclosure and adjacent area.

The elephant census results (annually recorded by Whyte)[1] were used to calculate the elephant densities in the different landscapes for the period 1985 to 1997 (Table 4). The annual game census results, for the period 1983 – 1997, were used to calculate impala densities in the different landscapes (Table 4).

Data analysis

All variables were examined in Landscapes 5, 12, 17 and 23, an area immediately adjacent to the roan enclosure (23A) and the area within the roan enclosure (23B). As no marula individuals were recorded in Landscape 23, a nested design of landscapes within geological types could not be used for data analysis; neither was it possible to compare the roan enclosure to the surrounding landscape 23 in which it was situated. Maximum interpretative value was gained from the roan enclosure data set by including it in the general analysis of the landscapes. All normally distributed data sets (height, log-transformed crown diameter, GBH) were examined using analysis of variance (ANOVA). Densities were examined using a negative binomial regression model with a log link, whereas proportion data was analysed with logistic (binomial) regression analysis. Overdispersion in binomial models was corrected using the William's procedure (Williams 1982).

Densities and proportions for the lower canopy were calculated by pooling belt transect data within each road transect, thus yielding 20 values per landscape (numbers 5, 12, 17, 23). Data for the three larger belt transects conducted adjacent to the roan enclosure (23A) were analysed separately, while belt transects in the roan enclosure (23B) were pooled for each of the four burn blocks. For mature tree variables, all data recorded in the belt transects conducted in the roan enclosure, were pooled. In order to prevent pseudo-replication in analysing the height and GBH of mature trees, the averages for these parameters were calculated for each road transect. Linear regression analysis was used to determine the relationship between height and GBH for non-coppicing trees and was based on the ungrouped data.

[1] Whyte, I.J. Census results for elephants and buffalo in the Kruger National Park, Skukuza, National Parks Board.

Results

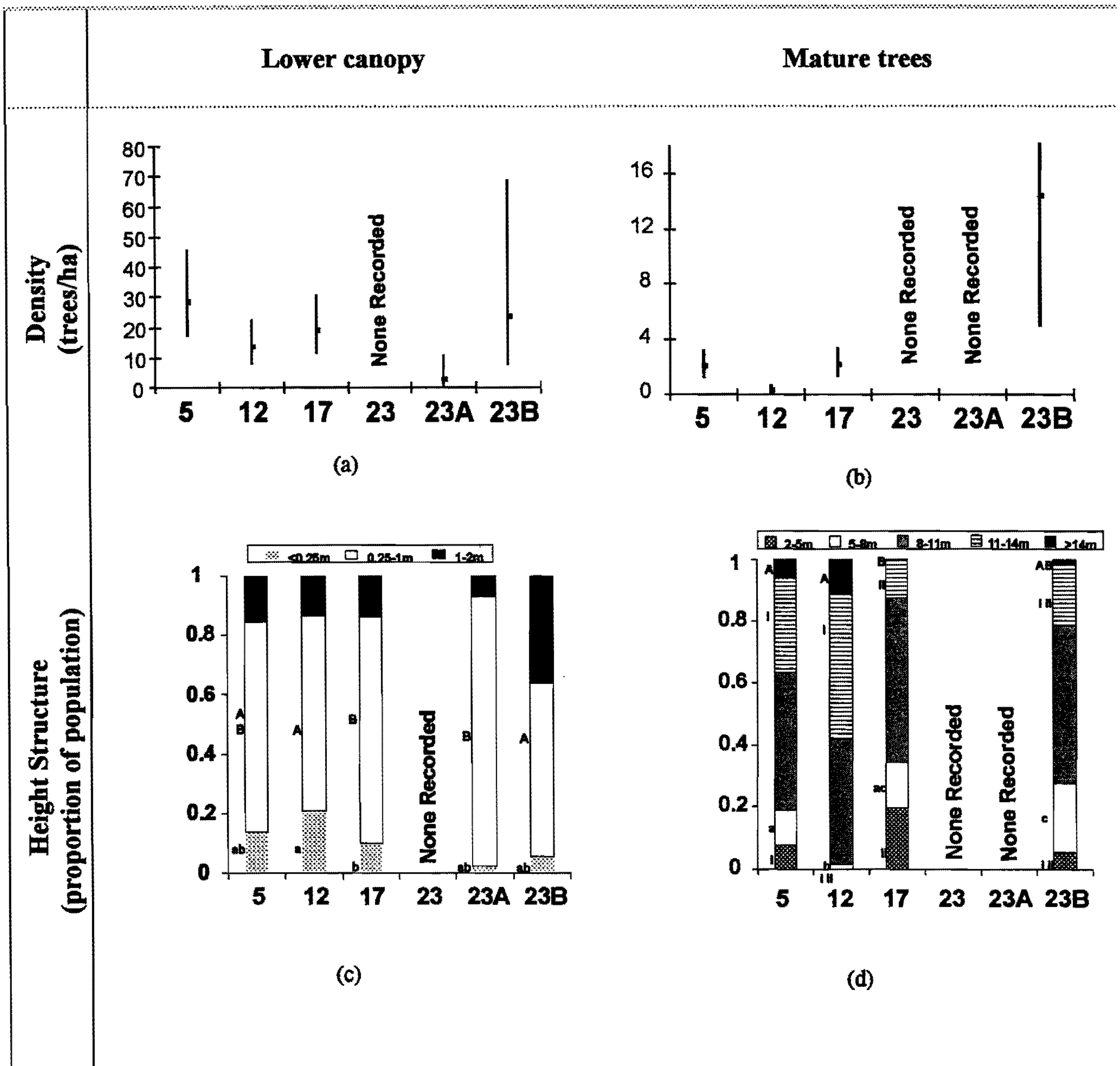
Figure 10 shows the density status and population structure of the marula population (lower canopy and mature trees) in the four landscapes and the roan enclosure surveyed in this study. It is important to note that neither mature trees nor individuals in the lower canopy were encountered in any of the road or smaller belt transects conducted in Landscape 23, although a conspicuous number of marula trees were recorded in the transects in and directly adjacent to the roan enclosure in the same landscape.

Lower canopy

The landscape effect on the density and structure of marulas in the lower canopy is summarised in Table 5. The number of marula trees in the lower canopy did not differ significantly between 30 m and 50 m from the road ($p=0.7152$). The proportion of single-stemmed individuals differed significantly across the different landscapes and between the different height classes (Figure 11). The structure (height and crown) of lower canopy individuals inside the roan enclosure was significantly larger than that of individuals recorded immediately adjacent to the enclosure (Figure 12).

Mature trees

The density of mature marula trees and the proportion of trees in each height class differed significantly between landscapes (Table 5). The average height and girth differed significantly across landscapes (Figure 13). The relationship between height and GBH is given by: Height=4.595+3.816*(GBH) ($r^2=38.5\%$; $p<0.00005$). However, this relationship differed between landscapes ($r^2=51.1\%$; $p<0.00005$). The relationship in granite landscapes (Landscapes 5 and 12) differed significantly from that in the basalts (Landscapes 17 and 23), where the relationship in Landscape 17 and the roan camp (23B) also differed significantly from one another.



* Different letters indicate significant differences between landscapes at p=0.05

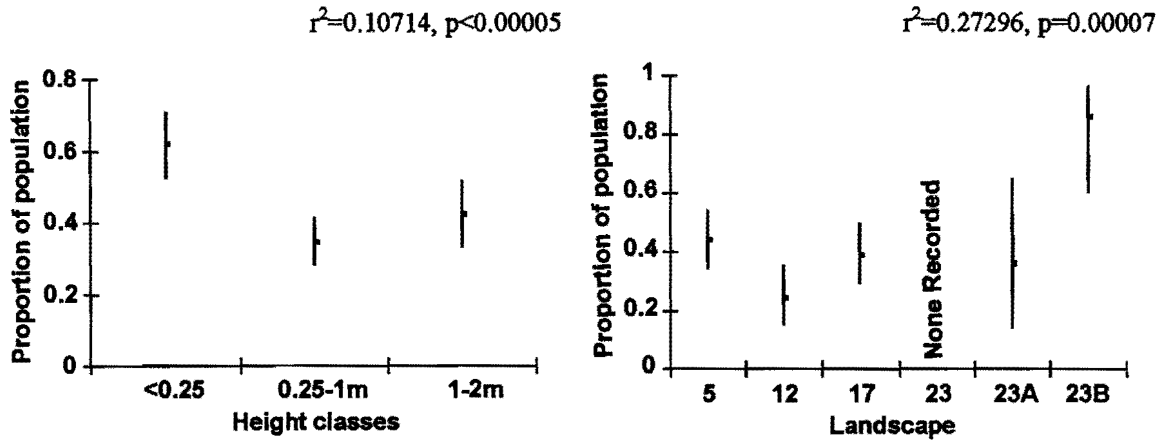
Landscapes: **5** = Mixed *Combretum/Terminalia sericea* woodland; **12** = *Colophospermum mopane/Acacia nigrescens* savanna; **17** = *Sclerocarya birrea/Acacia nigrescens* savanna; **23** = *Colophospermum mopane* shrubveld; **23A** = Area immediately adjacent to roan enclosure; **23B** = Roan enclosure

Figure 10. Landscape differences in density and population structure of *Sclerocarya birrea* in the Kruger National Park

Table 5.

Landscape effects on lower canopy and mature marula trees.

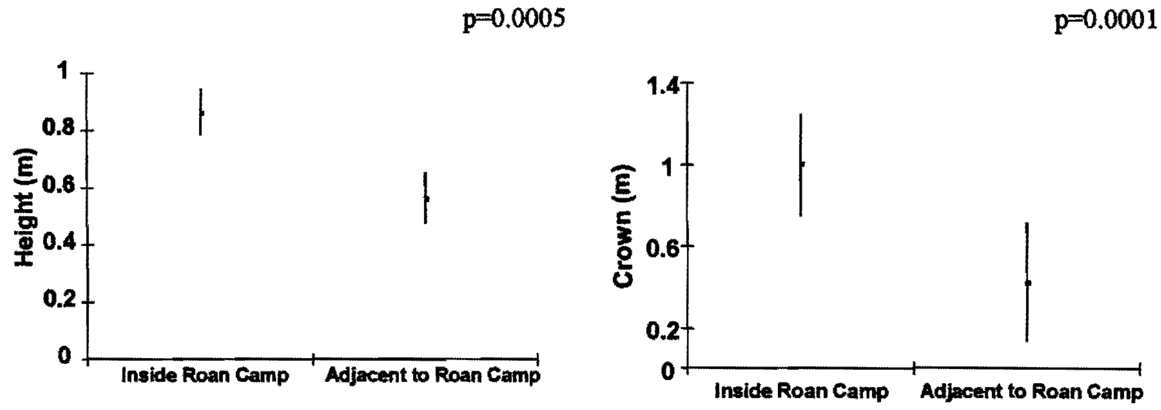
Parameter	Landscape Effect	Internal Contrast
Density: lower canopy	r^2=0.13573; p=0.04162	Figure 10a
Density: mature trees	r^2=0.72486; p<0.00005	Figure 10b
Height Structure: lower canopy		
• <0.25 m (class A)	r^2=0.05909; p=0.00585	Figure 10c
• 0.25 – 1 m (class B)	r^2=0.14840; p=0.01800	
• 1 – 2 m (class C)	NS	
Height structure: mature trees		
• 2 – 5 m (class D)	r^2=0.25615; p=0.00014	
• 5 – 8 m (class E)	r^2=0.24538; p=0.00042	Figure 10d
• 8 –11 m (class F)	NS	
• 11 – 14 m (class G)	r^2=0.34451; p<0.00005	
• >14 m (class H)	r^2=0.28382; p=0.00045	



(a) (b)

Landscapes: **5** = Mixed *Combretum/Terminalia sericea* woodland; **12** = *Colophospermum mopane/Acacia nigrescens* savanna; **17** = *Sclerocarya birrea/Acacia nigrescens* savanna; **23** = *Colophospermum mopane* shrubveld; **23A** = Area immediately adjacent to roan enclosure; **23B** = Roan enclosure

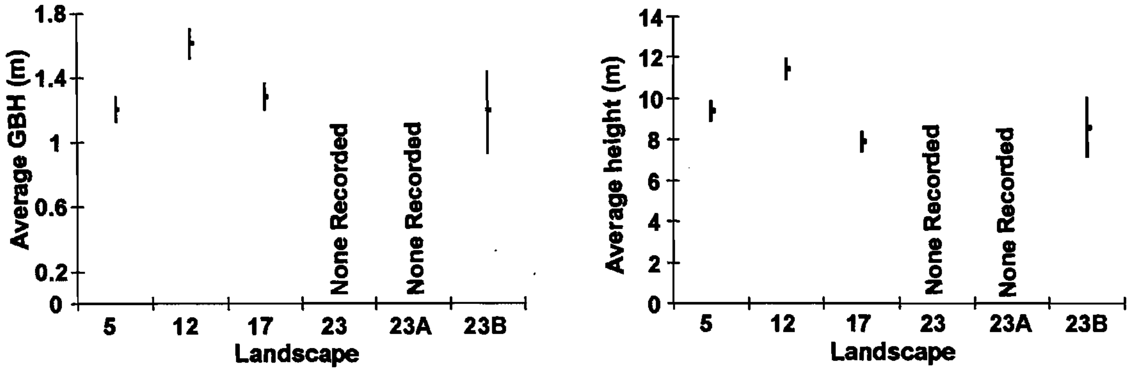
Figure 11. Variation in proportion of single stemmed individuals between (a) height classes and (b) landscapes.



(a) (b)

Figure 12. Exclosure effects on (a) the height and (b) the crown diameter of marulas in the lower canopy.

P<0.00005 P<0.00005



(a) (b)

Landscapes: **5** = Mixed *Combretum/Terminalia sericea* woodland; **12** = *Colophospermum mopane/Acacia nigrescens* savanna; **17** = *Sclerocarya birrea/Acacia nigrescens* savanna; **23** = *Colophospermum mopane* shrubveld; **23A** = Area immediately adjacent to roan enclosure; **23B** = Roan enclosure

Figure 13. Landscape effects on (a) average height and (b) GBH of mature trees.

Discussion

The fact that the only significant number of marula trees recorded in Landscape 23 were located in or around the roan camp, appears to indicate that certain areas within this landscape are suitable to marula trees and that the vegetation diversity in Landscape 23 has changed significantly since the construction of the roan enclosure in 1967. At that time three different vegetation types (including *Sclerocarya birrea/Acacia nigrescens* savanna) were recorded in the roan enclosure, and also occurred at least in the area surrounding the enclosure (Joubert 1970). Gertenbach (1983) classified this landscape as mopane shrubveld with three grassland variations, indicating that homogenising of the tree layer of this landscape must have occurred prior to this classification. It thus appears as though marula trees were historically present in this landscape, but that management practices such as increased elephant populations and a fixed fire policy have contributed to the decline of marula trees in this landscape.

Since marula trees are particularly selected for by elephants in the Kruger National Park (Trollope *et al.* 1998), one of the long-term factors contributing to the lack of marula trees in Landscape 23 could be that elephants have re-colonised the northern basalt areas of the Kruger National Park since 1905 (after being hunted to near extinction in the Lowveld prior to 1903 (I.J. Whyte, In prep. 2000)), whereas the southern parts on basalt and granite were only re-colonised after 1937. Re-colonisation of the northern granite areas (Landscape 12) only commenced during 1958 (I.J. Whyte, In prep. 2000). Van Wyk & Fairall (1969) reported severe elephant damage to *Colophospermum mopane* (mopane), *Grewia* species and *Combretum apiculatum* in the northern part of the Park. Species such as marula, *Acacia tortilis* and *Combretum imberbe* were at that time also severely browsed, but in comparison with other species, less uprooted (Van Wyk & Fairall 1969). Van Wyk & Fairall (1969) further reported that vegetation utilisation was at that stage very limited in the southern region. The dominance of mopane in Landscape 23 may have caused specific selection and consequent severe over-utilisation of marula individuals over an extended period, which resulted in the near removal of marulas throughout the landscape except in the roan enclosure. Guy (1976) estimated the average number of trees a single elephant may push over per day was as high as 4.2 trees. However, other macro-scale processes, such as the effect of global climate change, should not be discounted as contributing factors in the observed vegetation change in this landscape. The analyses of M.C. Rutherford, G.F. Midgley, W.J. Bond, L.W. Powrie, R. Roberts, J. Allsopp (In prep. 2000) indicate that there may be a major rearrangement of species in the Savanna Biome, with some species showing marked reductions to their current ranges while others expand into previously unsuitable climatic areas. Viljoen (1988) speculated that the change in vegetation in the *Sclerocarya birrea/Acacia nigrescens* savanna between 1944 and 1981 could be ascribed to the intense drought during the 1960's in combination with frequent burning and elephant impact.

An important issue raised by these findings is the process by which marula re-establishment can occur in Landscape 23 and the time-frame required for such a process. As mature trees are virtually absent, the only significant remaining source of marula fruit in this landscape is located within the roan enclosure which has been protected from elephants (one of the few dispersing agents of the marula seed (Lewis 1987)) since 1964. Results obtained by Whyte (1993) and Hall-

Martin (1984) indicated that elephant clans generally restrict their home ranges to either basalt areas or granite areas. The elephant clan in Landscape 23 monitored by Whyte (1993), did not move out of their home range into other landscapes, except during extreme droughts. Thus marulas are unlikely to spread from the adjoining granites into Landscape 23 and re-establish from that source. Furthermore, the clay soils limit the formation of deep root systems and water availability through an extended period of the year (Jachmann & Croes 1991), reducing the possibility of re-establishment of seedlings and successful population growth. Successful establishment of seedlings can, therefore, only take place for a short period during the rainy months.

Density

It appears as if seedling recruitment is taking place uniformly, and hence, that neither geology nor rainfall play a detrimental role in seedling establishment, since there was not a significant difference in the density of seedlings across Landscapes 5, 12, 17 and inside the roan enclosure (Figure 10a). However, these results indicate that a continuous rate of seedling regeneration is occurring, in contrast to Walker *et al.* (1986) who suggested that regeneration of marula is highly episodic. The lower density of seedlings directly adjacent to the roan enclosure could be due to increased herbivory. The fact that no marulas in the lower canopy were recorded throughout Landscape 23 indicates that dispersion of seeds, and hence regeneration of the marula population is not taking place in this landscape. Results therefore, do not support Lewis (1987) and Haig (1999) who suggested that small browsers, especially impala, were the main cause for seedling mortality and the lack of regeneration.

The fact that mature marula tree densities did not differ significantly between Landscapes 5 and 17 (where Landscape 5 yielded a higher annual rainfall than Landscape 17), and that the density in the roan enclosure was significantly higher than in all other landscapes (Figure 10b), indicates that the density of mature marulas respond to factors other than rainfall and geology. The significantly higher density of trees in the roan enclosure can be explained by the fact that the enclosure was constructed in 1967, and the vegetation was therefore protected from elephant impact for most of the time since the dramatic increase in elephant numbers that occurred during the 1960's. The lower density of trees in Landscape 12 can probably be ascribed to increased herbivory pressure as a result of less diverse vegetation, since soils are similar to Landscape 5, which has more mature marulas (Figure 10b). This supports the result of Lewis (1987) who found increased browsing pressure for seedlings in areas with lower species diversity, hence resulting in less recruitment into the upper canopy. Anderson & Walker (1974) found that elephants will forage on a favoured species until food becomes less available, when they will move on to the next favoured species. The lower marula seedling density directly adjacent to the roan enclosure could be attributed to a lack of seed producing trees in this area. The mature marula trees within the roan camp (specifically those closest to the fence) are most probably the source of these seedlings.

When examining the density of marula trees in the lower canopy at different distances (30 and 50 m) from the road, it appears as if 30 m is far enough from the road not to have been impacted on by increased runoff or disturbance from elephants walking along the road

Population structure

Examining the distribution of GBH measurements across the landscapes, it appears that all girths up to 2.4 m are well represented across the total data set. The number of trees recorded with a girth exceeding 2.4 m (estimated age of 183 years (Haig 1999)) declined sharply. This indicates that regeneration of marulas occurred across the entire period of time, and it does not appear as though recruitment events are directly influenced by climatic or rainfall cycles. However, the population structure is probably affected by the interaction between climate, rainfall, herbivory and fire.

When examining the overall structure of individuals in the lower canopy, the general indication is that new regeneration occurs continuously. The only significant difference in class A was found between Landscapes 12 and 17, where Landscape 12 yielded a higher proportion of new seedlings (Figure 10c). The average elephant density between 1985 and 1997 in Landscape 12 (5.7 elephants/km^2) is much higher than the density in Landscape 17 (2.7 elephants/km^2), and the higher number of elephants may promote the germination as well as seed dispersion of marula trees (Lewis 1987). The undulating terrain of the granites also contributes towards the establishment of seedlings, as they are more protected from fire and herbivory than on the open plains of the basalts. The slightly higher proportion of new seedlings in Landscape 12 when compared to Landscape 5 could be due to less competition from vegetation in a landscape with less diverse plant species composition. The greater proportion of individuals in class C in the roan enclosure indicates that low herbivory impact provides the opportunity for marula individuals in the lower canopy to grow beyond the fire sensitive height of 1.5 m as determined by O.S. Jacobs & R. Biggs (In prep. 2000). As opposed to these seedlings, the lower canopy adjacent to the roan enclosure has a high proportion of individuals in class B due to exposure to annual burning in combination with herbivory. This supports O.S. Jacobs & R. Biggs (In prep. 2000) who found the combination of annual burning and herbivory prevents marula trees in the lower canopy from developing into the upper canopy. The larger structure (height and crown) of marulas in the lower canopy within the roan enclosure compared to those encountered directly adjacent to the roan enclosure (Figure 12) further reflects the impacts of increased herbivory and fire frequency on individuals adjacent to the roan enclosure.

In general, the structure of mature trees on the granite substrates shows a high proportion of mature trees, differing from the structures on basalt which shows approximately stable height class distributions with successful regeneration (Figure 10d). It appears that less recruitment of individuals into the upper canopy is occurring on granite than on basalt. Various studies conducted on granites (Walker *et al.* 1986; Lewis 1987; Gadd 1997) revealed similar marula population structures with a lack of immature trees (<7 m). Although it appears that geology is important, the elephant densities could also play a major role in determining the population structures on the different substrates, as the granite areas in the Kruger National Park have a higher density of elephants. The proportion of trees in each height class was similar in Landscape 17 and the roan enclosure, and can probably be ascribed to low elephant impact (2.7 elephants/km^2). The proportion of trees in class F did not differ between any of the landscapes and the roan enclosure, and correlates with the previous population structure studies on marula (Walker *et al.* 1986; Lewis 1987; Gadd 1997), indicating that the structure is less affected by varying environmental factors once they reach this height class. Jachmann & Bell (1985) found that trees higher than the preferred feeding level (>7 m) were in general harder to break or push over by elephants.

The structure of the marula population in Landscape 12 is extremely unbalanced with a high proportion of bigger trees as opposed to individuals less than 8 m. The significantly higher average GBH and height in Landscape 12 (Figure 13) are a reflection of this skewed population structure. The high elephant density (5.7 elephants/ha) and low vegetation diversity probably enhanced the elephant impact on the 2-8 m classes, yielding the current unbalanced structure. Results of this study further show that the mature marula trees in Landscape 12 are older trees (according to GBH the average age is approximately 120 years (Haig 1999)), which are probably too big to be affected by elephants. These mature trees were well established when elephants started re-colonising the area in 1958 (I.J. Whyte, In prep. 2000). However, it is believed that the lack of immature trees in this landscape is related to increased elephant impact since re-colonisation. The lack of recruitment into the upper canopy and the gradual death of the existing mature trees as they reach the end of their life cycle, leads to a situation where there is no source of new seeds and hence no new seedling recruitment. This process, which is believed to have led to the virtual extinction of marula trees in Landscape 23, may currently be taking place in Landscape 12. Stewart & Veblen (1982) found that, when most of the mature trees of a population are the same, or nearly the same age, they will tend to senesce and die at about the same time.

GBH is not a very good predictor of height and can therefore not be used for predicting the height of trees with broken trunks. The granites with sandy, well-drained soils enhance growth as opposed to the clay soils of the basalts, resulting in different relationships between height and GBH for basalt and granite. For a given GBH, the predicted height is greater for the roan enclosure than for Landscape 17, possibly as a result of herbivory impacts in Landscape 17.

Single vs. multi-stemmed individuals

The high proportion of single-stemmed individuals in the lowest height class (A) is due to the fact that they are mainly new seedlings. Once the seedlings grow beyond 0.25 m, the stem morphology becomes predominantly multi-stemmed due to fire and herbivory impacts (Figure 11a). The higher proportion of single-stemmed individuals in the roan enclosure than in any of the other landscapes (Figure 11b) can be attributed to protection against herbivory. The proportion of single-stemmed individuals in Landscape 12 was significantly lower than in Landscape 5 (both on granite) and is probably due to increased herbivore pressure as result of the less diverse vegetation within Landscape 12.

Conclusion

The marula population in less diverse landscapes appears to be more susceptible to herbivory impact. The current status of the marula population in the landscapes under review is as follows: *Landscape 23:* The marula population appears to have become extinct. *Landscape 12:* An unstable population structure for the marula exists, with no recruitment of individuals into the upper canopy. Existing mature trees are predominantly older trees at the end of their life cycle, and their death may in time lead to the extinction of the population as the seed source disappears. *Landscape 5 & 17:* The population structures in Landscape 5 & 17 appear to be healthy, with a good distribution of individuals throughout the different height classes.

As opposed to previous vegetation studies (Walker *et al.* 1986; Gadd 1997), high recruitment rates were found throughout the study area in the Kruger National Park. It therefore appears as if sufficient regeneration is taking place, but that a combination of factors is preventing successful recruitment into the upper canopy. Geology and rainfall appear not to be the dominant factors contributing to the differences in the population structure between the different landscapes. Results indicate that marula populations can establish well on both the basalt and granite substrata under favourable conditions. Results further indicate that seedling mortality can not be related to increased herbivory by small browsers such as impala, but that a combination of browsing pressure and fire influences the structure of the lower canopy. The main impact on the mature marula trees could be related to elephant densities as well as the vegetation diversity.

Whyte, Biggs, Gaylard & Braack (1998) proposed a new elephant management policy in order to control the impact of elephants on the biodiversity of the Kruger National Park. The proposed new elephant impact zones (I.J. Whyte, In prep. 2000) are as such that Landscape 12 and most of Landscape 23 fall within the low elephant impact zone, while Landscapes 5 & 17 fall within the proposed high elephant impact zones. Most probably, the healthy populations of Landscapes 5 and 17 will not be as susceptible to the high elephant impact due to more diverse vegetation, but will not sustain the higher impact for excessive periods. Monitoring will be necessary to determine when structural diversity of the marula population in these landscapes is being lost, and clear thresholds of potential concern (TPC's) should be formulated against which such change can be measured. Existing TPC's for rare plants are based on the decline in numbers and recruitment of an order (taking into account the probable biology of the species) that would cause conservation concern, and obvious evidence of "non-natural" threats which constitute persuasive proof on a scale likely to be leading to such declines. Results of this study indicate that TPC's have been reached in Landscapes 12 and 23 and highlights that TPC's can be quantified by similar studies on other key species. Once stand structure has become homogenous through the action of any single agent or combination of factors, the population is set to undergo synchronous mortality (Stewart & Veblen 1982). TPC's should therefore be identified as to protect the important tree species from developing even age population structures.

A further area requiring research as highlighted by this study is the dispersion mechanism of the marula seed. The dispersion of marula seeds across the fence of the roan enclosure could not be attributed to elephants, indicating that other dispersal mechanisms exist. The succession process (re-colonisation and establishment) of marula trees in an area which has been depleted from a seed source should also be investigated. In the light of the policy of the South African National Parks to conserve all native species, it is hoped that results of this study will contribute to the formulation of future management strategies.

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THE IMPACT OF THE AFRICAN ELEPHANT ON MARULA (*SCLEROCARYA BIRREA* SUBSP. *CAFFRA*) TREES IN THE KRUGER NATIONAL PARK

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Abstract

Previous vegetation studies in the Kruger National Park have showed 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 utilised 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 5 m. Main stem breakage by elephant was the main cause of the 7% mortality observed in the marula population.

Key words: damage, population structure, savanna, utilisation

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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.

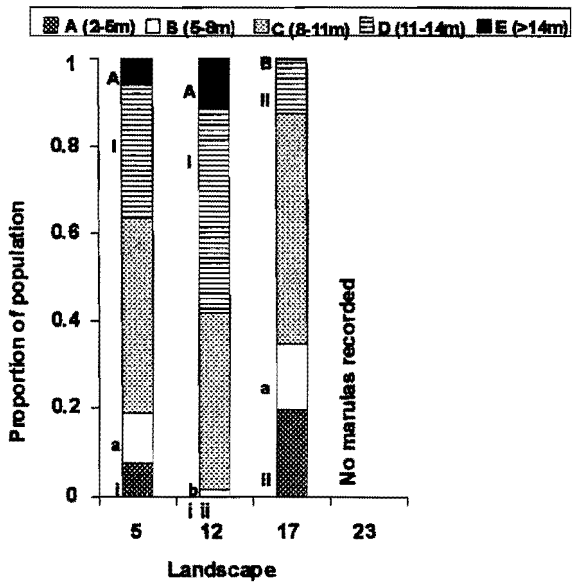
The severe impact that elephants have on marula populations has been documented in private protected areas in the South African Lowveld (Gadd 1997; Weaver 1995). Gadd (1997) found that marula was one of the trees most utilised by elephant and that recruitment and regeneration of these trees were very weak. Weaver (1995) found that the impact was particularly pronounced on marula and *Acacia nigrescens* in the Klaserie Private Nature Reserve, where marula was 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 to 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 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 (<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 – 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 are more a social display than a feeding necessity, although, Coetzee *et al.* (1979) found that marula trees were utilised 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. O.S. Jacobs & R. Biggs (In prep.2000 b) found no significant differences in the density of marula seedlings (<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 (I.J. Whyte, In prep. 2000). 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 *Colophospermum mopane/Acacia nigrescens* savanna (Landscape 12) differed significantly from the other landscapes (O.S. Jacobs & R. Biggs, In prep. 2000 b) (Figure 14). O.S. Jacobs & R. Biggs (In prep. 2000 b) 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.



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

* Different letters indicate significant differences between landscapes at p = 0.05.

Figure 14. Landscape differences in the population structure of *Sclerocarya birrea* in the Kruger National Park (Source: O.S. Jacobs & R. Biggs, In prep. 2000 b).

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 characterised 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), i.e. 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.

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 (>2 m in height) was examined and assigned to one of the following size classes: A = 2-5 m, B = 5-8 m, C = 8-11m, 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 stepsiceros*), 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 recognised by scorch marks on dead branches or a peeled and dark bark surface (Coetzee 1983).

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 to 1998 (I.J. Whyte 1998) [1]were used to determine the mean elephant densities (elephants/km^2) in the three landscapes.

Results

Tables 6 to 8 summarise the results of this study. The mean elephant densities per landscape for the period 1985 to 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. The majority of these trees had been felled and thus elephant damage seems to be the major cause of tree mortality. The proportion, as well as the nature of dead trees did not differ between marula populations in the different landscapes (Table 7; A).

[1] Whyte,I.J. 1998. Census results for elephants and buffalo in the Kruger National Park, Skukuza, National Parks Board.

Table 6.

Summary of results.

Parameter	Composition of parameter	Landscape	Composition across landscapes	Height class	Composition across height classes	Damage class	Composition across damage classes	Internal contrasts (Table)
A **Dead Trees**	r^2=0.36567 p<0.00005	NS	Fire: NS Standing: NS Uprooted: NS	-	-	-	-	Table 7 (A)
B **Damage Class**	r^2=0.36364 p<0.00005	r^2=0.54545 p<0.00005	Light: r^2=0.19181 p=0.00403 Moderate: NS High: NS Extreme: r^2=0.27144 p<0.00005	r^2=0.08642 p=0.00158	Light: r^2=0.68515 p<0.00005 Moderate: r^2=0.33664 p<0.00005 High: r^2=0.22599 p=0.00182 Extreme: r^2=0.81155 p<0.00005	-	-	Table 7 (B)
C **Damage Agent**	r^2=0.41206 p<0.00005	-	r^2=0.25039 p=0.00289	-	r^2=0.29934 p<0.00005	-	r^2=0.30609 p<0.00005	Table 7 (C)
D **Bark Damage**	r^2=0.49002 p<0.00005	r^2=0.53125 p<0.00005	<50: NS 50-100: NS Ring: NS	r^2=0.18987 p<0.00005	<50: NS 50-100: NS Ring: NS	r^2=0.34574 p<0.00005	-	Table 7 (D)
E **Branches**	-	r^2=0.20339 p=0.00744	-	r^2=0.09467 p=0.00906	-	r^2=0.82192 p<0.00005	-	Table 8 (A)
F **Coppice**	-	r^2=0.22368 p=0.00061	-	r^2=0.66288 p<0.00005	-	r^2=0.97487 p<0.00005	-	Table 8 (B)

* r^2 refers to proportion of total deviance explained by model

** p-values adjusted for multiple testing according to the Bonferoni Theorem

Internal contrasts in proportions of dead trees, degrees of damage, agents responsible for damage and types of bark damage across landscapes, height and damage classes.

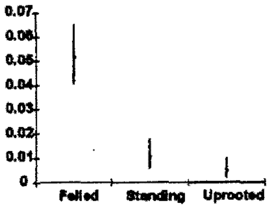
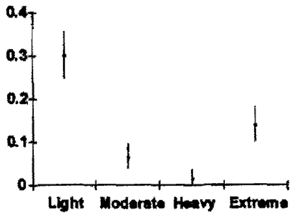
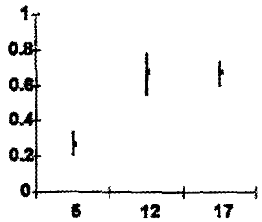
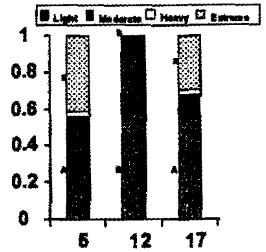
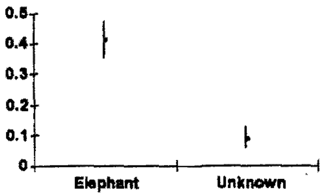
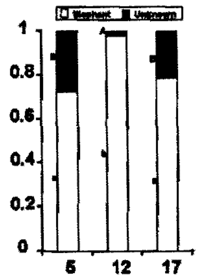
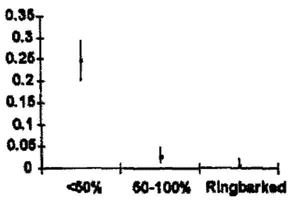
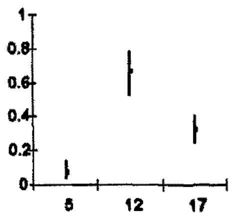
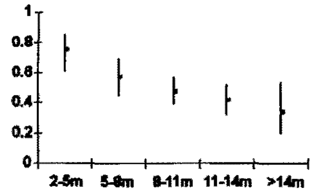
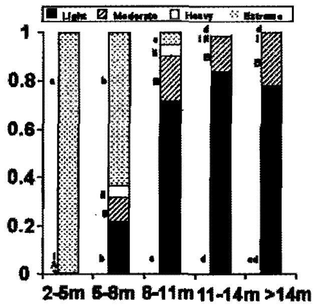
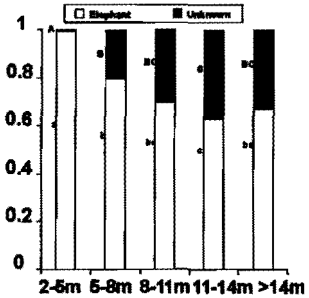
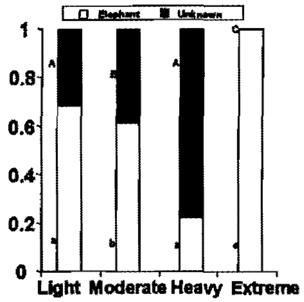
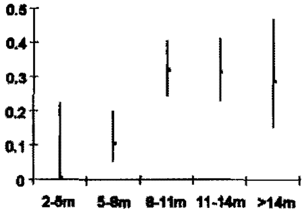
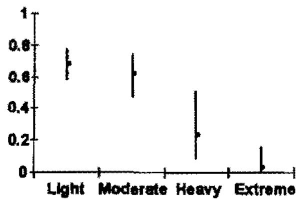
Parameter	Composition of parameter (Proportion of total sample)	Landscape ** (Proportion of sample per landscape)	Composition across Landscapes ** (Proportion of affected sample)
A **Dead Trees**		NS Average = 6.94%	NS
B **Damage Class**			
C **Damage Agent**		-	
D **Bark Damage**			NS

Table 7 continued ....

Table 7 continued

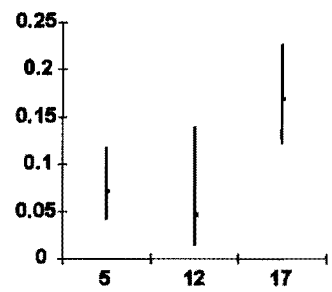
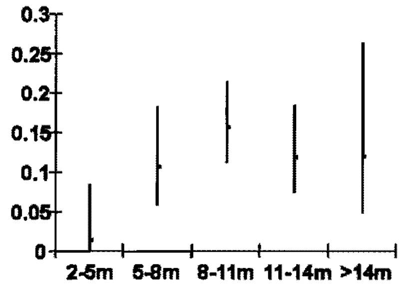
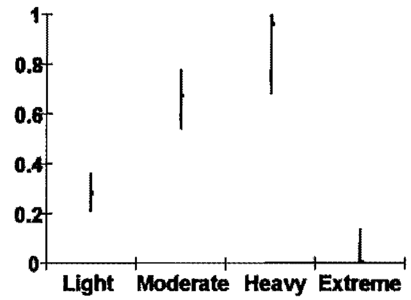
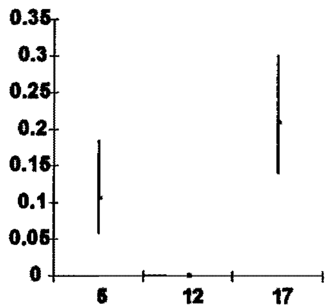
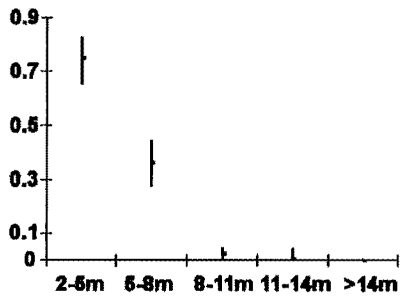
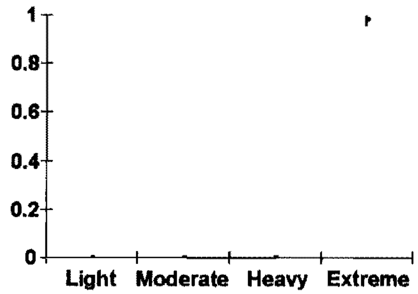
Parameter	Height classes (Proportion of sample per height class)	Composition across height classes (Proportion of affected sample)	Damage class *** (Proportion of sample per damage class)	Composition across damage class *** (Proportion of affected sample)
A Dead Trees	-	-	-	-
B Damage			-	-
C Damage Agent	-		-	
D Bark Damage		NS		-

* Common letters indicate parameters not differing significantly

** 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

Table 8
Proportion of sample suffering branch and main stem breakage impacts across landscapes, height and damage classes

Parameter	Landscape ** (Proportion of sample per landscape)	Height Classes (Proportion of sample per height class)	Damage Classes *** (Proportion of sample per damage class)
A **Branches**			
B **Coppice (Main stem breakage)**			

** 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

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 (Table 7; B). A higher proportion of the damage in Landscape 12 was attributable to elephant (Table 7; C). Landscape 12 showed mainly bark damage (Table 7; D), whereas damage in Landscapes 5 and 17 also consisted of a significant proportion of broken branches and main stem breakages (coppicing trees) (Table. 8; A & B).

Height class differences

Examining the damage across height classes, there seems to be a gradual decline with shorter trees suffering more damage than taller marula trees. 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 (Table 7; B). The damage across all height classes was mainly ascribed to elephant impacts (Table 7; C). Trees in the 8-14 m height classes had predominantly bark damage (Table 7; D) and broken branches, while damage to shorter trees consisted predominantly of main stem breakages resulting in coppicing (Table 8; A & B). Bark damage to all height classes was predominantly light (<50% bark removed from trunk circumference) (Table 7; D).

Damage class differences

Elephant seemed to be the dominant agent causing extreme damage (Table 7; C), mainly in the form of main stem breakages, resulting in trees coppicing (Table 8; B). Light and moderate damage (also ascribed to elephant impact) involved bark damage, whereas almost all heavily damaged trees had broken branches (Table 8; A).

Discussion

This study provided an evaluation of the status of marula utilisation 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) was the main cause of the 7% mortality in the observed marula population, and this supports the findings of Gadd (1997). Thus, results indicate that elephant impact is the main cause of mortality amongst the marula trees (>2 m) of the Kruger National Park. The proportion of dead trees did not differ across different landscapes, indicating that mortality is taking place uniformly across the landscapes.

Living trees

Structural changes

Approximately 55% of the surveyed marula population had suffered damage of some kind, with about 15% of all recorded damage being extremely heavy. Extreme damage entails mainly broken main stems, from which the marula trees would probably not be able to recover (Barnes 1982), thus changing the population structure towards the shrub category (<3m). Of the sample in the 2 – 5 m height class, 78% trees were coppicing. This 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 causes a proportion of trees previously not affected by fire, to be susceptible to fire impacts. O.S. Jacobs & R. Biggs (In prep. 2000 a) 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

The greater proportion of damage in the damage classes were ascribed to elephant damage, except in the case of the high damage class where damage was mainly recorded as unknown. The largest proportion of heavy damage was recorded on trees between 5 – 11 m, which could be ascribed to branch breakage due to elephant, giraffe or wind. However, branch breakage appears to be a minor form of damage as only 10% of the surveyed population had broken branches. Gadd (1997) found that marula trees could survive any branch breakage if less than 75% of damage occurred to an individual tree. 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 (Table 7; A). 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.* 1997).

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), suggesting that elephant select the smaller trees in preference to the larger ones, as found by Van Wyk & Fairall (1969) and Anderson & Walker (1974). Approximately 99% of the population sampled in class A yielded extreme elephant damage, mostly due to main stem breakage. This class includes the preferred level of elephant feeding, estimated between 2 – 3 m (Jachmann & Croes 1991). Jachmann & Bell (1985) found that trees, higher than the preferred feeding level, were pushed over or felled. This can explain the high proportion of extreme elephant damage in class B (5 – 8 m). Elephant impact seems to decrease with increase in height, where classes C, D and E showed virtually no signs of heavy or extreme damage, and experienced mainly light damage due to bark stripping. Results therefore indicate that trees >8 m are not as severely impacted on by elephants as those <8 m. This supports Jachmann & Bell (1985) who found that trees >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 <8 m are therefore probably more uprooted and foraged upon, and this could explain the smaller proportion of trees <8 m throughout the different landscapes as found by O.S. Jacobs & R. Biggs (In prep. 2000 b).

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 (O.S. Jacobs & R. Biggs, In prep. 2000 b) showed a highly skewed structure (Figure 14). 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. O.S. Jacobs & R. Biggs (In prep. 2000 b) found the marula populations in Landscape 5 and 17 to have a good distribution of individuals throughout the different height classes (Figure 14). The nature of the elephant impact in these landscapes did not differ significantly (Table 7; B) where both yielded predominantly light and extreme damage. The population structure in Landscape 12, however, comprises mainly of trees >8 m (Figure 14) and yielded light bark damage (<50%) with no heavy or extreme damage. Thus, it appears as though the higher proportion of extreme damage in Landscapes 5 and 17 correspond to the higher proportions of small trees (2 –5 m) encountered in these landscapes. When examining damage to the different height classes, 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 O.S. Jacobs & R. Biggs (In prep. 2000 b) 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.

O.S. Jacobs & R. Biggs (In prep. 2000 b) further stated that Landscapes 5 and 17 appear to have healthy populations. However, results of this study indicates that more than 60% of the trees in classes A and B are 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 coppicing between 2 – 5 m, 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, poses a serious concern as it appears that successful recruitment into the upper canopy is not occurring (O.S. Jacobs & R. Biggs, In prep. 2000 b), 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 (O.S. Jacobs & R. Biggs, In prep. 2000 b) 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.

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