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ELEPHANT EFFECTS ON VEGETATION

CHANGES IN VEGETATION IN THE KNP RELATED TO ELEHANT ACTIVITY

MICHELLE HOFMEYR AND HOLGER ECKARDT

Elephants are major agents of change and are often indicated as those large herbivores possessing the ability of changing entire ecosystems in terms of vegetation structure and composition, thereby affecting a whole series of other ecosystem components as well. The exclusive role of elephants as agents of change could thus far not be completely isolated from the multitude of factors involved in ecosystem dynamics.

The Kruger National Park is one of the largest conservation areas in Africa (Eckhardt *et al* 2000). Since it's proclamation in 1926, it has been closely monitored and managed, making it one of the largest and most intensely managed savanna areas in Africa (Eckhardt *et al* 2000). Early studies on vegetation were mostly of descriptive nature, forming part of the inventory phase which is a qualitative assessment of vegetation types and their distribution according to environmental gradients. While these types of studies have been completed long time ago, little attention has been given since to the dynamics of the woody vegetation, which are still poorly understood (Zambatis 1997). Of particular importance now is the role which elephant, fire and artificial water provision play in these dynamics. These need to be addressed as a matter of urgency ((Zambatis 1997). During the 1980's, the need for monitoring the herbaceous layer was expressed by Kloppers (pers comm.), emphasizing the importance of having a monitoring system in place which would be able to report on the status of grasses in particular, but also including forbs. In 1989, a veld condition assessment (VCA) was initiated. These 500 VCA sites are spread throughout the KNP covering all 35 Gertenbach (1983) landscapes. The initial surveys focused on key grass species, measuring standing crop and grass composition. The need for further detailed information on woody plants led to the VCA's being expanded in 2002. The woody VCA surveys provide a quantified evaluation of woody species (shrubs and trees), structure and fire/elephant impact. The surveys are done triennially at the end of the wet season (March/April). This will provide valuable information, as part of an on-going monitoring system, which will reveal trends in woody vegetation changes throughout the KNP.

The feeding behaviour of elephants plays an important role if one wishes to understand the ecological role elephants fulfill. It seems that there is not too much known about this particular issue. Several questions come to mind, such as what are the benefits of being a mixed feeder, why do elephants change their dietary preferences between seasons, what are their dietary needs and how do they satisfy these. Knowing the answers to the last question would help one to understand why elephants are so selective when it comes to utilizing certain plant species as well as plant parts such as roots, leaves, twigs, branches, fruits, flowers and bark. Is it the palatability, the nutrient status or both that affect elephant feeding behaviour. The social behaviour of elephants should also not be overseen since it has certain implications for the woody vegetation. Aggressive behaviour often results in uprooting or breakage of large trees.

Since elephants are mixed bulk feeders, they have the advantage of changing between woody and herbaceous components and can even afford to ingest low-quality food characterized by low-protein and high fibre contents. They compensate for the low-quality food intake by simply consuming huge amounts of material. This, together with their often-destructive feeding behaviour, has large-scale implications primarily for the woody vegetation. Extended intensive utilization of patches or communities more often than not alters the structure and sometimes even the composition of the vegetation.

Fire is another one of the driving factors affecting vegetation dynamics, especially those of the woody component. Much has been said about it elsewhere with most of the work being derived from the experimental burn plots (Trollope & Potgieter 1985; Enslin *et al.* 2000;

Brönn *et al.* 2001). Fires in Kruger are generally of low intensity and therefore only seldom change species composition. Structural changes are usually caused in the lower height strata (<3 m), resulting in individual plants having to regrow from ground level. Different landscapes or vegetation types respond differently to varying fire intensity and frequency. High-intensity fires have resulted in lower numbers of shrubs per hectare in the *Sclerocarya birrea-Acacia nigrescens* veld on basalt soils, but on the *Colophospermum mopane* veld on similar soils the shrub density increased through coppicing. Frequent fires, on the other hand, tend to suppress the woody layer by keeping it at lower heights on all soil types. The majority of grasses in Kruger are perennial and resprout from existing tuft bases after a fire. Annual grasses regenerate from seed. Recently burnt areas usually experience an influx of herbivores and associated increased grazing pressure, often exacerbated by long dry periods preceding and following such fires. It is, therefore, not the fire impact *per se* causing changes in the vegetation, but the interaction of fire and concentrated herbivory.

There have been a number of specific studies relating to vegetation dynamics in the KNP situation. One of the earliest publications dealing with prescribed elephant densities based on vegetation amongst others, is the one of Pienaar *et al.* (1966). An awareness of vegetation impacts was created by van Wyk & Fairall (1969) where they concluded that the KNP is sensitive to elephant impacts. The following is a sample of several studies relevant to vegetation dynamics, alluding to the plight of certain larger tree species in particular.

A species-specific impact study by **Engelbrecht (1979)** in the Punda Maria area demonstrates the different ways in which elephants utilize knobthorn trees of different age classes. Virtually all younger adult trees were pushed over but hardly used at all, probably because of the protection rendered to the main stem by the many thorny branches. Out of a total of 951 trees surveyed, 65% sustained damage to their stems and or bark. Knobthorn trees' ability to recover from severe damage through a self-healing process is insignificant, which means that the life span of a damaged tree is significantly reduced.

Coetzee *et al.* (1979) conducted a relatively similar study, investigating elephant damage to marulas in the central parts of the KNP. This study revealed that elephant damage is associated with distance from roads, *i.e.* the highest proportion of damages occurred within 10m away from roads. This particular finding could, however, not be confirmed by Engelbrecht's (1979) study. It is also suspected that debarking and bark utilization is a seasonal phenomenon, associated with wet climatical phases.

Trollope *et al.* (1998) did a subjective comparison of aerial photographs of the four major landscape types of the KNP for three different dates, *i.e.* 1940, 1960 and 1986/89. According to this study, no significant changes occurred in the density of large trees on the granites between 1940 and 1960, whereas a moderate decline occurred on the basalts. However, during 1960 to 1986/89 dramatic declines in large tree densities in all landscapes were observed. This particular trend coincides with the period during which sharp increases in elephant numbers were experienced as well as systematic burning programmes implemented. It seems that species diversity had not been affected but rather structural diversity, where the woody vegetation was being transformed into short woodland interspersed with a low density of large trees.

Eckhardt (2003) compared fixed-point photographs of 60 different sites for 1977/80, 1990 and 2002. Of these 60 sites, only two experienced a net increase in large trees, nine experienced no change and the remaining 49 sites a net decrease. This trend can be observed throughout the KNP, but is more evident on the clayey soils such as those derived from basalts, gabbros and shale. Relating this trend to distance to water points, no correlation could be found. The possible reason for this is that water distribution in the landscape is so abundant and widespread that elephant impacts are equally well spread over the entire Park.

Baxter (2003) conducted a modeling exercise on elephant impacts on woody vegetation and how this affects biodiversity. From this work, it becomes clear that the attributes of

specific trees must be taken into consideration before appropriate management actions are implemented to deal with these issues.

Jacobs (2001) conducted an autecological study of marulas in the KNP, examining the impact of elephants and fire on this species in four different landscapes. According to this study, marulas are experiencing large-scale changes in their structure, characterized by a reduction in the number of larger trees and a simultaneous increase in the number of those size classes susceptible to fire. The increase in the latter size class is not so much ascribed to recruitment, but rather because of supplementation by the large tree classes after experiencing severe physical damage to their morphology. The same study investigated the status of marulas on some of the experimental burn plots, determining the effect of different fire treatments on this species. From this study, it is clear that fire changes the structure and morphology of the woody vegetation, but not the composition and diversity. Intense fires cause high mortality rates amongst seedlings and saplings, thereby suppressing the recruitment into higher size classes.

Stevens (2001) emphasizes the importance of a combination of factors determining tree loss. Even though elephants are often responsible for taking out trees, it should be seen against the background primary factors geology, topography and climate which create conditions characterized by other core environmental factors such as competition, soils, fires and rain. While elephants and soil sodicity were identified as core factors in tree mortality, these factors in turn are continually modified by factors such as water movement, nutrients and trampling.

The work of **Levick (2001)** focuses on the boundaries between rivers and uplands within and outside the roan enclosure on the northern plains. Since boundary zones are regarded as highly diverse patches in terms of species richness, structure and function, they are favoured habitats by many herbivores. The structure and composition of the woody vegetation outside the enclosure has been severely altered by large mammalian herbivores. The boundary areas appear more sensitive to browsing disturbance than the surrounding patch types and are usually first in showing signs of change. Levick (2001) suggests that these sensitive areas act as indicators of change in a landscape. Monitoring attempts must focus on these local scale boundary zones and use them as barometers of ecosystem health.

Bezuidenhout (2004) reflects on the impact elephants have had on the vegetation in Marakele National Park since reintroduction. So far, elephant impact has been restricted to certain vegetation types, converting thickets into closed shrublands and closed woodlands into open woodlands. These are the more sensitive vegetation types, preferred by elephants and therefore prone to such changes. Elephant density for the whole of the Park will have to be adjusted accordingly so as not to result in complete changes of these vegetation types and net loss of species.

Nel (1988) surveyed the area north of Punda Maria, concentrating in the areas around Pafuri. The project was initiated from a report in 1977 that elephants were de-barking a large number of baobabs, as observed during the aerial census. The project sampled baobabs north and south of the Luvuvhu river. The project was motivated by the concern for the number of visible young baobabs and the visible damage to older trees due to elephant impacts. The project also investigated the number of other herbivores in the area from game count data and a cursory review of blocks burnt in the fire regime. Although the data from 2000 surveyed individual trees, was not statistically analysed, graphs showed that there were fewer trees in the smaller size classes south of the river (an area which had a high elephant number) as opposed to the area north of the Luvuvhu river. High elephant numbers south of the Luvuvhu river were attributed as the cause of low numbers of small trees. High mortality rates observed in 1983-1985 were attributed to a combination of drought conditions and elephant utilization. *Sterculia rogersii* was also noted as an incidental sighting during the project, with only few individuals in steep inaccessible areas having no elephant utilization.

Whyte (1996) conducted a survey of baobabs in northern KNP. It was estimated that the KNP has a population of about 20 000 trees, but is of the opinion that between 1985 and 1995 approximately 1000 of these trees died. Results indicated that baobabs north of the Luvuvhu river had a population with a higher proportion of younger trees than in the older/

larger size classes. The area south of the Luvuvhu river showed a declining proportion into the smaller size classes, suggesting that recruitment may be declining. A higher incidence of elephant damage to trees was found south of the river, when compared to the surveyed area north of the river. Lower damage north of the river was attributed to lower elephant densities in this area. The concerns the report identified included a lower rate of recruitment south of the river due to elephant numbers and elephant utilization of trees reducing the survival rate during drought years. The report cautioned that elephant population at the time (1996) seemed to be putting the baobab population under pressure. Due to the number of other species utilizing baobabs, baobabs were identified as a “keystone species”, whose decline would adversely affect many other species.

Hofmeyr (2002) found that baobab utilization by elephants appears to be of low impact at present elephant densities, with only a small percentage of the population very severely damaged. Trees vulnerable to elephant impacts are those growing in flat, open areas close to water and next to elephant paths, such as low-lying areas between the Luvuvhu and Limpopo Rivers. These trees could potentially die-out if elephant numbers increased significantly. Trees growing on rocky outcrops, on steep slopes, amongst dense vegetation and in areas inaccessible to elephants are likely to persist in the population. Baobab trees will persist in areas where elephants are not able to reach them, such as steep inclines and hillsides. These areas may serve as a source to repopulate areas where trees have been lost or reduced due to elephant pressures. Of the elephant damage to adult trees, most of the damage is superficial and not recent. Elephants may utilize baobabs on a seasonal basis, particularly eating the bark towards the end of winter when other vegetation is limited. The indications are that the baobab population is experiencing a lack of recruitment into the smaller size classes. In addition elephant damage in certain localized areas may cause some trees to become stunted and non-reproductive. These are both areas of concern for the population as a whole. *Sterculia rogersii* trees are very sparsely distributed in the landscape and are found to be in low numbers. As a result of this, this species is in more danger of severe elephant impacts than the baobabs. Further surveys over larger areas need to be conducted to determine if there are any smaller trees, the level of damage to adult trees and how these trees are distributed in the landscape. Marula and false marula appear to be affected by fire as smaller trees are kept trapped in the grass layer by fire and are potentially non-reproductive individuals in the population. Elephants are utilizing the trees but very few trees are directly killed by elephants. Most of the mortality is in the form of severe bark stripping and ring-barking. A combination of elephant damage in the form of bark stripping, burning of the exposed main trunk and high winds blowing weaken trees over is affecting the larger trees in the population.

Kelly (2000) conducted a survey of the effects of elephant utilization on the *Sterculia rogersii* and *Adansonia digitata* populations of the Kruger National Park. The population structure of neither species has been shaped by elephant utilization. Trees are inclined to be limited to the north of KNP due to suitable climate and low incidence of frost. SCD (Size class distribution) north of the Luvuvhu River is apparently “healthy” with more young trees than old trees and 25% of the population occurs in the smallest size class. The mean GBH of trees in the northern section is 3.96m and in the south is 4.5m. Mortality of baobabs or recruitment of seedlings into the population has not been consistent. The star chestnut population shows that recruitment has declined in recent decades. The utilization of trees is higher south of the Luvuvhu river as a result of higher elephant densities. Recent baobab damage has been greater north of the Luvuvhu River. Baobab mortality is lower than in other areas where elephant and baobabs co-exist. It appears that elephants are not playing a significant role in mortality of either tree species. Results of study are inconclusive in proving elephants play a significant role in structuring the populations of both baobab and *Sterculia*. Kelly suggests that the management of factors other than elephant is required to improve regeneration rates of these species.

Gaylard (in prep) has studied elephant impact on woody vegetation in relation to water distribution. Also how this affects the heterogeneity of piospheres and areas between these. Significant differences in impact to vegetation has been found between isolated and closely-spaced waterholes as well as between the former and areas between closely-spaced and isolated waterholes. Heterogeneity is compromised where waterholes are closely-spaced.

The KNP finds itself in a unique position by possessing several en/exclosures of different sizes on different geological substrates. Makhohlola (vegetation/fire), Hlangwini, Buffalo, Capricorn and N'washitshumbe camp (breeding), and Nkuhlu and Letaba (elephant/fire/vegetation), are all camps erected to serve different purposes. However, their locality with regard to vegetation types, geology and proposed elephant impact zones means that they hold immense potential for studies related to elephant/vegetation/fire interactions. It is believed that some of these camps will provide very useful information in this regard, while the Nkuhlu and Letaba exclosures were specifically built for this purpose. These en/exclosures served at varying degrees as study areas in the past, while the N'washitshumbe camp had been the focus area of many a study so far. This enclosure has been identified as valuable area to monitor for vegetation changes as elephants have been excluded since its construction in 1967. The enclosure is 309ha in size and is located in Landscape 23 on basalt, in the northern arid savanna near Shingwedzi. The vegetation within the enclosure consists of mopane woodland savanna, grassland savanna and *Sclerocarya birrea/ Acacia nigrescens* savanna (Joubert 1970). The enclosure has not been subjected to a fixed burning program and the different blocks have been burnt on a random basis throughout the years with a mean fire period of between 2-3 years. The burning program within the camp was therefore not much different from the triennial fire regime throughout all landscapes of the KNP (Jacobs 2001), although records indicate that there could be some seasonal differences as to when areas within the camp were burnt. The diet of the roan in the enclosure consists primarily of grass, although they do occasionally browse green leaves of young shoots of shrubs and favoured trees (*Dalbergia melanoxylon* and *Lonchocarpus capassa*) during excessively dry periods (Joubert 1970). During the survey in the roan enclosure, none of the marulas located showed any signs of browsing (**Hofmeyr 2003**). The estimated number of marula trees within the enclosure is 1025, giving an estimated density of 3.317 trees per hectare. This is compared to a density of 0.004 trees per hectare outside the enclosure. No false marulas have been found. Within the roan enclosure an interesting pattern has emerged from the initial surveys. The trees in the size classes 40-80cm circumference are the most dominant in the camp. These are the size classes that are poorly represented in areas of the KNP outside the roan camp. This has implications for marulas, indicating that trees are escaping a "fire trap" effect or new recruits entering the population. This has prompted the further investigation and a search for landscapes in the park that have trees of the size class 50-100 cm circumference. Few areas have shown trees in this size class and have not been encountered during further field investigation. All the trees located during the survey showed some signs of previous fire damage and in some cases trees were severely scarred with the heartwood exposed. This indicated that fire can, even at lower frequencies, cause lasting damage to trees, which may take several years to recover. Smaller trees are particularly susceptible as they can lose a year or twos' growth.

The subject of elephant/fire/vegetation interactions is receiving more attention than ever before. Currently, there are a number of research projects dealing with one or several parts of this issue, aiming to get a clearer understanding of the mechanisms and the way different components are related to each other. The findings derived from these studies will hopefully assist with providing a more comprehensive and better-informed understanding of vegetation dynamics and the relationship to associated agents of changes.

In the context of the KNP, it is generally accepted that there is no conclusive proof showing that elephants are the sole modifiers, whether directly or indirectly, of vegetation structure, composition and function. Ecosystem processes are complex and, as can be inferred from

various studies, are usually driven by a combination of various factors, some of which are fire, rainfall and water distribution (Viljoen 1988; Trollope *et al.* 1998; Eckhardt *et al.* 2000; Gaylard 2003). Kruger has been exposed to different fire regimes in the past, each having had specific consequences for the vegetation and heterogeneity. More notable changes were caused by the rigid triennial burns which resulted in holding the vegetation in a fire trap zone below a certain height and thereby prohibiting tree recruitment. To some extent the effect of this burn practice on the vegetation can be inferred from the experimental burn plots. The distribution and high density of artificial water points before the time when many of them were closed down, impacted negatively on landscape heterogeneity, with closely-spaced waterholes creating a uniform utilization of the vegetation. According to Gaylard (2003), widely spaced or isolated waterholes are more conducive to heterogeneity, creating patches of different intensities of utilization by elephants and other herbivores.

Notwithstanding the complexities of ecosystem dynamics and the role different factors play, it nevertheless becomes clear from those areas where elephants are kept that the latter have the capability of changing entire landscapes or vegetation types. This is evident from the various studies conducted in eastern Africa (Buechner & Dawkins 1961; Glover 1963; Laws 1970; Leuthold 1977; Pellew 1983; Dublin 1995) and South Africa (Viljoen 1988; Trollope *et al.* 1998; Hiscocks 1999; Eckhardt *et al.* 2000, Jacobs 1997??). Feeding habits and behaviour of bull elephants is known to directly affect larger trees. Excessive bark utilization, uprooting of trees and braking of branches usually impacts negatively on large tree populations. This type of utilization may be sustainable in the longer run only if elephant numbers fluctuate, but not with continuously increasing numbers. It is not known whether the declining trend in large tree numbers will eventually stabilize at a lower level in the high impact zones, however, it is unlikely that large trees will be completely lost from these areas. A possible scenario that could develop is the near to total absence of large trees on the basalts of the high impact zones. This loss in structural diversity, also called structural homogenization, may have various ecological consequences and is not acceptable in terms of our biodiversity mission. Threshold of potential concerns (TPC's) are formulated in such a way so as to give recognition to the dynamic nature of ecosystems, but in the same light also provide the necessary measures needed to protect them from complete destruction.

The spatial extent of changes one should allow is an issue of scales and may vary according to different peoples perceptions. By 'sacrificing' an entire region to high elephant impacts for an extended period with the ultimate intention to swop high and low impact zones once certain TPC's have been exceeded, may sound acceptable. However, one should keep in mind that these impact zones are not homogeneous and may consist of various types of landscapes each with its own specific characteristics. From an elephant's point of view, certain landscapes are more suitable than others and therefore might have to take the bigger brunt of extended impacts. As an example one could use the *Acacia welwitschii* thickets on Karoo Sediments of which the larger part falls into the southern high impact zone. This particular landscape consists of highly nutritional and productive vegetation and therefore experiences constant herbivory pressure. While a TPC for the whole impact zone might not have been reached yet, the concerned landscape might have undergone serious changes exceeding all TPC's by far. The question arises whether it is acceptable to sacrifice large tracts of a landscape while the TPC for the impact zone as such has not been reached. One could look at this concern from two different sides, one arguing that once this landscape has been transformed and consequently lost all its attributes which were favoured by elephants in the first place, the latter will be forced to leave this landscape and search for alternative areas. On the other hand, there are people claiming that this type of landscape evolved under conditions of heavy utilization and therefore is resilient enough to buffer such changes.

Perhaps a more flexible approach should be applied, allowing large scale changes in the environment within the framework of predefined TPC's, but at the same time exercising sufficient caution and sensitivity so as not to allow the complete alteration of a landscape within an impact zone. This alteration may be in terms of either one of composition, structure or function or all together.

Research requirements

- Elephants feeding behaviour for knp
- Detailed assessment of current vegetation status in park (sensitivity analysis) leading to a synthesis of current vegetation data (landscape/ land type) and to produce an estimate of areas that are potentially vulnerable to elephant impacts and set up monitoring programmes accordingly
- Detailed information on location/ extent and vulnerability of rare plant species
- The role of trees (especially large trees) in ecosystem productivity and in general
- Integration of current vca woody data into current understanding of vegetation dynamics
- Key-stone tree species recruitment dynamics need further investigation

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ELEPHANT-INDUCED CHANGES TO THE COMPOSITIONAL AND STRUCTURAL DIVERSITY OF RIPARIAN WOODY VEGETATION IN RELATION TO SURFACE WATER DISTRIBUTION

ANGELA GAYLARD

Introduction

Elephant impact studies traditionally predict that increased elephant populations will reduce an area's diversity, following the Intermediate Disturbance Hypothesis. However, these studies are scale-neutral and do not take patchy elephant impacts, which may mitigate against the adverse consequences for diversity, into account. Other research that I performed showed that the intensity of elephant impacts in riparian zones was spatially variable in relation to the locality's surface water context (specifically water proximity and density). I was interested to test whether/how this varying elephant impact intensity in relation to surface water distribution had produced distinct differences in the compositional and structural diversity of riparian trees, particularly considering the abundant supply of artificial water sources and the current density of elephants.

Methodology

I performed vegetation surveys in the riparian zones of seasonal rivers in northern KNP, noting the composition and structure of woody vegetation at varying distances from surface water. Since fire is negligible in riparian zones, water-dependent browsers were expected to be the primary drivers of any woody compositional and structural diversity differences related to surface water distribution. Elephant and impala were the only water-dependent browsers, but it was not possible to differentiate between the effects of these species without an enclosure study.

Principal Components Analysis was performed to determine whether there were particular suites of species and/or size classes of woody species that characterised areas with different surface water distribution attributes.

Results

1. Species composition did not appear to have a strong association with surface water distribution (proximity and density), although two species (*Hexalobus monopetalus* and *Nuxia oppositifolia*) were more strongly associated with riparian patches experiencing the lowest elephant impact, i.e. between isolated waterpoints.
2. Similarly, the structural composition of riparian trees was not particularly strongly associated with surface water distribution, the strongest association being the size class <20 cm.
3. However, the structural composition of riparian trees was more strongly associated with surface water distribution attributes than was species composition.

Discussion

1. The fact that two species in the low impact intensity patches of the riparian zone did, in fact, show an association with surface water distribution attributes, provides some initial support for the predictions of the IDH that patchy elephant impacts will allow for particular suites of species in different parts of the landscape.
2. Similarly one structural class (<20 cm) showed the strongest association with surface water distribution attributes, and represented the seedling size class. Along the Chobe river in Botswana, impala (the only water-dependent browser other than

elephant) have been found to be the primary removers of the seedling size class. It is therefore difficult to separate the effects of elephants and impalas in this case.

3. Two possible explanations exist for the fact that the previously demonstrated surface water differences in elephant impact intensity have not resulted in particularly different suites of species or structural differences in the riparian zone:
4. elephant impact intensity even at the most isolated waterholes may not be high enough to eliminate competitively dominant plant species, or to provide favourable conditions for impact tolerant species, as the IDH predicts. This scenario would suggest that local elephant densities, even at the most isolated waterholes, are low relative to the current abundance of waterholes.
5. elephant impact intensity is already so high that the zones of impact around even the most isolated waterholes have coalesced, leaving the entire riparian landscape with homogeneously distributed impacts on the high end of the IDH curve. This scenario would suggest that the natural spatial and temporal heterogeneity of elephant impacts needs to be restored (by reducing elephant populations and/or closing artificial waterpoints) in order to restore the maximum diversity of these riparian zones. However, the previous impact intensity study has demonstrated that elephant impact piospheres are, in fact, still intact at the more isolated waterholes.
6. The fact that structural diversity seems to have a stronger association with surface water distribution in the study area than compositional diversity suggests that structural diversity is affected by elephants before compositional diversity.

Management implications

1. The results of this study suggest that current elephant densities have not yet reached a level where they are significantly altering either the compositional or structural diversity of riparian woody vegetation
2. The results also suggest that current surface water densities should be reduced in order to re-establish the natural spatial and temporal variation of surface water distribution, as well as to reduce the proportion of the landscape that has closely-spaced waterholes. It is suggested that this would produce patchy elephant impacts that lead to higher compositional and structural diversity of riparian woody vegetation
3. Monitoring of changes in the structural diversity of riparian woody vegetation at particular distances from water would provide an earlier warning signal of changes to diversity by elephants than monitoring changes to species diversity of riparian woody vegetation

Accuracy of understanding

1. Since riparian woody composition and structure were not strongly associated with surface water distribution, despite the previously demonstrated relationship between elephant impact intensity and surface water distribution, this understanding should be classified as well-supported hypothesis at this stage.
2. However, this study established the fact that structural diversity (measured as size class distribution) responds more rapidly than compositional diversity (measured as species composition) to differential impact intensity related to surface water distribution.

Biodiversity consequences

1. The results of this study suggest that manipulation of surface water distribution can influence the spatial extent of elephants' influence on riparian woody compositional and structural diversity
2. Results further suggest that an overabundance of closely-spaced waterholes has homogenised the compositional and structural diversity of riparian woody vegetation in the study area

Future research

Future research should focus on:

1. similar vegetation surveys in the upland savanna, in order to establish the extrapolatability of these results outside of the riparian zone
2. performing similar PCA's on species diversity and structural diversity using, for example, an index such as the Shannon-Wiener index which provides a measure of evenness

Key publications

- GAYLARD, A. R.N. OWEN-SMITH AND J. REDFERN. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. In: du Toit, J., Rogers, K.H. and H. Biggs. The Kruger Experience: ecology and management of savanna heterogeneity. Island Press.
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SPATIAL DEMOGRAPHY OF SELECTED TREE SPECIES IN THE KRUGER NATIONAL PARK, IN RELATION TO ELEPHANT IMPACTS.

MICHELE HOFMEYR

Based on advice from KNP Scientific Services staff/ Wits academic staff, together with findings of past research, the following species were selected:

1. Baobab - *A digitata* (major species)
2. Common Star Chestnut - *S rogersii* (subsidiary species)

These two species appear to be distributed in similar habitats, preferring dry, rocky areas (pers. obs.). This will allow simultaneous sampling of both species in selected landscapes. Both species are also favoured by elephants (Kelly 2001 and pers. obs.).

1. Marula *Sclerocarya birrea* (major species)
2. False Marula *Lannea Schweinfurthii* (subsidiary species)

Marula trees are widespread throughout the park and are apparently targeted by elephants, which uproot the trees with their destructive feeding habits (Jacobs 2002b). False Marula trees have a similar distribution to Marula in the KNP and are also apparently targeted by elephants (Zambatis pers. com.). These factors make the False Marula a suitable species for comparison to Marula.

The aim of the study is to integrate current data and knowledge of these species into population viability models that accommodate spatial distribution, temporal variability in recruitment in response to rainfall and other factors, growth and mortality patterns and the effects of disturbances such as fire and elephant impacts. The study has attempted to document the spatio-temporal variation of elephant distribution and hence ecological pressure on these tree species and refine over time appropriate conceptual or more formalized models that will help guide managerial decisions with regard to the maintenance of biodiversity and ecosystem processes in protected areas.

Tree species selected for this study and proposed conservation status in the KNP

SPECIES	HABITAT	DISTRIBUTION	PROPOSED STATUS in KNP (in relation to elephant impacts)
Adansonia digitata (Baobab)	Well-drained soils of granitic origin	Restricted to the north of the KNP, but scattered individuals occur south to the Olifants river	Vulnerable
Sterculia rogersii (Common star chestnut)	Stony/ well drained areas.	Rare throughout the KNP but fairly common in the Pafuri area	Vulnerable
Sclerocarya birrea (Marula)	All soil types	Through-out, most abundant on the Lebombo Plains – (basalt)	Keystone species for biodiversity–vulnerable to elephant impacts in certain areas
<i>Lannea schweinfurthii</i> (False Marula)	Well-drained sand soils	Throughout the KNP, but more abundant around Skukuza and between Satara/ Tshokwane.	Vulnerable

Baobabs (*Adansonia digitata*)

Baobabs occur in semi-arid areas south of the Sahara, where the annual rainfall is in the range of 150 to 1500mm (Fenner 1980). Baobabs are also found from sea-level up to areas 1250m in altitude (Fenner 1980). Its range extends across the African continent south of the Sahel region, also into east, central and southern Africa (Fenner 1980). The species occurs from Ethiopia southwards to Botswana, Mozambique and South Africa (van Wyk 1972).

Van Wyk (1972) noticed that from local distribution, baobabs in the Kruger National Park, are more abundant in rocky areas, such as the Lebombo Mountains and the ridges between Punda Maria and Pafuri. Exceptions to this occur where a few individuals occur on plains, on alluvial silt soils and even on sandy soils. Van Wyk (1972) noted the greatest numbers of baobabs growing on dolerite or precipitations of Karroo sediments, although isolated specimens may be found on granite and basalt.

On poor, shallow soil thick roots radiate from the stem and are still visible above ground as much as 10 m from the tree (van Wyk 1972). The extensiveness of the root system may limit the density of the baobabs themselves (Fenner 1980). From aerial surveys the individual trees appear rather evenly distributed, suggesting a mutual antagonism probably caused by competition for water. The shallow root system typical of baobabs indicates an adaptation to the rapid absorption of water from the surface layers of the soil. This is useful in areas where most of the annual rainfall is in the form of occasional heavy showers in which there may be run-off on the hard soil surface. An extensive shallow root system may provide the most effective means of exploiting these situations (Fenner 1980).

Marula (*Sclerocarya birrea*)

S. birrea is a well known and valuable tree. It occurs throughout the KNP and is abundant on the Lebombo Plains (basalt). It is a medium size tree (up to 15m) with a round spreading crown (Venter and Venter 1996). Marulas grow easily from seed and is one of the fastest growing trees in South Africa with a growth rate of up to 1.5m per year (Venter and Venter 1996.) *S. birrea* has a warm-temperate to tropical distribution (van Wyk 1974). In the KNP the species occurs widely on sandy granitic soils but on the drier, clayey basaltic soils, is restricted to wetter climates with normal annual rainfall exceeding 500mm (Coetzee *et al* 1979). Marula populations on the basalt plains between Satara and Lower Sabie, typically occupy the mesic sites. These are predominantly the convex upper parts of the gently undulating basalt plains, where soils are leached with a comparatively low clay content (Coetzee *et al* 1979).

False Marula (*Lannea Schweinfurthii*)

This tree occurs throughout the KNP, but is more abundant in and around Skukuza and also between Tshokwane and Satara (van Wyk 1994). It is a small to medium sized deciduous tree with a straight stem and spreading crown (van Wyk 1994). The vegetative parts of this tree are widely utilized by browsing animals (van Wyk 1994).

Results

Baobab and Star Chestnut

Trees in inaccessible areas, such as close to water and on flat, open ground are more susceptible to elephant utilisation and damage than areas reducing elephant access - such as steep inclines and concealment in dense vegetation.

There appears to be low numbers of small trees (young trees) and no seedlings were found during survey, indicating poor recruitment for baobabs. Due to the longevity of these trees it is not expected that many seedlings or younger trees would be encountered. This could indicate some type of episodic recruitment strategies or that other herbivores may be preventing seedling survival.

Baobab utilization by elephants appears to be of low impact at present elephant densities, with only a small percentage of the population very severely damaged.

Trees vulnerable to elephant impacts are those growing in flat, open areas close to water and next to elephant paths, such as low-lying areas between the Luvuvhu and Limpopo Rivers. These trees could be under threat of greater utilisation if elephant numbers increased significantly.

There are indications that a source/ sink relationship may be occurring within the KNP baobab population. The isolated populations of baobabs occurring on rocky hillsides have more variation in size classes (ie: trees represented in more size classes both smaller and larger trees). Trees occurring on flat areas are mainly in the larger size classes. Should these trees decrease in number and density due to increased pressure from elephants, populations from elevated areas could be a possible source of seed to replace trees lost. Recruitment will depend on the vectors of seed dispersal, a suitable rainfall event to stimulate germination, low fire frequency and low herbivore pressures. The hillsides and elevated areas could thus serve as the source while the low-lying/ flat areas, where trees are accessible and utilised by elephants, act as a sink in the population.

Marula and False Marula

Fewer false marulas have been located along transects than marulas. False marulas appear to grow in small groves or patches of trees of the same size class.

Very few marula trees show recent or fresh utilisation. Most of the scaring and bark damage appears to be healing. More false marulas show fresh utilisation but most of the utilisation and bark damage was also very old and beginning to show signs of healing.

Both marula and false marula show a high level of non-utilisation (no damage to the trees) although the false marula population has a higher level of very severe utilisation. A number of the trees in the moderate to severe categories show a stunted growth form with the top branches being broken off. Many of the severely utilized trees show coppice re-growth.

Size class distributions for marula show a high number of trees in 1-2m size class. False marulas have a high number of individuals in the 0-1m size class. Many of these small trees have been burnt and show coppice re-growth. Very few small marula trees (less than 0.5m) have been located on the transects surveyed in the Skukuza and southern areas.

The false marulas grow in clumps of groves together and there is a possibility that a number of the coppice growth seen is from roots of other individuals ie: vegetative growth of one individual and not a group of separate trees.

The dense grass layer and the number of trees found in a coppicing state indicate that fire may be hindering the growth of trees above the grass layer, as determined by Jacobs (2001). Of the coppice trees for both species found on transects almost every tree has a thickened stem base and evidence of burnt dead stems. This indicates that the trees may be older than a tree of 1 years growth and may have suffered repeated burning.

No trees were found to be inaccessible to elephants. Both marula and false marula showed similar levels of utilisation. Of the trees found dead for both species, none could be attributed directly to elephants. Most of the dead trees showed signs of old elephant utilisation that had since healed but exposed wood had burnt during seasonal fires and weakened the tree.

The trees were hollow in some cases and appeared to have been blown over by the wind. The age of utilisation for both species was very old to old with most of the bark damage healed completely or the formation of thick scar ridges on damaged areas.

Marulas showed more signs of fresh utilisation in the form of bark stripping in small patch. None of the small coppice trees showed signs of elephant browsing or bark stripping.

Small seedlings encountered were below the grass layer and not highly visible. None of the coppice marulas or seedlings above and below the grass layer showed signs of browsing. Each tree was carefully inspected to note any leaves or shoots eaten off but none were found. A number of fresh marula coppice shoots were found in burnt areas but none of these showed signs of browsing.

Not many species were noted as nesting in both marula and false marula. Only 2 trees were recorded with buffalo weaver nests in the lower branches of tall trees. A few trees were noted as hollow but did not house beehives or show signs of animals living there. A few trees had squirrels feeding on the fallen kernels of old fruit.

Some trees appeared to produce fruit more prolifically than others based on the amount of dried seeds seen. Fruiting trees attract many animals and elephant activity was noted by signs of mud rubbed off on the bark and the grass trampled beneath the tree while the elephants searched for fruit. Very few trees had broken branches or had been pushed over by elephants in order to get to the fruit.

Fire does appear to be playing an important role in keeping individual trees in a coppicing state for both species as most coppice growth showed some signs of being previously burnt. The dense grass layer has the dual effect of protecting the young tree/ coppice growth from drying out during the end of the hot summer but increases the risk of creating a hot fire during the winter burns, which could kill the young tree. Tall trees of both species, in the 100-300cm stem circumference size classes, also showed signs of burnt bark.

Elephants appear to be weakening taller trees by repeated exposing the softer inner wood by debarking patches. This effect is exacerbated by frequent fires, which burn the exposed inner wood. The inner wood is also attacked by wood-borer, which creates further weakening. Although elephants do feed on tree by debarking, trees show an ability to heal wounds, although the process is slow and scar tissue seldom grows over to cover the entire exposed area.

Summary

The indications are that the baobab population is experiencing a lack of recruitment into the smaller size classes. In addition elephant damage in certain localized areas may cause some trees to become stunted and non-reproductive. These are both areas of concern for the population as a whole. Baobab trees will persist in areas where elephants are not able to reach them, such as step inclines and hillsides. These areas may serve as a source to repopulate areas where trees have been lost or reduced due to elephant pressures (source/ sink scenario). Of the elephant damage to adult trees, most of the damage is superficial and not recent. Elephants may utilize baobabs on a seasonal basis, particularly eating the bark towards the end of winter when other vegetation is limited.

Sterculia rogersii trees are very sparsely distributed in the landscape and are found to be in low numbers. As a result of this, this species is in more danger of severe elephant impacts than the baobabs. Further surveys over larger areas need to be conducted to determine if there are any smaller trees, the level of damage to adult trees and how these trees are distributed in the landscape.

Marula and false marula appear to be affected by fire as smaller trees are kept trapped in the grass layer by fire and are potentially non-reproductive individuals in the population. Elephants are utilizing the trees but very few trees are directly killed by elephants. Most of the mortality is in the form of severe bark stripping and ring-barking. A combination of elephant damage in the form of bark stripping, burning of the exposed main trunk and high winds blowing weaken trees over is affecting the larger trees in the population.

As elephants are classified as mega-herbivores (Owen-Smith 1992), consuming large amounts of vegetation, it is anticipated that they will have an impact on their habitat. In the scope of this project, the trees surveyed show that elephants are playing a role in both the

population dynamics and population structure, although impacts are not highly detrimental to the populations. Elephant impacts may be seen as seasonal and localized ie: in areas close to water or on trees that are accessible above the grass layer and the surveyed populations are not in danger of immediate extinction. The project has also served to highlight that a-biotic factors are playing an important role in the distribution and structure of the selected tree species, particularly the role of fire in the landscape.

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A SURVEY OF THE IMPACT OF HABITAT MANIPULATION AND ELEPHANT ON SOME ASPECTS OF BIODIVERSITY IN THE SABI SAND WILDTUIN

MIKE PEEL – UNPUBLISHED REPORT JULY 2003

Background

Savanna systems are characterised by a structure that can best be described as a wooded grassland where the woody vegetation comprises mature trees and shrubs and where the herbaceous (or non-woody) layer is dominated by perennial grasses.

A comparison of the 1944 and 1986 aerial photographs of the Lowveld exhibit a pattern of increasing woody plant density over extensive areas (e.g. Figure 1). In the Sabi Sand Wildtuin (SSW) anthropogenic impacts were highlighted by Tinley (1979) who described the underlying causes of the so-called 'bush-encroachment' problem in the SSW.

The resulting management approach that was proposed for the SSW by Tinley (1979) was to clear contour seepline grasslands of trees and shrubs. Large tracts of the SSW have thus been cleared/thinned over the past 20-25 years using a variety of chemical and mechanical methods. In the SSW we have therefore moved from what was perceived to be a 'bush encroached' situation, to a much more open situation due to the extensive habitat manipulation programme. With the removal of the fence between the KNP and the SSW in 1993 there was a dramatic increase in the number of elephant in the area. This expansion of range by the elephant from the KNP is natural but under present conditions, with a no-cull policy in the KNP, there is a concern that there is

overutilisation of habitat within the SSW.

The effect of the habitat manipulation programme and the increasing elephant population in the SSW therefore presents a number of challenges in terms of ecological management and monitoring of the reserve.

The aim of this survey was therefore to assess the ecological impact of the habitat manipulation programme and elephant on aspects of the biodiversity of the SSW.

Results and discussion

The following observations were made on the habitat manipulation vs. untreated sites (ns=not significant and s-significant):

1. The tree diversity index was higher in the untreated areas (ns);
2. There are more favoured browse species on the untreated areas (s);
3. There is a greater diversity of structure on the untreated areas (s);
4. Related to the above, this measure indicates a more even distribution of structural classes in the untreated situation (s);
5. Tree structure similarity indicates a less even distribution of tree structure as measured by height class in the habitat manipulation sites (most of the structure in the habitat manipulation areas is limited to the short tree layer and the very tall (say >10m) tree layer);
6. The mean similarity index of grasses between habitat manipulation areas and untreated areas is only 0.4 (out of a possible 1);
7. The frequency of occurrence of dominant species showed that there were more palatable, productive shade loving grasses such as *Panicum maximum* and *P. coloratum* in the untreated areas (s);

8. Microhabitat diversity was used as a surrogate for the possible presence of smaller creatures such as invertebrates, frogs, reptiles and small mammals. There was a higher availability of habitat in the untreated (s); and 9. There was higher evenness of habitat types (from small logs to large stumps) in the untreated area (s).

The following observations were made regarding elephant impact:

1. The severity of elephant impact has shown a marked increase across all damage classes (whereas the elephant were making use of the excellent grass production following the recent wet seasons it appears that they have now switched their attention to shrubs and trees due to the prevailing dry conditions);

2. In terms of percentage damage per height class, there was an increased selection for larger trees (29 % from 19% in the 2-5m height class and 28% from 18% in the >5m height class). This situation can be problematic where structure has largely been homogenised by habitat

manipulation. There was also the increase in the percentage of the 1-2m height class impacted upon indicating a focusing on a wider range of tree size selection;

3. There was a general marked increase in the impact of the percentage of each species sampled. These increases occurred in both the 'taller' tree species such as *Sclerocarya birrea* and *A. nigrescens* and the shorter height classes (species such as *Dichrostachys cinerea*, *Grewia* spp. and *Albizia harveyii*). The latter would account for the increase in impact in the

impact on the 'shorter' height classes (see above); and

4. Of all of the species impacted upon, *Combretum apiculatum*, *C. zeyherii*, *Acacia nigrescens* and *A. gerrardii* make up the greatest percentage (48%).

Summary

1. The habitat manipulation programme has had an overall negative impact on the biodiversity of the SSW; and 2. There was an increased impact on the woody layer by elephant during the last year. As stated was precipitated by the drought that forced the high number of elephant to turn their focus from the grazing component to the tree component. Of concern is the general increase in the severity of the impact, and the increase in the percentage of 3 structural classes that are being impacted upon, viz. the 1-2m, 2-5m and > 5m height classes; and

3. While some habitat manipulation is in fact necessary to mitigate against anthropogenic impacts, the large-scale habitat manipulation has reduced the biodiversity within the SSW. The current high numbers of elephant and their impact on the vegetation (in particular the tree layer) has exacerbated the situation.

A clear protocol, embedded in a comprehensive ecological management plan, is required to address the current approach to among others habitat manipulation and large herbivore (in particular elephant) management.

The plan would ultimately provide the following for any ecological issue that may arise in the SSW:

1) Threshold's of Probable Concern (TPC's) that:

- Provide **Hypotheses** of the spatial and temporal limits of natural ecosystem flux;
- Provide **amber lights** for managers (and scientists); and
- Are described by upper and lower limits of change in selected ecological **indicators**.

From the above ecological variables of importance would be monitored and adjusted accordingly and when appropriate. As the monitoring/research programme starts providing relevant information management may find that certain initial guidelines may need to be adjusted upwards or downwards. Thus an adaptive management approach to the management of the SSW is proposed.

**THE INFLUENCE OF HABITAT MANIPULATION ON HABITAT SUITABILITY FOR
HERBIVORES IN CONJUNCTION WITH THE AFFECT OF ELEPHANT IMPACT ON THE
VEGETATION OF THE SABI SAND WILDTUIN**

JONATHAN SWART – SABI SAND WILDTUIN – UNPUBLISHED REPORT MARCH 2003

Conclusions

In general the forage value in terms of the nutritional value of grasses in the manipulated cleared areas of the Sabi Sand Wildtuin appears to be suitable for plains game such as zebra and wildebeest. Nitrogen (N) levels give an indication of the palatability of the grasses and the amount of available bulk protein. The levels of nitrogen obtained from this investigation are similar to those obtained in a previous study in the KNP (C.C. Grant, personal communication). Even though on the whole, similar nutrient values occur in the KNP and SSW, there are still subtle differences within the SSW, which are probably important in terms of habitat selection for species such as zebra and wildebeest. The gradual increase in the nutrient value of grasses between the northwest of the SSW and the northeastern region correlates with the higher densities of zebra and wildebeest in the northeastern region. This gradual change in nutrient levels between the west and east is probably related to the changing geological forms along this continuum. It would be interesting to see if a similar relationship exists between the eastern SSW and the KNP. Generally, the forage value in terms of the composition of grass species in the manipulated cleared areas of the SSW (except for the Contour Seepline habitats) appear to be somewhat below average and this is mainly because of the low ratio of decreaser to increaser 2 grass species. Since zebra and wildebeest are regarded as bulk roughage grazers they tend to select areas where there are a higher proportion of nutritious or more palatable grass species rather than select nutritious species within communities (Ben-Shahar & Coe 1992). Thus an area with a high proportion of decreaser grasses should be more suitable in terms of forage value.

In general the lack in structure of the woody component of the manipulated cleared areas appears to be largely responsible for the decline in the number of more palatable decreaser grass species and an increase in the less palatable increaser 2 species. The manipulated cleared areas compare favourably with wooded areas that were not manipulated in terms of the nutritional value of the grass layer, however, with the exception of the Contour Seepline habitats, they did not compare favourably in terms of grass composition for the reasons mentioned above. Even though the grass cover appeared better in the cleared areas, the grass nutritional value and composition remains paramount in terms of herbivore habitat selection. The manipulated cleared areas do however appear to increase the availability of suitable habitats for herbivores such as zebra and wildebeest. This is supported by the number of animal droppings that were recorded in the cleared areas. Herbivores such as impala, zebra and wildebeest utilise these manipulated cleared areas as foraging refuge sites to avoid predation, particularly in the evening when good visibility becomes more important. Thus, these animals may be utilising these areas for reasons other than the higher nutritional value of grasses or higher proportion of palatable grass species. The short grass probably creates easier grazing conditions and by making less contact with the vegetation the parasite load may also be reduced. The timing and frequency that the manipulated cleared areas had been slashed were not taken into consideration during this investigation because of the high number of permutations and also much of this information was not available. These factors probably play an important role in determining the composition of grass species in cleared areas and may also influence their nutritional value. For example, different grass species flower at different times of the year and if certain species were cut before the seeds matured then this would alter the seedbed and thus influence their reproduction. In addition, most grass species go through a period of autumn rest when nutrients are transferred from the leaves to the roots where they are stored so that they are available to the roots for the following growth season. If the grasses are cut during this

period the nutrients are transferred back to the leaves for renewed growth thus exhausting the nutrients from the roots and in turn reducing the competitive advantage of these grasses at the beginning of the following growth season.

The elephant impact on shrubs and small trees in the manipulated cleared areas is insignificant in comparison to the impact in the wooded areas. On the other hand the proportion of elephant impact on the larger trees in manipulated cleared areas is considerably larger than that of wooded areas. This occurs not only because there are fewer trees in the cleared areas but also because the diversity of tree species in the cleared areas is considerably lower than in wooded areas. In addition, there are mainly larger trees in the cleared areas leaving the elephants less of a variety to forage on.

The current status of the overall elephant impact appears to be at a critical stage. In other words if measures are not taken to reduce the number of elephants in the SSW the reserve runs the risk of having the habitat drastically altered and several targeted tree species reduced to critical numbers.

**ELEPHANT IMPACT ON TREES SURROUNDING ARTIFICIAL AND NATURAL
WATERPOINTS IN SABI SAND WILDTUIN, SOUTH AFRICA.**

KAY HISCOCKS (LATE), MIKE PEEL AND JUDITH KRUGER – UNPUBLISHED 2003.

Abstract

Game lodges, such as those within Sabi Sand Wildtuin (SSW), rely on high quality animal sightings per guest for photographic safaris. Natural and artificially provided water determine the distribution of animals and are therefore important factors in tourism-based operations. An increasing elephant population in SSW is having a greater impact on the vegetation surrounding waterpoints than occurred in the past.

This study investigated the impact of elephants on the woody vegetation surrounding an artificial waterpoint that is permanently supplied with water and two natural, seasonal, pans. There was no difference between the tree diversity of the three sites. In the worst case, 85% of the trees survived utilisation by elephant. Evidence of heavy utilisation was recorded on 64% of the trees at the artificial waterpoint and 36% and 37% at the seasonal pans respectively. Elephants showed a preference for certain trees, especially Acacia species. Sixty-seven percent of Acacia species at the artificial waterpoint showed major structural damage compared with 41% and 47% at the seasonal pans. (It was concluded that)The artificial waterpoint showed a higher degree of tree mortality and structural damage than the seasonal pans due to year round utilisation mostly by adult elephant bulls.

**THE IMPACT OF ELEPHANTS (LOXODONTIA AFRICANA) ON THE LIMPOPO
RIPARIAN FORESTS IN THE SEMI ARID REGION OF THE LIMPOPO PROVINCE**

GCO DE BEER

INTRODUCTION

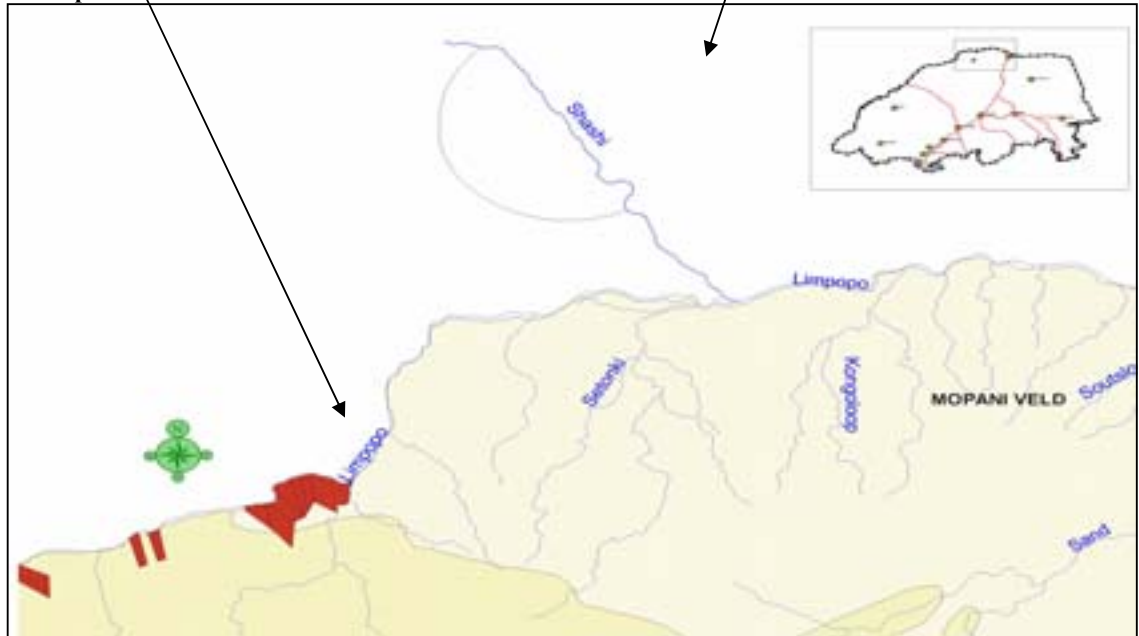
The Limpopo riparian forest has been under severe pressure by agricultural and infrastructure development since 1978 and has been identified as an endangered plant community. Damage to the forest between the Shashe and Motloutse Rivers in recent years by the Tuli elephant has become more evident.

The natural habitat of the Tuli elephant, which historically migrated from Botswana into Zimbabwe and South Africa, is steadily decreasing as a result of increased development resulting in the Tuli elephant population (which is not controlled) being forced into the Tuli block which has common boundaries between Botswana, Zimbabwe and South Africa. Increased agricultural development and the security and veterinary fences towards South Africa have hindered migration of elephants, which has resulted in concentrations of large numbers of elephants in the Limpopo riparian forest.

Cattle farming and development

Hunting pressure and settlement

Veterinary fence and Agricultural development



Aim

The study was conducted to determine the impact of elephants on the Limpopo riparian forest between 1999 and 2003.

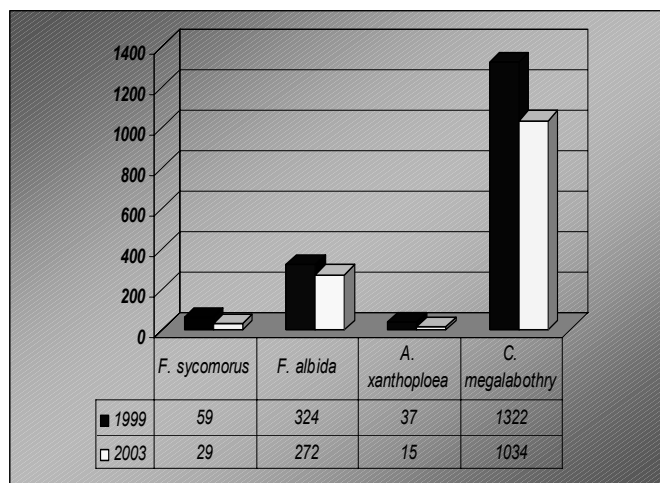
Methods

Specific trees such as *Ficus sycomorus*, *Feadherbia albida* and *Acacia xanthophloea* (preferred by elephants) and *Croton megalabotrys* (not preferred by elephants) were studied in twenty transects (500 x 20 m) on the lower river fringe. Data such as stem circumference, height, type and % elephant damage were recorded. Information regarding elephant movement was obtained from landowners.

Results

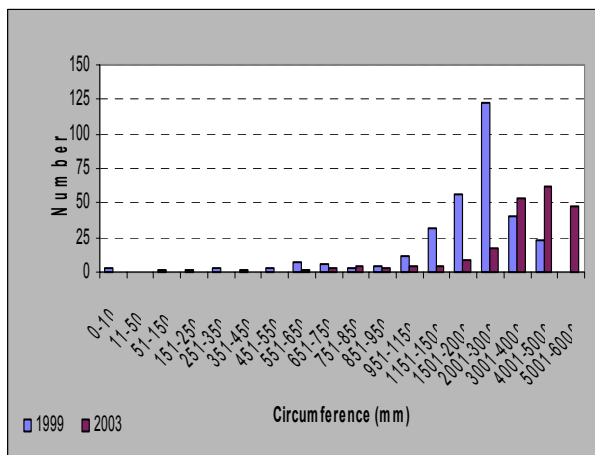
Results of the study show a decrease in the density of all tree species over a six-year period.

Change in tree density

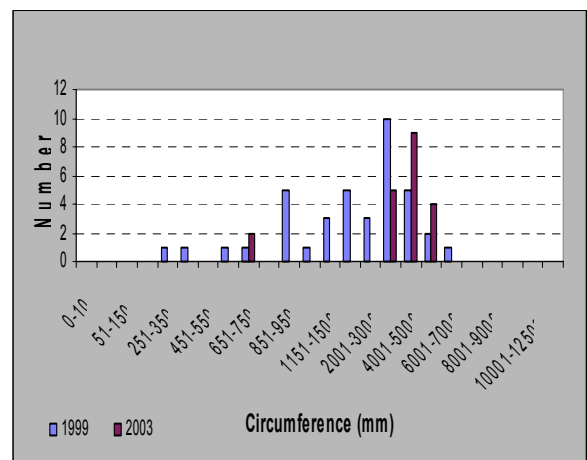


Change in population structure

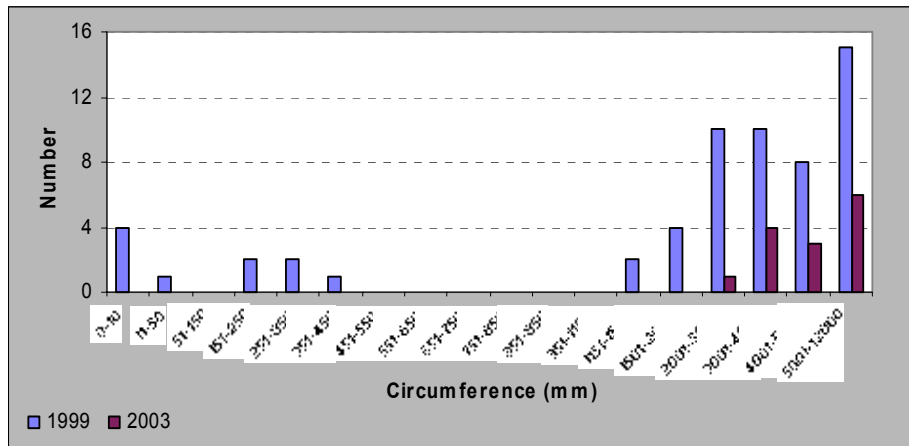
A. xanthophloea
sycomorus



Feadherbia albida

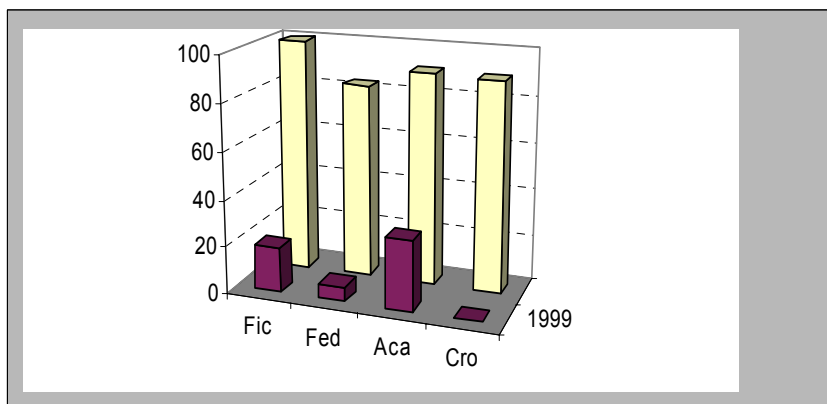


Ficus sycomorus



Small trees of *F. sycomorus*, *F. albida* and *A. xanthophloea* disappeared completely whilst larger trees declined drastically in number.

Change in utilization pattern from palatable species to all species

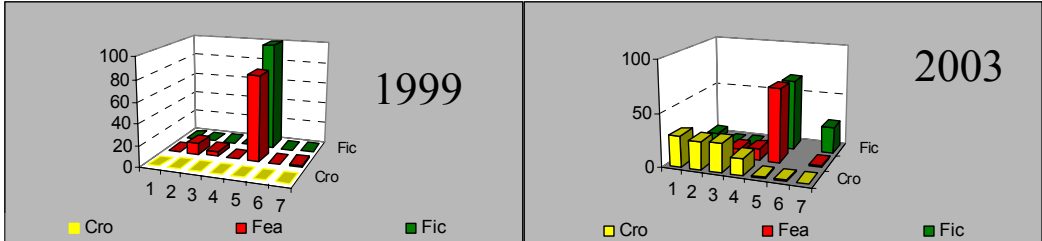


The decline in tree numbers is accompanied by an increase in type of elephant damage, especially ring barking.

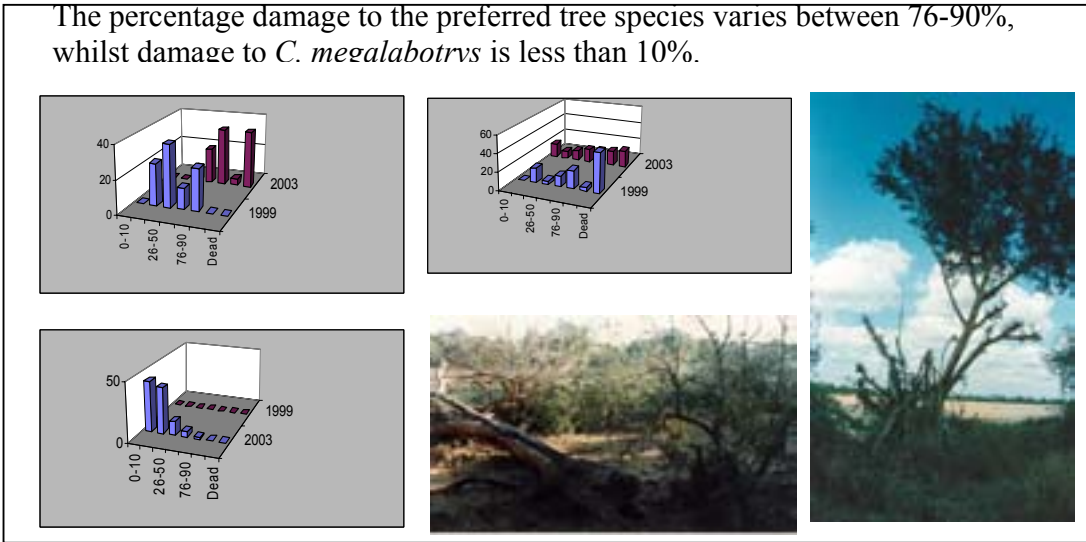
Change in type of elephant damage

- 1 = tertiary branches broken,
- 2 = secondary branches broken,
- 3 = primary branches broken
- 4 = main trunk broken,
- 5 = ring barking,
- 6 = pushing over living trees,

7 = dead trees



The percentage damage to the preferred tree species varies between 76-90%, whilst damage to *C. megalabotrvs* is less than 10%.



CONCLUSION/ DISCUSSION

Although elephant numbers were estimated at 500 (1980) it is believed that the numbers are continuously increasing. Trans border-movements by elephants are steadily increasing as well as the time spent in the forest. The concentrations of elephants here could also be caused by severe drought in Botswana, hunting pressure and continuous development that decreases the size of habitat (spatial limitation). The elephant population exceeds their forage supply as is evident in the decrease in tree species density and increase in damage. This includes *C. megalobotrys* trees, where damage was limited to individual trees in 1999.

Bearing in mind the increased agricultural activities and development planning of future dams in the Limpopo River system, the elephant migration route will be increasingly blocked, forcing elephants into smaller areas, which will eventually lead to the breakdown of the system. The degradation of the forest is evident in the change in closed canopy to open canopy forest.

Control of elephant numbers is inevitable to ensure the continued existence of this once highly productive vegetation system. Further degradation of the system will ultimately lead to a loss in biodiversity and land degradation.

Arid nature of vegetation caused pressure on riparian vegetation



Degradation from closed canopy forest to open canopy forest



RECOMMENDATIONS

- In order to minimize the increased elephant damage to the Limpopo riparian forest it is recommended that:

- Elephant numbers be determined by relevant stakeholders according to the ecological capacity.
- A Management Committee consisting of members from Botswana, Zimbabwe and South Africa should be established in order to exchange data regarding the numbers of elephant, their movements, size of existing suitable habitat and trends in habitat degradation.
- The control of elephant numbers be implemented to prevent further deterioration of this important river vegetation.

A NEIGHBOUR'S PERSPECTIVE ON THE NEW MANAGEMENT POLICY OF THE KRUGER NATIONAL PARK

MICHELLE D. HENLEY

This report is based primarily on research conducted within the Associated Private Nature Reserves (APNR) on the western border of the Kruger National Park (KNP). The APNR covers an area of approximately 1800 km² which is open to the KNP which itself has recently become part of an even larger Transfrontier Conservation Area (Braack 2000). The fences were removed between the APNR and the KNP in 1993/1994, to create a greater KNP conservation area (Joubert 1996). In the sections that follow I will highlight some of the results of these studies under specific headings which are relevant to this debate and also draw on studies conducted elsewhere.

Factors affecting an elephant management policy

Carrying capacity: a popular misconception

Historically the objective of elephant culling in the Kruger National Park was to maintain a stable population density of one elephant per square mile (0.4 elephants/km²). This was the prevailing policy between 1967 and 1994 (Whyte 2001). While the concept of a static carrying capacity within a dynamic environment no longer has scientific validity (Macnab 1985, McLeod 1997), regrettably the idea that KNP can only support a population of 7 000 elephants has become so deeply entrenched within the minds of the general public that the current population of 11 454 (I.J. Whyte pers. comm.) is unquestionably viewed by some as an overpopulation and in itself the primary reason to control elephant numbers. The revised KNP elephant management policy of the (Whyte *et al.* 1999) has moved beyond absolute numbers and rather focuses on attempting to maintain the processes that uphold ecosystems. It is important that this refinement to the policy be conveyed clearly to the broader public so that the current situation, and projections into the future, may be evaluated rationally. A meaningful debate cannot take place when the objectives of the elephant management policy are clouded.

Ecosystem resources influencing elephant populations

Dispersal and colonisation

A current study of elephant movements within the APNR, using GPS-satellite telemetry indicates that bulls do colonise new areas. A mature large tusked bull, Mac includes in his range both the KNP and APNR and the (Henley & Henley 2004). This option has only been available to him over the past 10 years; since the fence that separated the two areas was dropped. Anecdotal reports from land owners and rangers who were familiar with the area over this period suggest that he expanded his range from within the KNP to incorporate the APNR. Furthermore, having survived a period of hunting large-tusked bulls within the APNR would serve to corroborate the idea that Mac moved from the KNP into the APNR, rather than visa versa.

The increase in the APNR elephant population based on annual aerial surveys has been greater than predicted from the natural growth rate of elephants found elsewhere (de Villiers 2004). These results indicate an influx of elephants from the KNP since the removal of the boundary fence separating the reserves. The potential therefore exists for dispersal of elephants from the Kruger into surrounding areas, for example into Mozambique's Limpopo National Park. Under natural circumstances, local over-utilisation of woody vegetation by elephants within the KNP could be prevented by dispersal. Bulls are generally the first to colonise new areas (Hall-Martin 1992, Whyte 2001). Cows have the added burden of ensuring the safety of younger family members within the herd and consequently they may tend to take fewer risks than bulls (Sukumar 1991).

The colonisation of new areas by bulls could be of particular importance as bull groups have been found to have a heavier impact on the vegetation than family units (Greyling 2004) and all possible attempts should be made to encourage dispersal of particularly bulls as a natural population regulatory process. Furthermore, dispersal could be driven by a build up of densities of animals and pre-emptive culling could further disrupt this process if source areas are prevented from reaching high densities of elephants.

Mac's home range exceeds an area of 5 000 km² and spans both the proposed high density and low density management zones within the KNP (Henley & Henley 2004). The fact that an elephant's home range may be greater than the proposed management zones implies these zones do not contain separate elephant subpopulations that can be treated as discrete source and sink populations. This has implications for the effectiveness of the proposed zonation strategy in that many elephants may rearrange their pattern of range use to occupy preferentially the safe, high density zones.

At a fundamental level, any evaluation of elephant numbers should take into consideration the differences in foraging strategies between adult males and breeding herds. My research within the APNR (Greyling 2004) serves to corroborate the findings of Stokke & du Toit (2000) who, in the Chobe National Park, Botswana found that bull elephants not only ate different plant species when compared to family units but also utilised different plant parts (Stokke & du Toit 2000). Within the APNR, although bull groups and family fed on similar species, their diets differed in the plant parts ingested.

These results indicate that ecologically we cannot treat all elephants as a single unit when considering the factors that govern their movements and their consequent impact upon the vegetation. Different patterns of dispersal and resource partitioning between the sexes could be one way of meeting the nutritional requirements of the population during periods of resource limitation. It is apparent that an understanding of the patterns of movement of elephants the east and west of the KNP are of significance to all the above.

While elephants should disperse once their resource base becomes heavily utilised, an extensive network of artificial water points may interfere with this process. Elephants may remain in the proximity of the many water sources during the dry season instead of seeking out areas offering them more suitable food resources. In the dry season elephants tend to congregate near perennial rivers and more persistent water sources, thereby localising/diminishing their impact at a landscape scale. In the wet season when water is freely available, their impact will be more evenly spread across the landscape. The overall impact of elephants on the woody vegetation should also be lower in the wet season because woody species don't constitute such a large proportion of their diet. A dry season dietary shift to browse was confirmed within the APNR by carbon isotope analysis of faecal samples where a diet dominated by woody browse in the dry season (80%), reached near equal proportions of grass:browse by the wet season (Greyling 2004). Furthermore, impacted woody species would be most likely to recover in the growing season as well as during the coming dry season when elephants would, under natural circumstances, tend to move away from these impacted areas in search of water. Artificial water points thus potentially decrease both spatial and temporal heterogeneity (Walker & Goodman 1983). The KNP is currently decreasing the number of artificial water points (Whyte 2001), and this practise should be continued as far as possible and the public informed accordingly.

Climatic influence

While elephants may be more resistant to short-term climatic variability than other animals, this should not detract from the fact that they still are sensitive to them. The occurrence of oestrus in elephant cows could directly be related to short term rainfall cycles with their consequential increase in grass greenness indices (I. Douglas-Hamilton pers. comm.). Within the APNR the relative abundance of musth bulls is correlated with the mean monthly rainfall. The proportion of musth bulls peaks from March through to May. This is the most suitable time for bulls to come into musth. Cows that conceive during these

months will give birth 22 months later from January through to March, the second half of the peak rainfall period. By implication, these cows would have access to the most nutritious food resources when their physiological needs are greatest, *i.e.* during late pregnancy and early lactation (Henley & Henley 2004). Whyte (2001) also recorded an increase in breeding activity in cows in response to rainfall but also after a two month time-lag. Moss (1988) mentioned that within Amboseli National Park breeding females stopped reproductive activity for two years after a severe drought. These findings serve to highlight the fact that elephant reproductive physiology is tied to prevailing environmental conditions and that elephants are not immune to climatic variability.

Principal woody forage species

Contrary to popular opinion, elephants do not feed on all available forage. Various studies have concluded that a small number of woody species contribute a large proportion to the overall diet of elephants (De Villiers 1994). During the dry season elephants, within the APNR typically ate a narrow range of woody species (6-8 spp.). *Grewia* species were the principal food to both family units and bull groups. Results indicate that up to 38% of bull groups and 41% of family unit's diet consisted of *Grewia* spp. *Grewia* has been described as a multistemmed shrub widespread throughout the KNP, especially on basaltic soils in knobthorn veld (Van Wyk 1988). This woody species is abundant within this area, and is frequently being cleared in sections of the APNR to prevent bush encroachment.

Favoured woody species

When considering which plant species are favoured by elephants, one has to also take their availability and not only their acceptability into account. Within the APNR, five woody plants - the common false thorn (*Albizia harveyi*), mopane (*Colophospermum mopane*), zebra-wood (*Dalbergia melanoxylon*), sickle bush (*Dichrostachys cinerea*) and false marula (*Lannea schwieinfurthii*) were identified as plants favoured by both bulls and breeding herds. In addition, bull groups favoured marulas (*Sclerocarya birrea*). These six woody species together with *Grewia* spp. were utilized during 72% and 70% of all feeding events by bull groups and family units respectively (Greyling 2004).

To briefly focus on elephant impact on marulas: previous work conducted within the APNR (Haig 1999) has indicated that although elephants are impacting on the mature marula trees, regeneration of this species is being prevented by herbivory from smaller ungulates. The impala (*Aepyceros melampus*) population has increased substantially in the area and this species was found to be the main agent responsible for the lack of regeneration of marula trees. Impalas were also found to be the responsible for the lack of regeneration of *Acacias* in Lake Manyara National Park, northern Tanzania (Prins & Ven der Jeugd 1993) and for restricting the regeneration of the riparian woodland in Chobe National Park (Sharpe *et al.* 2004). Marula trees in the Kruger Park appear to be affected by fire as smaller trees are kept trapped in the grass layer by repeated burning and remain potentially non-reproductive individuals in the population. A change in the burning regime could potentially "release" these trees from a "fire trap" and allow recruitment into the population. Elephants are utilizing the mature/ adult marula trees, but very few trees are directly killed by elephants. A combination of elephant damage by bark stripping, burning of the exposed main trunk and high winds blowing weaken trees over a number of years and is affecting the larger trees in the population (Hofmeyr 2003).

The roan enclosure, in the northern basaltic region of the KNP, has been used retrospectively as an exclusion plot to measure the effect of elephant impact and other herbivores on marulas (Jacobs & Biggs 2002). Other than roan (*Hippotragus equines*), a few grey duiker (*Sylvicapra grimmia*) and steenbok (*Raphicus campestris*) large herbivores, including elephants have been excluded from the enclosure. The enclosure was erected in 1967; the same year the culling programme was implemented in the KNP. Results show that within this enclosure high densities of marulas including mature trees occur while no

mature trees are found within the surrounding landscape. The results therefore verify that elephants do have an impact on the mature canopy of specific tree species within particular vegetation types. However, an important point has been overlooked. The culling programme did not prevent, the disappearance of mature marula trees from this landscape.

Owen-Smith (1988) makes the observation that elephants will still have an impact on their favoured plant species, even at low densities. Pellew (1983) found that mature umbrella thorns (*Acacia tortilis*) were being lost at a rate of 6% per annum despite an elephant density of 0.2 elephants/km². Trollope *et al.* (1998) also concludes that culling has not prevented a change in the structural diversity of the woody vegetation in the KNP. Culling can therefore not be seen as a way of preventing elephants selecting for favoured species but merely an attempt to slow the process down. The question remains how did elephants co-exist with these tree species historically, and what has changed in the process of adult tree mortality and regeneration?

The importance of historical perspectives

In many African parks the recent vegetation structure and composition developed in the absence of elephants over a 70-100 year period (Sharpe *et al.* 2004), largely as a consequence of excessive hunting in the 1800's and early 1900's. Elephant populations within most protected areas are still recovering from low densities caused by intensive ivory hunting at the turn of the previous century. Although the vegetation is being modified by increasing elephant numbers, we are still unsure whether long term food production for elephants is being increased or decreased or whether the vegetation is not merely reverting to a historic state reminiscent of times when elephants were unaffected by hunting (Owen-Smith 1988). If the vegetation is reverting back to a previous state or in the process of establishing a new stable state, then we may be attempting the impossible task of sustaining high elephant densities whilst seeking to maintain the characteristics of the vegetation that would only have persisted if no or few elephants were present (Gillson & Lindsay 2003).

Final recommendations

When considering changes in the vegetation due to impact by elephants the most important step would be to determine the percentage of trees killed per annum and whether recruitment by surviving saplings and seedlings can maintain the tree population (Owen-Smith 1988). If this is monitored over a sufficiently long period, KNP could potentially predict changes in species composition and structure over time. The condition of the system can thus be assessed although this gives little or no insight into the numerous underlying processes that affect the status of the components (mature trees and elephants) in an ecosystem (Caughley 1983, Sinclair 1983, Owen-Smith 1988). If continuity of a mature canopy is desired, then recruitment is essential (Pellew 1983b).

Wildlife management policies should not be based primarily on subjective interpretations of the current state of an ecosystem. Rational strategies require appropriate ongoing monitoring to specifically test cause-effect relationships (Joubert 1983). To achieve this, a monitoring programme will need to be put into place that would not merely track changes but also look at causal effects by creating control areas which separate the effects of elephants from those of climatic variability, fire and other herbivores. An effective way in which these objectives can be met is by exclusion experiments (Sinclair 1983, Mallan 1992). It would be important to ensure that exclusion plots are erected in each of the management zones proposed by the new KNP management policy.

To briefly summarise the points discussed above and conclude:

- 1) The idea that the KNP has a static elephant carrying capacity is acknowledged by wildlife ecologists and managers to be an inappropriate basis for population control. However the concept persists and is still frequently invoked as the most

pressing reason for culling. Before there can be an informed debate there needs to be a widespread understanding of the objectives of the elephant management policy.

- 2) New areas were recently made available for elephants to colonise in the expanded Limpopo conservation area. This may be driven by nutritional, social and safety issues within the new habitats.
- 3) Elephants exhibit measurable sex-related differences in forage use and this should be born in mind when evaluating the potential impact of a population on resources.
- 4) Elephants are influenced by short-term climatic cycles, although to a lesser extent than many other large herbivore species.
- 5) Staple food species do not include woody plants of conservation concern.
- 6) Concerns about the impact of elephants on aesthetically appealing mature trees may not be addressed through culling alone or at all. Factors influencing the patterns of tree regeneration need to be evaluated to understand and manage the process.
- 7) Historic elephant population densities in the KNP area need to be thoroughly investigated as the concept of biodiversity includes both temporal and spatial variability.
- 8) Exclusion plots in the evaluating the effects of elephants, other herbivores, fire, and climate on the woody vegetation dynamic should be an integral element of an adaptive management strategy.

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**THE COMPARATIVE USE OF WOODY SPECIES IN DIFFERENT HABITATS BY
ELEPHANTS IN TEMBE ELEPHANT PARK, MAPUTALAND, NORTHERN KWAZULU-
NATAL.**

W.S. MATTHEWS AND B. R. PAGE

Abstract

Tembe Elephant Park's elephant population was the last naturally free roaming elephant of KwaZulu Natal. The area was proclaimed a reserve in 1983 and the south, west and eastern borders were fenced with a game proof and electric fence. In 1989 the northern border with Mozambique was fenced. When TEP was proclaimed many of the large species of mammals were absent or at very low numbers. The elephant population estimated of TEP was 120 at time of study, based on past records, aerial surveys and local knowledge. The sex ratio was biased towards bachelor bulls (1.5:1) (Ostrosky (1987, 1988, and 1989).

Tembe Elephant Park is located within the Maputaland Centre of Endemism (MC), which to date the MC has 230 endemics and near-endemic species and/or infraspecific taxa (Van Wyk 1994). Eighty-four Maputaland Centre endemics have been recorded for the study area (Matthews *et al.* 2003). The use of woody species by elephants in different vegetation types in Tembe Elephant Park (TEP) was investigated using a Point Centre Quarter sampling design. The habitat and species use is based on a detailed survey carried out during the year 1996. The technique was modified to reduce sampling intensity by measuring distances in each quarter to individuals in five different height categories at each point. Samples were located in seven different vegetation types and the intensity of utilization of individuals of different species measured by estimating the proportion of the canopy volume that had been removed by elephants. A classification of species into utilisation categories was produced which enabled assessment of the importance of different species to elephants, and also of the potential impact of elephants on different tree species. Ninety of the 137 species encountered in the study were utilized. Thirteen species were selected for, 32 were used at random, 35 were avoided and at least 9 were rejected totally. Selection at the Family level also occurred. Tembe Elephant Park's elephant diet is bias towards dicotyledons through all seasons. Seventy five percent of the diet was made up by 7 species and 90 % by 13. Because the staple diet was made up by relatively abundant species, rarer species that are highly preferred may be threatened. Species were utilized with different intensities in different habitats, those that were selected for in one type were also usually heavily utilized in other types but with different intensities. The number of species that were utilized in any habitat was proportional to the number found in that vegetation type. The results suggest that elephants could have negative impact on the diversity of Sand Forest. The need for monitoring and further study in this regard is indicated.

Type, Intensity and Age of Utilisation

46 % of all trees examined were utilised. The most frequent type of use, by far, is the removal of one or a few branches. (Fig 1). The intensity of this use is mostly light, with 63 % of individuals having < 10 % of the canopy volume removed. 6 % of the individuals are relatively heavily utilised (50 - 90 % of the canopy removed), 3 % severely impacted on (90-99%), and 2 % being totally destroyed.

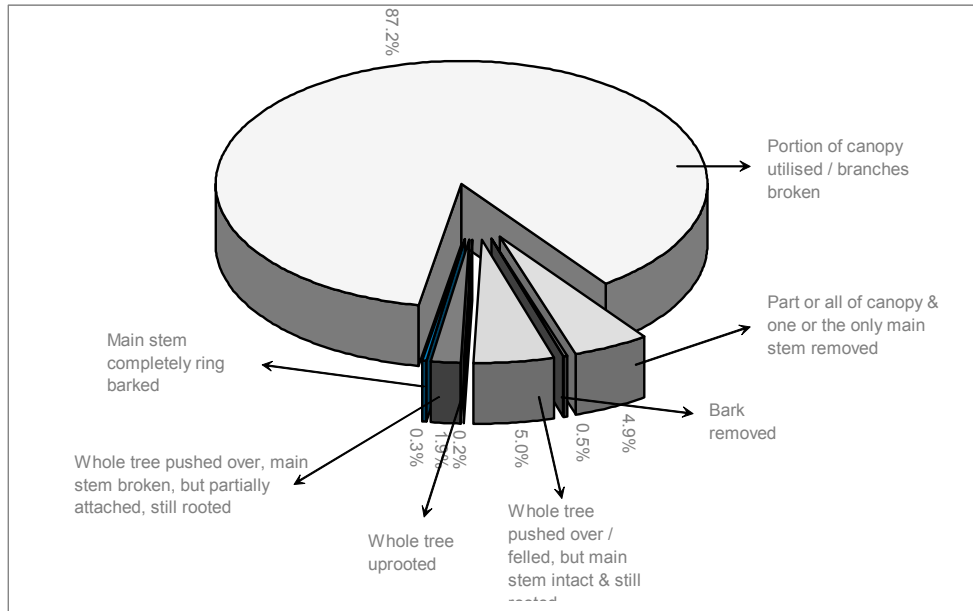


Fig. 1. Pie Chart of the Frequency of Utilisation of different Use Types

Utilisation is mostly more than 2 years old (Fig 2), which indicates that past feeding activity, consisted mostly of the removal of small amounts of foliage over successive relatively widely spaced intervals. It also appears that the rates of utilisation over the past five to seven years were not as high as at present (Fig. 2). The higher intensities of use now can be attributed to both a slight increase in elephant numbers and more intensive range use probably because the range has been reduced by fencing off part of the former range.

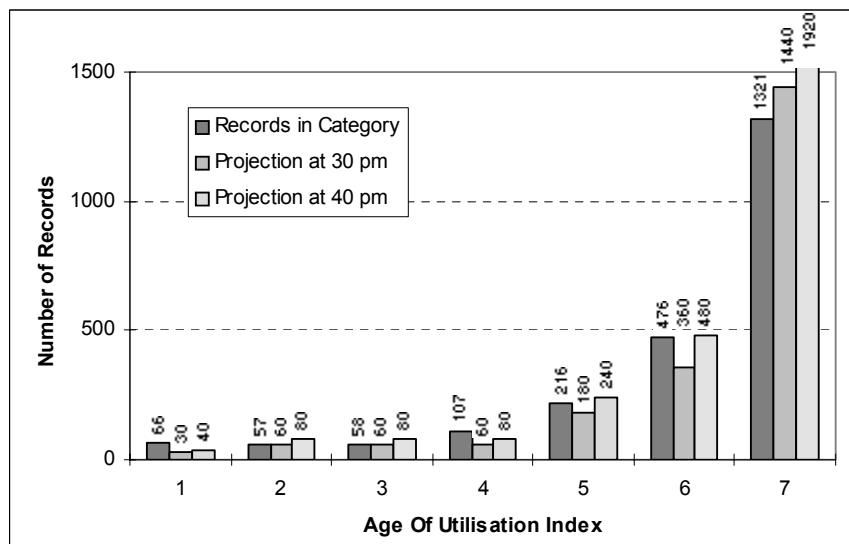


Fig. 2. Histogram of Number of Records in Each Age of Use Category and the Projections for Samples of 30, 40 and 50 Individuals Utilised per Month. Projections > 2 Years are for Total disappearance of signs of feeding Within 7 Years.

Habitat Use and Size Class Selection

Based on the percentage of individuals utilised in each habitat type, of the seven types, Open Woodland with high *Albizia adianthifolia* densities appears to be most heavily utilised, with about 60 % of the individuals having been utilised and about 30 % with more than 10 % of the canopy removed (Fig. 3). Utilisation in the other three woodland types is lower, but there appears to be little difference between them. The two Thicket types have lower utilisation than the previous four types, and Sand Forest the lowest of all.

A different picture emerges however, when the absolute quantities utilised (the density of utilised trees) in the different habitat types is examined. Whilst Open Woodland with high *A. adianthifolia* densities had a higher proportion of individuals utilised than in other types, the density of trees utilised was relatively low. The number of trees used per unit area in the different habitat types increases as density increases. Thus utilisation is highest in those habitat types with the highest tree densities (Sand Forest, Thicket, and Closed Woodland), and lowest in the types with the lowest densities (Thicket on Clay, Open Woodland and Sparse Woodland), indicating that whilst the proportion of individuals utilised were higher in the less dense habitats, a smaller absolute number of trees were utilised. The density of trees in the habitat type appears to also influence the percentage of individuals utilised, where a higher percentage is used in open habitats.

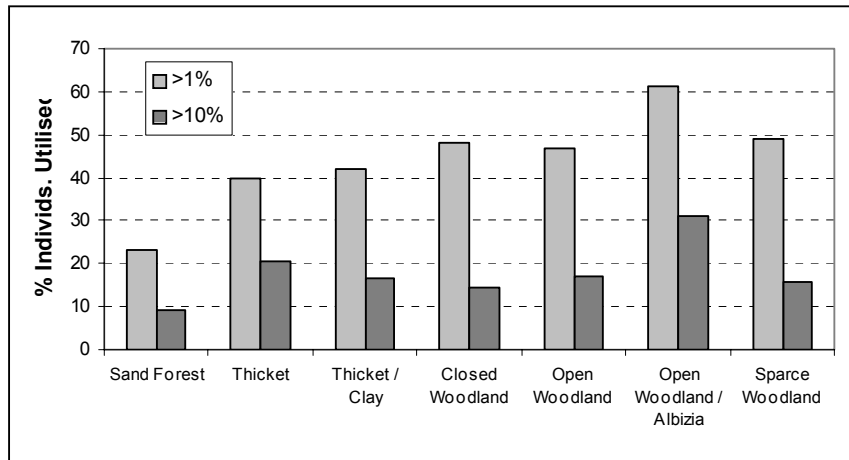


Fig. 3. Histogram of Frequency of Use in Different Vegetation Types for Individuals Utilised and Individuals with More Than 10 % of the Canopy Volume Removed.

The preferred feeding level does not appear to be different in different vegetation types. On the basis of percentage use, the 3 – 5 m class appears slightly more intensively utilised in Closed Woodland and Sparse Woodland, the 5 – 8 m level in Sand Forest, Thicket on Clay and Open Woodland, and the > 8 m class in Thicket and Open Woodland with high *A. adianthifolia*. (Fig 4). However, on the basis of the density of use the 3 – 5 m height range is used most in all habitat types. The greatest volumes are removed in the > 8m height class in all habitat types.

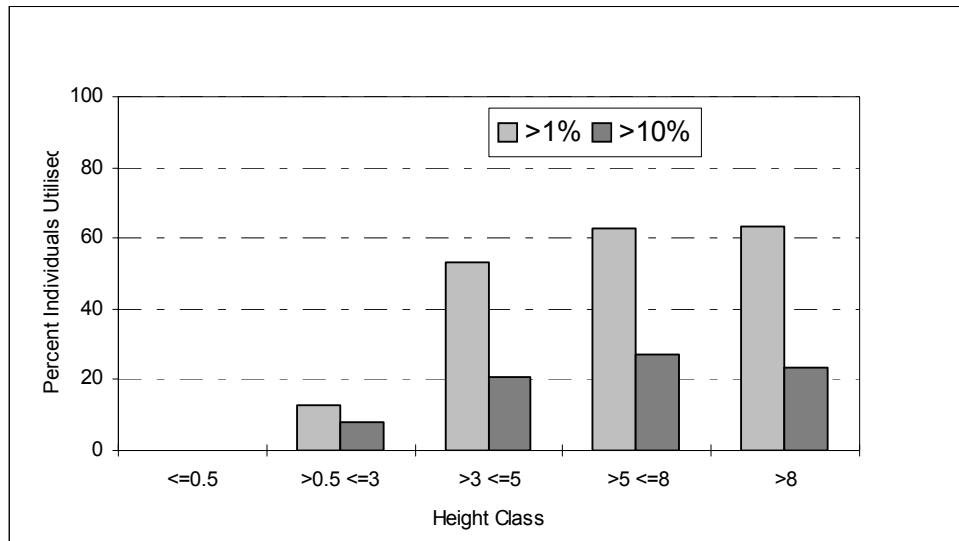


Fig. 4. Histogram of the Frequency of Use in Each Height Class in Each Habitat Type and for All Types Combined.

The comparatively high impact on in the taller height classes in TEP may be explained by the abnormally high proportion of bulls in the area. It should thus be born in mind that the results presented here may reflect an abnormal situation, and that the results for all analyses might be different with different sex ratios.

Some conclusions from study

- The numbers of elephants present in the area now covered by the Tembe Elephant Park prior to fencing, fluctuated seasonally. The exact numbers involved are unknown. The range utilised prior to fencing appears to have been slightly larger than at present. The current densities are thus higher than prior to fencing.
- Utilisation rates of trees in TEP are slightly higher now than they were prior to fencing. Currently around 2 trees are browsed per ha per elephant per year, or 161.5 trees browsed per elephant per day.
- Trees in the 3 m – 5 m height range are used more frequently than other height classes, but more material is removed from the 5m – 8m and > 8 m classes.
- The density of trees utilised is highest in those vegetation types with the highest densities of trees (Sand Forest, Thicket and Closed Woodland) and lowest in those types which is least dense (Thicket on Clay, Open Woodland and Sparse Woodland). However, in terms of the volumes removed, those habitat types with the highest abundance of large preferred trees (Open Woodland with high *A. adianthifolia*, and Open Woodland) have the highest volumes removed and those with the lowest (Sand Forest and Sparse Woodland) the lowest. Those with intermediate abundance of large preferred species (Thicket on Clay, Thicket, Closed Woodland) have intermediate volumes removed.
- Relatively few (five) species are strongly selected for or heavily utilised. Slightly more (nine) are lightly to moderately selected for. A much larger suite (nineteen) are randomly utilised or selected for in proportion to their availability in the habitat. A larger number still (twenty eight) are used at very low levels. Eighteen of these species are moderately to strongly rejected. A relatively large number (eleven species with samples of 3 or more) are totally rejected. (Table. 1).

- More species are utilised in diverse habitats than in less diverse habitats. The proportion selected appears to be constant at around 60 percent of the species available.
- Those species most highly selected for are used in all habitats in which they occur, but the degree of selection (the relative preference) is different in the different habitats, and appears to be influenced by the relative abundance of other forage species and other unknown factors.
- The bulk of the diet is made up by species which are relatively common, and which are strongly, moderately, lightly or neutrally selected for i.e. that belongs to Utilisation Classes (i) – (iv). These are *Acacia burkei*, *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Combretum molle*, *Dialium schlechteri*, *Sclerocarya birrea*, *Strychnos madagascariensis*, *Terminalia sericea* and *Trichilia emetica*.
- It appears that the suite of species, including both relatively common and rare species, that are strongly selected for are being utilised to the extent that they may be reduced to very low levels, or possibly local extinction. The threat to each of these species depends on the demographic responses of each one to environmental conditions, including utilisation by elephants. These species which include those from Utilisation Classes (i), (iii), (v), and (viii) are *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Antidesma venosum*, *Cassine transvaalica*, *Euphorbia tirucalli*, *Ficus stuhlmannii*, *Galpinia transvaalica*, *Garcinia livingstonei*, *Hyperacanthus microphyllus*, *Kigelia africana*, *Manilkara discolor*, *Newtonia hildebrandtii*, *Phyllanthus reticulatus*, *Syzygium cordatum*, *Sclerocarya birrea*, *Terminalia sericea*, *Tricalysia junodii*, *Trichilia emetica*, *Warneckea sousae* and *Wrightia natalensis*.
- More species are utilised in diverse habitats than in less diverse habitats. The proportion selected appears to be more or less constant at around 60 percent of the species available.
- Those species most highly selected for are used in all habitats in which they occur, but the degree of selection (the relative preference) is different in the different habitats, and appears to be influenced by the relative abundance of other forage species and other unknown factors.
- Several species which are Maputaland endemics with a limited distribution, and which have very little conservation status outside of TEP may be threatened by elephant impact. These are *Combretum mkuzense*, *Dialium schlechteri*, *Hyperacanthus microphyllus*, *Warneckea sousae*, *Tricalysia junodii* var. *junodii* and *Wrightia natalensis*.
- Sand Forest, a unique vegetation type, of limited distribution and area conserved, containing many Maputaland endemics, may be threatened as a type because of general thinning, as well as direct impacts on particular species.
- Because utilization is influenced by relative abundance, the classification presented here should be expected to change. For this reason only potential impact of elephants on any particular species can be predicted from this single survey. The accurate prediction required for the successful management of Biodiversity requires that all of the factors influencing demographics be established first and thereafter monitored continuously.

Irrespective of the accuracy of the density estimates, the approach provides useful information on the relative use of different species and the likelihood of impact on their abundance from elephant feeding activity.

The patterns of selection described above have obvious implications for the management of Tembe Elephant Park. Since more species are used in the more diverse habitats, but the staple diet is from species in a wider range of habitats, the potential exists for rare strongly selected for species to be heavily impacted on and extirpated. Cumming *et al.* (1997) have presented data that suggests that where elephant have been confined for a few decades, the biodiversity is substantially reduced. In conservation situations where elephants are contained and/or artificial waterholes are provided, the potential for substantial impact on the diversity of the area is increased. In the TEP situation, the data presented here suggest that several species have a high probability of being heavily impacted or eliminated from the Park. In particular the species *A. adianthifolia*, *A. versicolor*, *S. birrea*, *A. quanzensis*, *T. emetica*, *D. schlechteri*, *G. transvaalica*, *G. livingstonei*, *M. discolor*, *N. hildebrandtii*, *H. microphylla*, *M. sousae*, *T. junodii* and *K. africana*, require more intensive study of the factors influencing their growth and survival to establish if elephants are affecting their demographics or not.

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Table 1. Intensity of use classification for each species in each habitat type and for all types combined

* indicates where an average for the total area is anomalous, but where the vegetation types concerned have very low samples (< 3 individuals). VPD – Total Volume Removed For The Particular Species in the Total Sample / Preference Ratio / Mean Density for all Types in which the Species Occurs. H – High; M – Moderate; L – Low; T – Trace; S – Selected For; N – Neutral Selection; R – Rejected; C – Complete Rejection; R – Rare. Densities are categorised as high (>50 per ha), moderate (10 –50), low (1-10), rare (<1). CLS - classes.

Species	VPD	CLS
<i>Albizia adianthifolia</i>	HSL	i
<i>Albizia versicolor</i>	HSL	i
<i>Sclerocarya birrea sub. caffra</i>	HSM	i
<i>Terminalia sericea</i>	HSH	i

<i>Acacia burkei</i>	HNH	ii

<i>Acacia robusta sub. clavigera</i>	MSL	iii
<i>Azelia quanzensis</i>	MSL [#]	iii
<i>Trichilia emetica</i>	MSL	iii

<i>Combretum molle</i>	MNM	iv
<i>Dialium schlechteri</i>	MNM	iv
<i>Strychnos madagascariensis</i>	MNH [#]	iv

<i>Galpinia transvaalica</i>	LSL	v
<i>Garcinia livingstonei</i>	LSL	v
<i>Antidesma venosum</i>	LSL	v
<i>Manilkara discolor</i>	LSL*	v
<i>Newtonia hildebrandtii</i>	LSL	v
<i>Wrightia natalensis</i>	LSL	v
<i>Ficus stuhlmannii</i>	LSR	v
<i>Syzygium cordatum</i>	LSR	v

<i>Erythrophleum lasianthum</i>	LNL	vi
<i>Sapium integerrimum</i>	LNL	vi
<i>Ziziphus mucronata</i>	LNL	vi
<i>Balanites maughamii</i>	LNL	vi
<i>Commiphora neglecta</i>	LN [#]	vi

<i>Psydrax fragrantissima</i>	LNM	vi
<i>Pteleopsis myrtifolia</i>	LNM [#]	vi
<i>Spirostachys africana</i>	LNM [#]	vi
<i>Strychnos spinosa</i>	LNM [#]	vi
<i>Cordia caffra</i>	LNR	vi

<i>Cleistanthus schlechteri</i> v. <i>schlechteri</i>	LRL	vii
<i>Acacia senegal</i> v. <i>rostrata</i>	LRM	vii
<i>Psydrax locuples</i>	LRM [#]	vii
<i>Tabernaemontana elegans</i>	LRM [#]	vii
<i>Dichrostachys cinerea</i>	LRM [#]	vii
<i>Euclea natalensis</i>	LRM	vii
<i>Hymenocardia ulmoides</i>	LRM	vii
<i>Vepris lanceolata</i>	LRM	vii
<i>Drypetes arguta</i>	LRH	vii

<i>Hyperacanthus microphyllus</i>	TSL	viii
<i>Memecylon sousae</i>	TSL	viii
<i>Tricalysia junodii</i> var. <i>junodii</i>	TSL	viii
<i>Cassine transvaalensis</i>	TSR	viii
<i>Euphorbia tirucalli</i>	TSR	viii
<i>Kigelia africana</i>	TSR	viii
<i>Phyllanthus reticulatus</i>	TSR	viii

<i>Boscia foetida</i> sub. <i>rehmanniana</i>	TNL*	ix
<i>Canthium setiflorum</i> sub. <i>setiflorum</i>	TNL*	ix
<i>Euclea divinorum</i>	TNL [#]	ix
<i>Mimusops caffra</i>	TNL [#]	ix
<i>Rothmannia fisheri</i> sub. <i>moramballae</i>	TNL	ix
<i>Sideroxylon inerme</i>	TNL	ix
<i>Tricalysia delagoensis</i>	TNL	ix
<i>Drypetes natalensis</i>	TNL	ix
<i>Bridelia cathartica</i>	TNM	ix
<i>Lagynias lasiantha</i>	TNM	ix
<i>Rhus gueinzii</i>	TNM [#]	ix
<i>Acacia nilotica</i> sub. <i>kraussiana</i>	TNR	ix
<i>Berchemia zeyheri</i>	TNR	ix
<i>Combretum mkuzense</i>	TNR	ix
<i>Ekebergia capensis</i>	TNR	ix
<i>Schotia brachypetala</i>	TNR	ix

<i>Canthium inerme</i>	TRL [#]	x
<i>Monodora junodii</i>	TRL*	x
<i>Acalypha glabrata</i>	TRL	x
<i>Acridocarpus natalitius v. linearifolius</i>	TRL	x
<i>Ancylanthos monteiroi</i>	TRL	x
<i>Dovyalis longispina</i>	TRL	x
<i>Erythroxylum delagoense</i>	TRL	x
<i>Grewia microthyrsa</i>	TRL	x
<i>Margaritaria discoidea</i>	TRL	x
<i>Maytenus senegalensis</i>	TRL	x
<i>Ozoroa engleri</i>	TRL	x
<i>Pavetta catophylla</i>	TRL	x
<i>Phoenix reclinata</i>	TRL*	x
<i>Ptaeroxylon obliquum</i>	TRL*	x
<i>Vangueria esculenta</i>	TRL*	x
<i>Xylothea kraussiana</i>	TRL	x
<i>Zanthoxylum capense</i>	TRL*	x
<i>Acacia borleae</i>	TRL	x
<i>Grewia caffra</i>	TRM [#]	x
<i>Hyphaene coriacea</i>	TRM [#]	x
<i>Salacia leptoclada</i>	TRM	x
<i>Strychnos decussata</i>	TRM [#]	x
<i>Teclea gerrardii</i>	TRM	x
<i>Todallopsis bremekampii</i>	TRM	x
<i>Tricalysia capensis</i>	TRM	x
<i>Vangueria infausta sub. infausta</i>	TRM [#]	x
<i>Catunaregam spinosa sub. spinosa</i>	TRH [#]	x
<i>Cola greenwayi</i>	TRH [#]	x
<i>Brachylaena huillensis</i>	TRH [#]	x
<i>Croton pseudopulchellus</i>	TRH [#]	x

<i>Clausena anisata</i>	CM	xi
<i>Coddia rudis</i>	CM	xi
<i>Plectroniella armata</i>	CM	xi

<i>Coffea racemosa</i>	CL	xii
<i>Diospyros inhacaensis</i>	CL	xii
<i>Ehretia rigida</i>	CL	xii
<i>Euphorbia ingens</i>	CL	xii
<i>Gardenia volkensii</i>	CL	xii
<i>Haplocoelum gallense</i>	CL	xii
<i>Hyperacanthus amoenus</i>	CL	xii
<i>Mundulia sericea</i>	CL	xii

<i>Ochna arborea</i> var. <i>arborea</i>	CL	xii
<i>Ochna barbosae</i>	CL	xii
<i>Ochna natalitia</i>	CL	xii
<i>Oxyanthus latifolius</i>	CL	xii
<i>Strychnos henningsii</i>	CL	xii
<i>Suregada zanzibariensis</i>	CL	xii
<i>Tarenna junodii</i>	CL	xii
<i>Vitex amboniensis</i>	CL	xii
<i>Acacia karroo</i>	CR	xii
<i>Albizia forbesii</i>	CR	xii
<i>Casearia gladiiformis</i>	CR	xii
<i>Cassipourea mossambicensis</i>	CR	xii
<i>Combretum celastroides</i> sub. <i>orientale</i>	CR	xii
<i>Erythroxylum emarginatum</i>	CR	xii
<i>Euclea schimperi</i>	CR	xii
<i>Eugenia natalitia</i>	CR	xii
<i>Euphorbia grandidens</i>	CR	xii
<i>Lannea antiscorbutica</i>	CR	xii
<i>Manilkara concolor</i>	CR	xii
<i>Maytenus undata</i>	CR	xii
<i>Premna mooiensis</i>	CR	xii
<i>Pseudobersama mossambicensis</i>	CR	xii
<i>Thespesia acutiloba</i>	CR	xii

THE ROLE OF ELEPHANT IN CREATING DIVERSITY IN VEGETATION STRUCTURE, FUNCTION AND COMPOSITION, AND THE CONSEQUENCES FOR BIODIVERSITY

CHARLES KAY

A key question for elephant management is whether the current impact of elephants on vegetation is eroding ecosystem resilience and thereby threatening biodiversity. A historical perspective is essential to addressing this question, and ideally we would be able to compare changes in past elephant population densities and vegetation structure over long periods of time (say the last 500 years) in order to determine whether current elephant population density and vegetation structure is within the normal range of variability for the Kruger ecosystem. At present, however, there are very few data describing changes in vegetation and elephant population density over long time periods, and research opportunities exist to explore the relationship between long-term variability in vegetation and elephant abundance. For example, it has been suggested that elephants were historically of low density in the Kruger area, and that the current population of ~ 9000 is therefore too high to be sustained by the present vegetation cover (Whyte et al 2003). An alternative hypothesis is that savanna vegetation and elephant populations have varied over time, and that today's population increase represents a return to pre-ivory trade abundance. Comparison of palaeoecological, palaeoclimatological and historical data might provide possibilities for testing these two alternative hypotheses. The areas of uncertainty associated with the proposed research are:

- 1) The sources of possible historical data have not yet been fully investigated, though preliminary work suggests good potential (Beinart, Pers. Comm.)
- 2) The palaeoecological data now emerging from the Kruger National Park mainly show small scale changes in vegetation structure, and probably reflect the effects of localised disturbances rather than larger scale trends in elephant abundance (Gillson, in prep)
- 3) Correlation does not imply causality: a coincidence of change in elephant abundance and vegetation structure may be related to other factors e.g. climatic change. Thus it is essential that the results of the proposed study are embedded in the overall framework, which represents the interplay between numerous biotic and abiotic factors, including climate, CO₂ concentration, herbivory (elephants and other herbivores), human activity, fire, other disturbance, topography at different spatial and temporal scales (Coughenar and Ellis, 1993; Gillson 2004; Rogers 2003).

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VEGETATION – ELEPHANT INTERACTIONS

NORMAN OWEN-SMITH

Feeding and associated breakage of plants by elephants can vastly alter vegetation structure and composition at landscape scales. The consequences for biodiversity need likewise to be recognised at the regional scale. Accordingly attention needs to be directed more towards the regional distribution of such impacts and less towards the local effects.

From this perspective, predator-prey theory, developed for carnivores preying upon herbivores, has relevance. Ecologists accept that predators can eliminate prey populations locally from habitats where they might otherwise occur, unless escape through dispersal or other mechanisms enables the prey to keep one step ahead of the predator. Also crucially important are refuge areas where prey species can persist because defence mechanisms effectively counteract the predation hazard in such habitats.

Furthermore, the state of the vegetation is not static or fossilised in time. Some plant populations will be aggrading, others contracting, over prolonged periods, and there may be a patch-mosaic pattern of regeneration. In the recent past, South African savannas were generally more open in woody canopy cover than we see today, and in the distant past much more open. The extent to which the bush thickening is related to global warming, CO₂ increase or a alteration of fire regimes is uncertain. The absence of elephants for more than a century may well have contributed to the recent bush thickening.

The conversion of extensive areas of Kruger from savanna woodland to open parkland or even grassland through elephant impacts need not be detrimental. It could be viewed as restoring the conditions that were prevalent a few centuries ago. Elephant impacts may even be necessary to restrict the trend towards bush thickening, at high density levels than those current in Kruger. Extreme vegetation transformation not seem to be adverse for animal diversity, as shown by findings from the Norwegian BONIC team for the Chobe river front region of Botswana - not for large herbivores except perhaps bushbuck, not on small mammals, and not on game birds. Local elephant densities at this level (4-6 per km²) may be needed to open up such shrublands, which favour mainly impala.

Elephant impacts can suppress recruitment to the canopy layer by certain tree species. Variability over time in local impacts probably enables plant to escape from this suppression and grow beyond the vulnerable size classes. The relevant temporal variability is more likely to occur through a re-distribution of elephant presence rather than a change in elephant population abundance. It could be enabled by spatial variability drawing elephants away to other resources before local patches get too extremely depressed.

Management implications

The management need is to identify spatial regions where plant species threatened by elephant impacts can be enabled to persist. Relatively few tree species seem vulnerable: baobab, marula, kiaat. Baobabs seem secure for the time being on the rocky hillslopes where they are prevalent in northern Kruger. Marula have abundant regeneration that could quickly replace mature trees killed by elephants, if released from suppression by fire, browsers and elephants. This could be brought about by restricting the presence of elephant bulls during the dry season and increasing wet season grazing pressure in the upland regions where marula trees are prevalent, e.g. around Satara. None of the riparian woodland species seems to be threatened. Some tree species patchily distributed within mopane-dominated vegetation may be locally threatened if elephants concentrate their impacts disproportionately in these patches. Their loss could be detrimental for

regional diversity, affecting not only these but also the animals that depend on these patches (e.g. giraffe). More research is needed to establish the extent to which this is a problem, but the resurgence of marula within the roan enclosure testifies to the potential for such effects.

To my knowledge, current elephant impacts do not transgress or even approach the thresholds of potential concern that were set at a previous workshop. The only justification for contemplating population containment or reduction at this time is as a precautionary or risk-containment measure.

From this perspective, there is justification for designating botanical reserves, to ensure that vulnerable plant species or vegetation types will not be eliminated by elephants. I don't see any reason to expand these zones beyond those currently established in the south-west and north-west regions of Kruger, but further attention could be directed towards this question as an aspect of risk-containment. The only intervention needed over the remainder of the park might be disturbance culling to concentrate the elephant population within a narrower central region, in order to demonstrate the consequences of higher elephant densities before they become too widespread.

The management aim should be to safeguard threatened components of biodiversity or species while allowing natural processes to proceed little hindered within the context of the fenced park, even if they lead to vegetation states somewhat different from those that were prevalent within the memory of park visitors.

SOME RECENT FINDINGS RELEVANT TO THE ELEPHANT POPULATION QUESTION

BOB SCHOLES

This note briefly reports work-in-progress at the CSIR that has relevance to the issue of the long term consequences of various elephant management strategies. The work has been carried out under two projects: the 'Biocomplexity in African Savannas' project supported by the US National Science Foundation, and the 'Adaptation of biodiversity to climate change project', funded by AIACC.

The elephant-tree system has at least three stable states

Theoretical work in savanna ecosystem dynamics has predicted that mixed tree-grass systems have two potential 'end-point' stable states: one with a low tree cover and lots of grass (think of the open basaltic plains in the southern Kruger), and one with a high tree cover and very little grass (think of the Sabi river thickets). Much of the landscape is not actually in either of these states, but somewhere in between, in a 'disequilibrium' condition being moved around by disturbances, particularly fire and browsing, especially by elephants. If you change the level of disturbance, the system tends to track off towards one of the endpoints, depending on where it was when you made the change. There are many different theoretical treatments of this system, but they all tend to come to similar conclusions. Scholes (2004) is one example, and points out that the 'dense tree' state is much more resilient than the 'grassy' state.

Recent work, triggered by a reanalysis of Charlie Shackleton's PhD data on tree growth rates, suggests a mechanism for a third state. Long-standing insights from mathematical ecology tell us that in a 'predator-prey system' (in this case, think of trees as the prey, and elephants as the predator), a solution in which both predator and prey persist is only possible if the intrinsic growth rate of prey is substantially higher than the predator growth rate. Otherwise you end up with boom-and-bust cycles, and need to depend on refugia and spatial effects for a long-term persistence. From Charlie's data we know that the mean savanna tree growth rate is 3% per annum, and from KNP elephant data we know that the elephant growth rate is 6% pa. This suggests that a stable elephant-tree coexistence is not possible, and we should expect wild population fluctuations in both, and perhaps a patchy landscape at a large scale, with different patches in different stages of boom or bust. [I am keeping the argument simple: a full analysis has to include the fact that elephants actually mostly eat grass, but have a seasonal dependence on trees].

A recent re-analysis of Charlie's dataset (Shackleton and Scholes, in prep) shows that the intrinsic growth rate of trees has a strong dependence on stem diameter (figure 1). At the 'average stem diameter' of most mature savanna plots, tree mean annual increment is indeed about 3%, *but when the trees are small in diameter, even if there are many of them, the growth rate is much higher*. At the limit, the tree mean annual increment is in the region of 20% pa. This is much higher than the maximum growth rate of elephant populations, and therefore a stable state exists. This state has a high number of elephants, a high cover of coppiced trees (multiple stems, each with a small diameter), and a low grass cover.

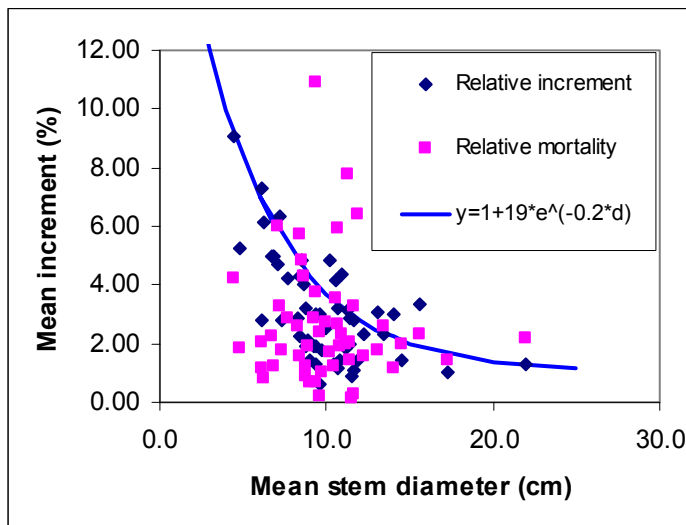


Figure 1. Tree mean annual increment as a function of the average stem diameter in the plot (ie, $200 \cdot \sqrt{\text{plot basal area}/\text{number of stems}/\pi}$) for 49 locations throughout the savanna biome in South Africa.

This theoretical finding accords with experience all over southern Africa: when the elephant populations become high, they tend not to crash, or migrate out and allow the woodland to recover, but remain high and the system gets stuck in a coppice state. This state may not persist forever. If elephant populations continue to climb, at some stage their browsing offtake will overwhelm even the high regenerative capacity of coppiced trees, and tree mortality will set in, leading to a treeless, grassless landscape, and eventual elephant population collapse. But the coppice state may last a long time: decades or more. After the elephant numbers have declined through mortality, out-migration or culling, the coppice state may still continue to persist for a very long time, simply because tree-on-tree competition prevents it from reverting to a more natural mixed tree size structure. The process of self-thinning is slow, especially when the competing stems are effectively clones of one another. The current extensive *mopane* coppice woodlands in many parts of the KNP and elsewhere may be a reminder of high elephant densities more than a century ago.

The habitat structure consequences of changes in the climate and atmospheric composition depend on elephant numbers, rather than the other way around.

There has been much speculation that the different response of trees and grasses to rising carbon dioxide concentrations in the atmosphere may tilt the tree-grass competition in favour of trees, leading to a more woody landscape in the future, and helping sustain higher elephant numbers [I simplify here; the full argument includes fire and browsers as well]. It is certainly true that at the low CO₂ levels that occurred in the Pliocene (180 ppm in glacial periods, and 280 ppm in interglacials) there are very dramatic differences in responses by trees and grasses. For instance, during the glacial that lasted up until about 20 000 years ago, there may have been much less tree cover, and possibly many fewer elephants. But at the levels predicted for the future (500 ppm or more), the difference between trees and grasses is much less – a few percentage points.

Trees and grasses also react differently to temperature and water supply, and these effects may overwhelm the CO₂ effect for the projected warmer, slightly drier conditions in mid-century (figure 2).

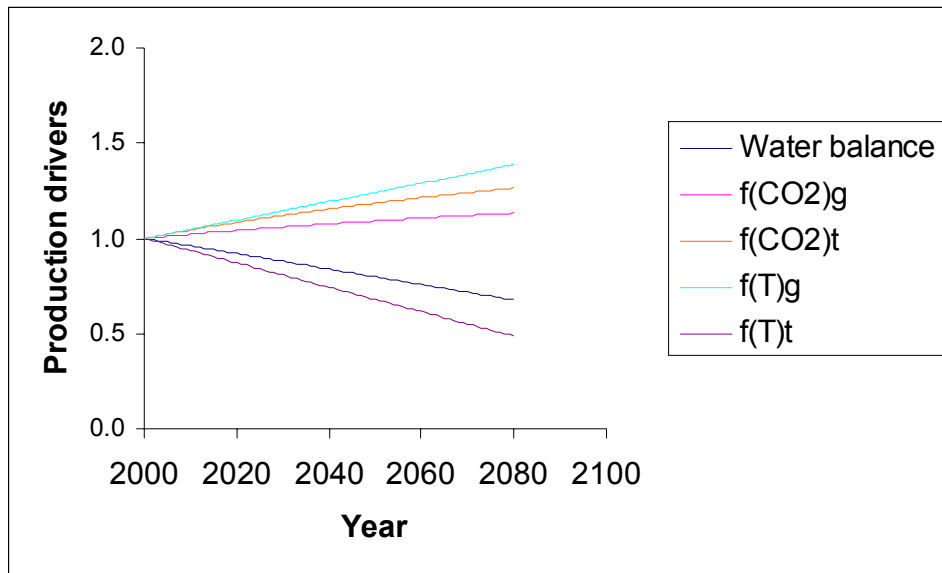


Figure 2. The effects of CO₂, temperature (T) and water balance on tree and grass growth during the 21st century, using the A2 scenario and the Hadley GCM projections.

A model that takes into account all these effects, plus tree-grass competition, fire and herbivory, suggest that the main determinant of the future habitat structure in the KNP is elephant density, rather than climate change (Scholes 2005).

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PREDICTING THE IMPACT OF ELEPHANTS ON WOODY PLANT DIVERSITY

T.G. O'CONNOR, P.S. GOODMAN AND B. CLEGG

(NOT TO BE CITED WITHOUT PERMISSION - An extended summary of a paper to be submitted for publication)

Introduction

- The elephant problem was identified in the 1960's as a result of the transformation of woodland and forest vegetation in East African parks resulting from increased elephant densities due to compression of populations as expansion of human populations occurred (compression hypothesis). The dramatic decline of the African elephant population in East Africa during the 1980's as a result of poaching alleviated concern about vegetation in affected areas, but the issue has persisted in southern African parks that were relatively unaffected by poaching, in most of which quasi-stable elephant populations were maintained by harvesting.
- In southern Africa, elephant populations have been re-established in a number of small to medium-sized reserves (<1000 km²) over the past few decades. These populations have been maintained at densities not expected to result in habitat transformation. There is widespread perception, however, albeit poorly investigated, that certain selected plant species are at risk of local extirpation in small to medium-sized reserves.
- African ecology lacks a predictive ability about the nature and extent of elephant impacts on vegetation. This is required for ensuring the co-existence of elephants and their selected food species. This lack of a predictive ability possibly owes mainly to the phenomenological nature of most research. There are many descriptive studies of elephant population numbers or trends, elephant diet, and their impact on woodlands at a point in time. There have been only a few process-based studies of this plant-herbivore dynamic, most of which have not directly addressed plant diversity.
- The aim of this paper is to develop predictions (an hypothesis) about which woody species are vulnerable to extirpation, and under what circumstances, in African savanna reserves. The hypothesis is founded upon a functional approach to the elephant-vegetation relationship. (1) The vegetation types and species selected by elephant and the manner in which they are utilized, is predicted. (2) The attributes of an individual plant and of a plant population that might render a plant species vulnerable to local extirpation by elephant impact are predicted. (3) The characteristics of a reserve or ecosystem that would predispose a woody species to extirpation by elephant are identified. Specifically, recognizing that elephant and selected plant species co-existed in historical times, what have been subsequent key changes that have rendered certain species more vulnerable.

Elephant foraging ecology: constraints

- Any animal has to meet its nutritional requirements within the constraints of its intake and digestive capabilities. On account of their very large body size, an elephant would have a low specific, but a large absolute, requirement for energy and nutrients. By comparison with a smaller-bodied animal, an elephant can utilize a large amount of food that does not have to contain relatively high concentrations of protein and energy. By comparison with a ruminant, however, the following characteristics and capabilities of their digestive system have consequences for the type of foodstuffs selected.
- Elephants are hind gut fermentors.

- Elephant are capable of a rapid rate of passage of material, even if coarse, through the gut because of its relatively simple structure (33 hours compared to 70-100 hours in cattle). Elephant digestion therefore contrasts markedly with ruminant digestion.
- As a result of the rapid rate of passage, the structural material of the cell walls (mainly cellulose) is passed out largely undigested.
- Accordingly, elephants are expected to be reliant mainly on soluble sugars and other cell contents as a source of energy.
- On account of the low level of cellulose digestion, cell contents must be largely released by rupture of cell walls during chewing rather than by break down of cell walls during fermentative digestion. Hence the presence of six sets of molars and death of the animal by starvation once the sixth set is worn out.
- Much of the cell content per unit feed may not be extracted, as evidenced by the large proportion of ingested cells that pass out intact (e.g. whole leaves and fruits).
- For an individual elephant to meet its nutritional requirements, it is proposed that it would need to process a large amount of food per unit time given its large absolute nutrient/energy requirement and low level of nutrient/energy extraction per unit of feed, and the above-listed constraints. This can be achieved because their digestive system allows for a high rate of passage, provided that intake rate is not limiting. This contrasts with the ruminant strategy of maximizing digestion per unit feed.
- Elephants are therefore predicted to maximize the intake of foodstuffs that result in the greatest amount of extractable cell contents that can be sequestered per unit time.

Elephant foraging ecology: consequences

- Elephant should minimize intake of senescent material because it contains little cell contents.
- Elephant should maximize intake of foodstuffs with a high proportion of cell contents (e.g. herbs with succulent stems in preference to those with woody stems; woody plants from which they can harvest leaves without having to harvest the supporting stems).
- They should strive to minimize intake rate by selecting foodstuffs with the shortest prehension and processing times.
- They should select foraging areas where vegetation with the above characteristics is most abundant, thereby reducing searching time and increasing intake rate.

Evidence in support of this hypothesis

- Recorded seasonal changes in diet are consistent with elephant ensuring a near maximum intake rate of material with a large absolute amount of extractable cell contents relative to what is available.
- In the markedly seasonal savannas of Africa, elephants select herbs and grasses during the rainy season, and browse, bark and roots during the dry season, with the amount of bark and roots increasing as the dry season progresses.
- Elephants consume herbs and grasses more rapidly than browse foliage, and consume browse foliage more rapidly than bark or roots, because of shorter search, handling and processing times. Consequently during the rainy season, when all forage types have high extractable cell contents, they favour herbs and grass over browse, bark and roots. When

herbs and grasses dry out during the early dry season, elephant select browse because it offers the greatest amount of extractable cell contents that can be harvested at the greatest rate of intake. During the late dry season when leaf fall is near complete, elephants consume a greater amount of bark and roots, despite the poor rate of intake achieved, because these forages have the greatest amount of cell contents at this time.

- Bark is consumed for the sugar-containing phloem tissue.
- Patterns of selection in order to maximize quality and quantity of intake are apparent for individual foraging components as well. They select soft, broadleaved grasses (e.g. *Panicum*, *Urochloa*) because these species possess the greatest ratio of cell contents to structural material. Grasses with long leaves have a greater proportion of supporting lignin.
- Bark is most consistently utilized when sap flow through phloem is most active during early spring.
- Their habit of pollarding trees is a tactic allowing elephant access to choice foliage on a tree's crown that can be rapidly harvested.

Key determinants of the individual and population response of woody plants to elephant utilization

- A population would tend toward local extirpation should the average rate of adult mortality consistently exceed the average rate of recruitment. For species selected by elephant, severe utilization is most commonly in the form of pollarding, ringbarking, uprooting, or repeated, severe defoliation of foliage.
- Mortality, however, depends on the ability of a species to regrow following severe utilization, especially coppicing ability. Elephants can therefore markedly affect the rate of adult mortality.
- Elephants are not known to influence materially the recruitment of small individuals.
- The species= attributes of an individual plant will influence the manner and extent of selection, type of utilization, tolerance of severe utilization, and the probability of mortality if severely utilized.
- Pollarding or uprooting result from an elephant pushing against the main stem of a tree to gain access to crown foliage or fruit. Whether the stem snaps or uproots depends primarily on the shearing strength of stem wood, the tensile strength of roots, and the inertness of the soil matrix.
- Excavation of roots depends on soil texture, with sandy preferred.
- Debarking depends on the ease with which bark can be separated from the underlying wood. Species with clean boles and with bark that strips easily can be easily ringbarked (e.g. *Kirkia acuminata*); species with single boles and whose bark has to be chiselled off rather than stripped (e.g. *Sclerocarya birrea*, *Schotia brachypetala*) can eventually be ringbarked; species with more than one main stem, but whose bark otherwise strips easily, can usually not be debarked on the inside of the stems (e.g. *Colophospermum mopane*); and bark structure of many species precludes effective debarking (e.g. *Combretum imberbe*).
- Activation of the bud bank (coppicing) and the vigour of coppice regrowth are key growth attributes determining an individual=s response to damage. The size of the bud

bank on the lower half of the main stem varies among woody species and declines with age. For example, pollarded *Commiphora merkerii* dies quickly whereas *C. mopane* does not usually die.

- Population decline resulting from elevated adult mortality would depend on recruitment and growth rates of individuals, both of which differ among species and are dependent on rainfall, fire, and the impact of other herbivores.
- Declining populations which experience infrequent recruitment of small numbers could reasonably be expected to be at greater risk of extirpation than populations experiencing ongoing recruitment with large numbers, other factors being equal.
- Seedling recruitment depends on rainfall in semi-arid and arid systems. The striking population size structure of some long-lived species in such systems indicates that successful recruitment may not occur for decades or centuries. Such species may be particularly vulnerable to local extirpation if adult mortality is increased.
- The influence of the Little Ice Age (1300-1800) on the dynamics of woody species in elephant-impacted savannas has probably been seriously underestimated. Climate was considerably cooler and drier in the summer-rainfall region of southern Africa during this period. Long-lived species which currently have mature populations (e.g. *Adansonia digitata*, *Combretum imberbe*, *Sclerocarya birrea*, *Xanthocercis zambesiaca*, *Sesamothamnus lugardii*, *Acacia erioloba*) may not have had significant recruitment events during most of this period..
- Punctuated recruitment patterns of woody species may also arise as a consequence of relaxation of browsing pressure, but such examples are expected to be uncommon because they require the constellation of a special set of conditions that would not be commonly met.
- Fire is a key regulatory agent of woody recruitment in savannas.

In summary: Population decline toward extirpation resulting from elephant use is expected to occur under the following conditions:

- elevated adult mortality resulting from pollarding, uprooting or ringbarking by elephant;
- the species lacks an adequate coppicing response, hence mortality rather than regrowth occurs;
- recruitment is inadequate to compensate for elevated mortality.

Local extirpation in relation to reserve or ecosystem characteristics

- It is assumed that elephant once co-existed with plant diversity. What changes have occurred such that local extirpation of certain species has become likely. This section develops a set of predictions about the environmental conditions and characteristics of a reserve under which selected, potentially vulnerable species might become locally extirpated.
- *Probability of encounter.* An increase in elephant-related mortality of trees requires that elephant encounter the trees, the probability of which depends on the elephant population and the environment. Increasing elephant density will obviously increase the probability of encounter, but the nature of this relationship at a specific location in the landscape will

depend further on environmental factors influencing elephant local density. The availability of water is an obvious influence.

- Risk of extirpation is greatest in reserves lacking spatial refugia from elephant utilisation. An inaccessible refuge would ensure persistence of a woody species but most woody species occurring on areas accessible to elephant are, however, absent from rugged terrain.
- Vulnerability of a woody species to extirpation by elephant depends on its distribution in relation to water. The foraging range of elephant is limited to approximately 15 km from water. Whereas individuals of a woody species occurring beyond this distance are secure against elephant impact, the probability of encounter between a tree within foraging range and an elephant should decrease with distance because of energetic constraints on foraging distance. The further the distances between watering points, the more secure a proportion of a woody species should be against elephant impact.
- Reserves in which there are no areas greater than 15 km from water would not have a refuge from elephant utilisation.
- *Grassland Degradation.* Elephant are preferentially grazers, their seasonal switch to browse occurring when the quantity and quality of appropriate grazing becomes depleted. Degradation by sustained, severe grazing has been most pronounced for semiarid environments, often to the extent that the perennial grass component has been eliminated. In such environments, elephant have a minimal grazing resource to consume during summer, and essentially subsist year-round on woody vegetation. A consequent prediction therefore is that elephants will have to concentrate year-long on woody material more in semi-arid than in mesic habitats. A compounding influence is that semi-arid regions are prone to a greater frequency of droughts of greater duration than mesic areas, during which grass production is reduced. Browse production is more stable but leaf fall occurs earlier. Drought years are therefore expected to be characterized by increased elephant utilization of the woody component commencing during the growing season, and an increase of debarking and uprooting earlier in the season. The prediction that elephant *per se* (i.e. independently of fire) have a greater impact in semi-arid than in mesic systems is consistent with available insight.
- *Elimination of predation.* Elephants have only two effective predators, humans and lions. We contend that predation by these two agents, individually or collectively, was sufficient to inhibit, possibly even regulate, elephant population growth in pre-colonial Africa. The absence today of either of these predators from many systems containing elephant has allowed elephant populations to increase to problematical levels. Mostly young calves are predated by lion, which appear to be particularly vulnerable when forced to undertake extensive movements during periods of nutritional stress. Continuing predation of young animals is expected to affect the population growth of a species with a long inter-calving period and low reproductive output.
- Elephants have been hunted by humans for at least 4000 years. Trade in ivory has underpinned many trading activities both within Africa and between Africa and neighbouring continents. These trade linkages ensured substantial elephant offtake throughout most of Africa since well before European colonialism.
- Hunting for ivory would have concentrated on large bulls, which exert a disproportionately greater impact on woody vegetation. Thus even if the total number of elephant removed was small, it would have alleviated considerably impact on woody vegetation.

- *Reversal of changes during elephant absence.* Elephant have been absent for well over a century in most areas in southern Africa that have had populations re-established, during which time substantial vegetation change has occurred owing to reduction of fire frequency, lack of elephant, and overgrazing. It is speculated that a number of species characteristic of rocky refuges (e.g *Kirkia acuminata*, *Sterculia rogersii*) have established outside of their refuges during this time. Current elephant impact on such species simply signifies a reversal of vegetation structure to times when elephant were present.

Elephant carrying capacity

Recommendations for elephant carrying capacity have been founded upon maintaining a sufficient food resource for the herbivore. The extirpation of some woody species by elephant is unlikely to have a material effect on the amount of available food although diet breadth would be reduced. The issue of maintaining plant diversity therefore relates to the density of elephant appropriate for ensuring the persistence of a plant species within a particular system configuration. This elephant density would be considerably less than that defined for maintaining a food resource for elephant. Defining a carrying capacity for elephant based on maintaining a sufficient food resource would, in fact, heighten the likelihood of extirpation of vulnerable woody species.

Conclusion

The species that would be most vulnerable to extirpation would exist under the following circumstances: (a) degraded semi-arid savanna in which suitable grass is infrequently available, hence woody species constitute the mainstay of the diet; (b) the species does not occur in inaccessible refuges; (c) distance from water is not a foraging constraint for elephant; (d) highly selected species; (e) the species is frequently subjected to pollarding or complete ringbarking; (f) the species has little or no resprouting ability so that mortality usually results from pollarding or ringbarking; (g) the species recruits infrequently and usually in small numbers; and (h) the species grows slowly so that adults are not easily recruited.

THE ROLE OF ELEPHANT IN CREATING DIVERSITY IN VEGETATION STRUCTURE, FUNCTION AND COMPOSITION, AND THE CONSEQUENCES FOR BIODIVERSITY

LINDSEY GILLSON

A key question for elephant management is whether the current impact of elephants on vegetation is eroding ecosystem resilience and thereby threatening biodiversity. A historical perspective is essential to addressing this question, and ideally we would be able to compare changes in past elephant population densities and vegetation structure over long periods of time (say the last 500 years) in order to determine whether current elephant population density and vegetation structure is within the normal range of variability for the Kruger ecosystem. At present, however, there are very few data describing changes in vegetation and elephant population density over long time periods, and research opportunities exist to explore the relationship between long-term variability in vegetation and elephant abundance. For example, it has been suggested that elephants were historically of low density in the Kruger area, and that the current population of ~ 9000 is therefore too high to be sustained by the present vegetation cover (Whyte et al 2003). An alternative hypothesis is that savanna vegetation and elephant populations have varied over time, and that today's population increase represents a return to pre-ivory trade abundance. Comparison of palaeoecological, palaeoclimatological and historical data might provide possibilities for testing these two alternative hypotheses. The areas of uncertainty associated with the proposed research are:

- 1) The sources of possible historical data have not yet been fully investigated, though preliminary work suggests good potential (Beinart, Pers. Comm.)
- 2) The palaeoecological data now emerging from the Kruger National Park mainly show small scale changes in vegetation structure, and probably reflect the effects of localised disturbances rather than larger scale trends in elephant abundance (Gillson, in prep)
- 3) Correlation does not imply causality: a coincidence of change in elephant abundance and vegetation structure may be related to other factors e.g. climatic change. Thus it is essential that the results of the proposed study are embedded in the overall framework, which represents the interplay between numerous biotic and abiotic factors, including climate, CO₂ concentration, herbivory (elephants and other herbivores), human activity, fire, other disturbance, topography at different spatial and temporal scales (Coughenar and Ellis, 1993; Gillson 2004; Rogers 2003).

Key Publications

- COUGHENOUR, M.B. & J.E. ELLIS (1993) Landscape and climatic control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. *Journal of Biogeography* 20: 383-398
- GILLSON, L (2004) Evidence of Hierarchical Patch Dynamics in an East African Savanna? *Landscape Ecology* 19: 883 -894
- ROGERS, K.H. (2003) Adopting a Heterogeneity Paradigm: Implications for Management of Protected Savannas. In DU TOIT, J.T., K.H. ROGERS & H.C. BIGGS (eds) *The Kruger Experience. Ecology and Management of Savanna Heterogeneity*. Island Press, Washington. pp 41-58
- WHYTE, I.J., R. VAN AARDE, PIMM, S.L. (2003) Kruger's Elephant Population: Its size and Consequences for Ecosystem Heterogeneity. In: DU TOIT, J.T., K.H. ROGERS & H.C. BIGGS (eds) *The Kruger Experience. Ecology and Management of Savanna Heterogeneity*. Island Press, Washington. pp 332-348

MODELLING ELEPHANT EFFECTS ON SEMI-ARID SAVANNAS.

PETER BAXTER AND WAYNE GETZ.

Introduction

High densities of elephants in African savannas have been blamed for shifts in vegetation community composition, with reductions in populations of rare, vulnerable and/or palatable trees, with implications for possible reductions in biodiversity. Models of elephant effects on savannas, however, have tended to over-simplify the vegetation components and to ignore environmental variability.

Methods

We developed a grid-based model of elephant-savanna dynamics, which differs from previous elephant-vegetation models by accounting for woody plant demographics, tree-grass interactions, stochastic environmental variables (fire and rainfall) and spatial contagion of fire and tree recruitment. The model projects changes in height structure and spatial pattern of trees over periods of centuries. The first implementation of the model is based on a long-lived, slow-growing tree species; we further adapted the model by including a second, more “r-selected” tree species to investigate the effects of elephant impacts on species composition. We investigated the effects of introducing an elephant population on long- and short-term trajectories of the plant community.

Results and Discussion

The vegetation component of the model produced long-term tree-grass coexistence and realistic fire frequencies. The tree-grass balance of the model was more sensitive to changes in rainfall conditions and tree growth rates while less sensitive to fire regime. Introducing elephants into the model had the expected effect of reducing tree cover, although at a fixed elephant density of 1.0 km^{-2} , woody plants still persisted for over a century. Rates of tree decline were in broad agreement with those reported in the literature and the vertical structure became less adult tree dominated at higher elephant densities, reflecting a shift towards a bushland structure within the increasingly grass-dominated community. We tested the effect of plant responses to elephant impact: for the single-species model, faster growth was a more successful strategy than elephant-enhanced germination or adult resilience to impact. The addition of the second, faster-growing, tree species to the model enabled both species to survive greater elephant densities. As elephant stocking densities were increased, the resultant savanna community changed from tree dominance to grassland while the tree community shifts towards the more “r-selected” species. Spatial heterogeneity of the woody plant component increases with elephant density and time. For the two-species model, resilience to impact (reduced mortality following use by elephants) was the more successful strategy and may act synergistically between tree species, with regeneration providing increased food supply while slowing the transition to grassland. Fire suppression also mitigated the effects of elephant damage.

Management implications

In the face of prolonged high elephant densities, the modeling results raise concerns about slow-growing trees, particularly those species that are preferentially used by elephants, and those with less resilient strategies to mitigate elephant damage at the individual or population level. Fire suppression alleviated the elephant effects even at modeled densities of 1 km^{-2} and therefore has management potential.

Where does this lie on the conjecture-hypothesis-fact spectrum?

Due to paucity of available data the model is not site-specific but has been parameterized using empirical sources from a variety of locations (mainly southern African). Elephant use of adult trees was parameterized from bull elephant data and may therefore over-estimate the magnitude of impact overall. Elephant population dynamics are not coupled to the model (this has previously been done but for simplified models with limited applicability). This emphasizes the role of models as exploratory rather than predictive tools.

Biodiversity consequences

We conclude that while elephants may cause woodland to decline, they can also enhance biodiversity at lower densities, and increase spatial heterogeneity.

Future research

As the models exhibit pronounced sensitivity to tree growth rates, they highlight the need for detailed height-related woody plant data in particular, especially for addressing changes in structural diversity.

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VEGETATION-ELEPHANT INTERACTIONS FROM AN EVOLUTIONARY PERSPECTIVE

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Summary

Elephant damage to trees in Kruger National Park has been well documented and for some species in some localities it is verging on local extinction and therefore has high thresholds of concern. However, what is less well known is why elephants damage trees and how they choose trees for targeting. In many cases elephant damage appears to be excessive, counter-productive and not a necessary product of feeding. Elephants do not always feed on trees they push-over, nor do they need to push-over trees to feed on them. Similarly, it is not obvious that they feed on all the bark that they strip. To properly manage elephants it is possible that further understanding is needed of the proximate and ultimate determinants of elephant behaviour in relation to the damage of trees and woodlands.

In terms of ultimate explanations at least three possibilities exist. Firstly, is the ecosystem engineering or farming hypothesis. Elephants are predominantly grazers and it is possible that their anti-tree behaviour has evolved for the conversion of woodlands to grasslands. It is not clear how the anti-tree gene would spread or rather, how the cheaters would be disadvantaged. Secondly, is the delinquent behaviour hypothesis. In this instance damage to trees is not directly selected, it may merely be aggressive behaviour following forms of stress applied by humans (notably culling, but also translocations and disrupting hierarchies). Thirdly, tree damage may be due to socio-sexual behaviour. For example, it appears to mainly be due to males and therefore it may have little to do with feeding.

In terms of proximate explanations much remains to be researched concerning how elephants select trees based on the tree size, local tree density, species composition and local environment. Species attributes such as bark thickness, toxicity, wood density and rooting depth may either explain elephant choice or elephant impact. Possibly plants have evolved defences against elephants such the knobs on *Acacia nigrescens* and an analysis of the biogeography of this trait would be interesting. Is this species prone to elephant damage because it has shallow roots and are knobs better developed in areas historically more likely to be frequented by elephants?

Research of diverse kinds is needed to understand which hypothesis best explains why elephants damage trees. Results from this can then be fed back into management. For example, if tree damage is associated with juvenile males in musth then an implication would be to maintain family hierarchies. If elephants preferentially target trees in open woodland, including toxic or non-fodder tree species then this may support the farming hypothesis and suggest that a long-term view of woodland succession is needed. Research can combine both experimental manipulations as well as observations. For example, the behavioural response of elephants to various experimental trees (e.g. poles) and the sound of trees falling can be noted in terms of response versus gender, size and group size. Finally, elephants may also be involved in other mutualisms with plants, for example seed-dispersal, and this also needs to be documented and considered.

SUMMARY AND CONCLUSIONS

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It appears from all the contributions received that there is general consensus on the dynamic nature of vegetation. Most people would agree that ecosystems are constantly changing, albeit within certain limits, and therefore implies that the vegetation is also subject to continuous change. Perceived changes, especially those not based on any scientific evidence, are often subjective and anecdotal, sometimes overestimating and sometimes underestimating such changes. The dominant agents of vegetation change in Kruger are fire and large herbivores. Both interact strongly with rainfall variability, particularly the occurrence of prolonged droughts. The outcomes of fire and herbivory are altered by management practices, such as the burning regimes applied and the provision of water where it was previously unavailable.

Trees have shown elevated adult mortality as a result of elephant utilization. In the Sabi Sand, habitat manipulation to combat bush encroachment has a negative impact on biodiversity. This is exacerbated by elephant impacts, switching to browse due to drought effect on herbaceous layer. All height classes showed an increase in impacts, although taller trees experienced the most impact. Elephants negatively affected the riparian vegetation along the Limpopo River. Trees are declining in numbers and seedlings are completely absent, especially certain species. Due to restriction of elephants to smaller areas, ie hunting pressure, drought and increased development in Botswana, they are forced to migrate to South Africa. The impact of elephants on the vegetation in the KNP has shown, so far, that only certain species are targeted. This is a clear indication of elephants' selective browsing behaviour, supposedly related to palatability and nutrient status of specific plant species. Since these species contribute largely to the tall tree component, even characterizing certain landscapes, losses in the numbers of these trees may result in structural homogenization at landscape scale. These and numerous other studies indicate the varying degrees of impacts elephants have on the ecosystem.

It is well documented that elephants, at various densities, will affect the landscape at different spatial and temporal scales. There are basically two groups that differ in their view to interpreting elephant-vegetation interactions. The first group recognizes these changes as an integral part of ecosystem functions and therefore sees no immediate need to address the problem. This group acknowledges the dynamic nature of vegetation and elephants and compares it to predator-prey cycles. This allows for varying degrees of changes in the vegetation at different spatial scales. This also potentially allows local extinction of plants in smaller areas, while similar populations still exist elsewhere (source/sink scenario). The emphasis is to rather focus on biodiversity at a regional scale, while allowing for small-scale changes in the landscape. The precautionary principle can be invoked to motivate for culling in specific areas.

The second group views changes to the landscape as undesirable, implying that ecosystems should be kept in a fixed state. Any changes need to be strictly controlled to maintain the system in a stable state. This can be achieved by an intensive management programme responding to slight changes in the vegetation and would necessarily involve controlling elephant numbers.

So far, few researchers have attempted to incorporate the long-term scale in their studies. This is primarily a result of a lack of information on the state of ecosystems of stone and iron-age periods. There is some evidence that suggests that elephants never occurred at high densities due to hunting pressure by native people. This view emphasizes the role native people played in shaping the environment through hunting and using fire, which impacted on fauna and flora. Thus the landscapes and ecosystems visible today have already been altered by the interventions of early man, which means that there is no "undisturbed natural harmony and equilibrium". Palaeoecological studies can provide some answers to this question, though it seems of limited

spatial scale only. Research indicates that local changes in vegetation structure are due to localized disturbances rather than large-scale trends in elephants. Apart from elephants acting as agents of change, there are also various other factors which need to be taken into consideration, such as climate change (increased temperature and CO₂ levels and decrease in rainfall), other herbivores, fire and human activity.

While it is widely accepted that some types of vegetation are more sensitive to elephant impacts, the resultant loss of vegetation structure and ultimately species extinction are not acceptable in terms of the SANParks biodiversity mission. In the Kruger Park none of the specific TPC's have been reached or exceeded. The removal or reduction of elephant numbers will form part of a large-scale experiment with high and low-impact zones where increases and reductions can be effected.

To guide management decisions regarding elephant-vegetation interactions the following are apparent:

- Lacking long-term window of observation to see what precipitated the current vegetation state.
- The desired state of vegetation needs to be determined by management, together with the level of flux/ change that will be tolerated in the system.
- A detailed synthesis of current vegetation information is required to provide support for selecting the desired state of vegetation. Factors influencing tree population dynamics and regeneration need to be integrated into the decision-support system.
- The role or combination of biotic and abiotic factors needs careful consideration in the context of ecosystem function and interaction with elephant impacts.
- Data generated from the Veld Condition Assessments needs to be analysed and used to predict potential vegetation changes over time.
- Exclusion plots will provide valuable information in evaluating the effects of fire, herbivores and climate on vegetation and should be an integral part of the monitoring system.
- Specific areas where rare species are potentially under threat need to be identified and safeguarded.
- While managers feel a sense of urgency to deal with the “problem” immediately, an informed decision will be more valuable once all information has been integrated and all possible outcome scenarios have been investigated with data/ model evaluation.

Trying to summarize all the contributions is not an altogether easy task. It shows that ecosystem dynamics are much more complex than initially assumed. Multiple factors play a role to varying degrees, depending on spatial and temporal scales. The challenge is not to unravel these complex systems by excluding certain environmental parameters, but to understand them in their entirety. To achieve this goal, a multidisciplinary approach similar to the KNP Rivers Research Programme is required. Excluding certain factors from an experiment automatically changes the dimension of such an approach. This is why the proposed elephant management plan with its high and low-impact zones provides the ideal opportunity to investigate and understand the dynamics of the larger system which is the KNP. It will be the collective responsibility of Kruger scientists and research partners to use this opportunity and explore all different avenues in order to create a clearer picture of elephant-vegetation interactions in the broader ecosystem context.