# An autecological study of the Marula (*Sclerocarya birrea*) in the Kruger National Park with specific reference to the relative impact from elephants and fire.

by

Olga Sanet Jacobs

Submitted in partial fulfillment of the requirements for the degree of

Magister Scientiae (Wildlife Management)

in the

Centre for Wildlife Management

Faculty of Biological, Agricultural and Information Sciences

University of Pretoria

Pretoria

Supervisor: Prof. W. van Hoven

Co-supervisor: Prof. G.J. Bredenkamp

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**Dedicated to my mother**

*"It's funny how those once so close and now gone, still so effect our lives....."*

# ABSTRACT

The South African National Parks expressed the need to implement autecological studies on specific rare indicator plant species to determine habitat requirements and sensitivity to disturbances. Previous vegetation studies in the Kruger National Park have shown a dramatic decline in the density of large trees in four major vegetation units of the Park. *Sclerocarya birrea* subsp. *caffra* (marula), one of the preferred tree species of elephant (*Loxodonta africana*), is considered as one of the more sensitive tree species in the Kruger National Park. The current damaged condition and reduction of mature marula trees in the Kruger National Park gave rise to a study on the marula population. There is a strong possibility that the problem is complex - elephants are probably killing the large marula trees by debarking them or pushing them over, while fire is preventing young trees from becoming established. The severe impact that elephants have on marula populations has been documented in private protected areas in the South African Lowveld, and the inclusion of the effects and interaction of fire in this study is the general recognition that elephants and fire can have a highly significant impact on vegetation structure. This study, therefore, focused on the marula population structure, with specific reference to the impact of elephants and fire in four major landscapes of the Kruger National Park.

Results of this study indicated that regeneration has been taking place uniformly throughout the landscapes, but that a combination of factors is preventing successful recruitment into the upper canopy. It is further indicated that diversity of vegetation plays an important role in determining herbivory pressure, and consequently influencing the marula population structure. The marula population in the *Colophospermum mopane* shrubveld has become virtually extinct, while the marula populations throughout the rest of the landscapes does not appear to be in a sustainable condition. More than half of the population surveyed suffered predominantly damage due to elephant activity in the form of bark stripping and felling, and elephants appear to play a role in changing the structure of the adult marula tree. The results also indicated that the lower canopy structure (individuals <2 m) was greatly affected by fire, whereas density was unaffected. The lower canopy generally responded to the interaction between frequency and season of burn, and not to the main effects of season or frequency.

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- The impact of the African elephant on marula (Sclerocarya birrea subsp. caffra) trees in the Kruger National Park

*African Journal of Range & Forage Science (In press):*

- The effect of different fire treatments on the population structure and density of the marula (*Sclerocarya birrea* subsp. *caffra*) in the Kruger National Park

**"Instructions to authors" followed throughout the thesis**

*Manuscript:* 1 mm margin on all sides of the sheet and in 1.5 line spacing. All pages are numbered sequentially.

*Title:* Brief and sufficiently informative.

*Abstract:* Concise, informative and not exceeding 150 words.

*Additional index words:* Up to five additional index words which are not included in the title, listed in alphabetical order.

*Introduction:* Outlines the problem in general and clearly state the study objectives.

*Intermediate section:* Study Area, Methods (Data collection, Data Analysis), Results, Discussion, Acknowledgement, References.

*References:* If the author's name forms part of a sentence, only the year of publication is enclosed in parentheses. If work by two authors is cited, both names are provided and separated by an ampersand. If work by more than two authors are cited for the first time, all the names are provided. Thereafter, only the first author's name is listed followed by the abbreviation *et al.*, a space, and the year of publication. References to several works, each by a different author, at a given point in the text, are separated by semi-colons and enclosed in a single pair of parentheses, and arranged chronologically, then

alphabetically. Only publications to which reference has been made in the text is listed alphabetically according to authors (upper case) and chronologically under each author, with the year of publication. Journal titles are abbreviated italicised.

*Section headings:* Headings are prepared as follows: major headings are in lower case, centered and bolded; second-order headings are in lower case, left justified and bolded; third-order headings are in lower case, left justified and italicised.

# INTRODUCTION

**Project motivation**

Elephant-induced damage to habitats seems to increase under conditions where elephant movements are restricted by neighbouring human settlements (Ben-Shahar 1993). Human modifications of the environment can intensify use of particular areas by disrupting traditional elephant pathways and prevent elephants from making large-scale movements in response to resource supply (Gadd 1997). In some conservation areas, elephant numbers increase, woody vegetation declines, and pressure mounts for controlling elephant numbers. Such a phenomenon has been termed the 'elephant problem' (Barnes 1983). Increasing densities of elephants are often blamed for decreasing woodlands but the exact dynamics of the relationship have evaded ecologists and managers for many years. A proper management policy regarding the control of elephant numbers requires information on the trends of the elephant population and, especially, their patterns of resource utilisation (Ben-Shahar 1993). Elephant control to promote the recovery of mature canopy woodland can be successful only if accompanied by effective fire protection (Pellew 1983).

That there has been a significant decline in the density of large trees in the Kruger National Park is confirmed by the visual appearance of the woody vegetation over much of the Park (Viljoen 1988). Viljoen (1988) conducted a preliminary survey on changes in the density of large trees in the *Sclerocarya birrea/Acacia nigrescens* savanna landscape of the Kruger National Park by using aerial photographs. The results showed that during the period 1944 to 1981 (37 years) the number of large trees decreased by 93.4% in the Satara area. A similar trend, but not as marked decline, was noted in the Lower Sabie area where during the period 1940 to 1977 (37 years) the large trees decreased by 49.6%. In both cases the major decline in the tree density occurred after 1965. Trollope, Trollope, Biggs, Pienaar & Potgieter (1998) found no significant changes in the density of large trees between 1940 vs. 1960 in areas with granitic soils, whereas a moderate decline in the vegetation occurred in the areas with basaltic soils on four of the major vegetation units in the Kruger National Park, i.e.

- **Landscape 5:** Mixed *Combretum/Terminalia sericea* woodland (Gertenbach 1983)
- **Landscape 12:** *Colophospermum mopane/Acacia nigrescens* savanna (Gertenbach 1983)

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- **Landscape 17:** *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* savanna (Gertenbach 1983)

- **Landscape 23:** *Colophospermum mopane* shrubveld (Gertenbach 1983)

Conversely during the period 1960 to 1989 there was a dramatic decline in the density of large trees in all four above mentioned landscapes, particularly in landscape 17: *Sclerocarya birrea/Acacia nigrescens* savanna on basaltic clay soils (Trollope *et al.* 1998). Results of Trollope *et al.* (1998) suggest that the changes in the woody vegetation do not involve a decrease in species diversity but rather a change in the structural diversity where the woody vegetation is being transformed into a short woodland community with a low density of large trees. There are strong indications that the reason for the decline in the density of large trees in the Kruger National Park can be attributed to the interactions of elephants and fire on the woody vegetation. These two factors changed dramatically during the post-1960 period. Firstly, there was a dramatic increase in the elephant population in the Kruger National Park between 1960 and 1970 (Trollope *et al.* 1998) when the elephant population increased from approximately 1100 in 1960 to over 8500 in 1970 (Whyte & Wood 1995). Secondly, a controlled burning program was introduced in the Kruger National Park in 1954 and has been maintained in one form or another until 1995. Research by Trollope, Potgieter & Zimbatis (1995) concluded that the veld was being burnt too frequently in the Park during the past, based on the present condition of the grass sward. This partly forms the basis for the current *Laissez Faire* burning program introduced, in an attempt to reduce the previously high frequency of fire (Trollope *et al.* 1998).

Concern about the potential impact that elephants may have on the *Sclerocarya birrea* (marula) population of the Kruger National Park gave rise to an earlier research project (Coetzee, Engelbrecht, Joubert & Retief 1979). Although results of this research suggested that the impact at that time did not constitute a threat to the marula population, there is now a growing concern among certain research and field staff members of the Kruger National Park that the marula population is deteriorating (Whyte, Pers. comm.)[1]. There is a strong possibility that the problem is complex - elephants are probably killing the large marula trees by debarking them or pushing them over, while fire is preventing young trees from becoming established. Whyte, Biggs,

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[1] I.J. Whyte. Scientific Services Section, Kruger National Park, Private Bag x402, Skukuza.

Gaylard & Braack (1998) suggested that elephants should not be viewed in isolation, but as one component of a broader, integrated system. They recommended that the elephant impact should be managed in conjunction with other ecosystem processes such as fire, to promote biodiversity in general. Fire and large herbivores are among the principal factors determining the balance between herbaceous and woody plants in savanna ecosystems (Ruess & Halter 1990). In revision of the research objectives for the Kruger National Park, the development of an understanding of different fire regimes, and the effect of natural fire in combination with elephants and other herbivores on the biodiversity at multiple scales has been identified as a priority for nature conservation (Freitag & Biggs 1998).

**The Elephant Factor**

*Management of elephants in the Kruger National Park*

As the flagship of South Africa's national parks, the Kruger National Park can be seen as a model for the management of large herbivores. The largest elephant population in South Africa is found within the boundaries of this wildlife sanctuary (Smit 1997). By 1920 the Kruger National Park, which was proclaimed in 1889, was one of the last four remaining areas in South Africa with elephants (Hall-Martin 1992a). Since 1920 elephant numbers have increased in the Kruger National Park to such an extent that 13 000 surplus elephants have been culled since 1976 (Hall-Martin 1992b). The control of elephants by means of culling was implemented in the Kruger National Park to maintain the population at a density considered suitable to the area. The last management policy limited the population to 7500 elephants (Smuts 1975) after the carrying capacity of elephants in the Kruger National Park was estimated between 6000 and 8500 (Joubert 1986). During 1996 a moratorium was placed on the control of elephants by means of culling (Smit 1997), and since then the population has grown to 8896 in 1998; the largest population to be recorded in the Kruger National Park (Whyte 1998).

Reviewing the gross elephant population structure in the Kruger National Park since 1967, Whyte & Wood (1996) found the mean values for the population structure ratio as follows: bulls – 15.78% and cows – 84.22%. Whyte & Wood (1996) also found that the migration of elephant bulls is restricted to the arbitrary regional boundaries and no long-term trends were detected.

Elephant breeding clans monitored by Whyte (1993), did not move out of their home ranges into other landscapes, except under extreme drought conditions. Culling operations, however, did result in sporadic fluctuation of movement to areas outside the regional home ranges occupied by breeding herds (Whyte & Wood 1996).

Whyte *et al.* (1998) proposed a new policy for the management of the elephant population of the Kruger National Park. One of the principles on which the policy is based, is that elephant populations which are confined - but whose growth is not limited through management - are very likely to ultimately increase in number until negative impacts on the system's biodiversity results (Whyte *et al.* 1998). They suggested that the Kruger National Park be divided into six zones (Figure 1). These are two botanical reserves, two high elephant impact zones and two low elephant impact zones. The management of these zones will be driven by "Thresholds of Potential Concern" (TPC's). These TPC's are specified limits of ecological change which should not be exceeded (Whyte *et al.* 1998). The specified management for each zone will be followed until there are indications that one or more of the TPC's have been reached or exceeded. It is expected that the population of these zones will increase at around 7% per year. In the low elephant impact zones the population will be decreased until one or more of the TPC's have been reached or exceeded. This decrease will be achieved through the reduction of the populations within these zones by 7% per year. In the Botanical Reserves, medium densities will be maintained (Whyte *et al.* 1998).

*Previous studies of Elephant Impact on Vegetation*

Of the megaherbivores, the elephant is singular in its ability to profoundly modify habitats. Where this occurs within protected areas the change may be such as to reduce biodiversity beyond the threshold of recovery in the long term. There consequently appears to be little alternative but to limit elephant numbers to commensurate with specified conservation goals (Taylor & Cumming 1993). A population limit was imposed to ensure the perpetuation of viable populations of all large mammal species in the Kruger National Park and to minimise excessive elephant damage to vegetation (Coetzee *et al.* 1979). Furthermore, vegetation structure favourable to elephant and other animals is maintained by limiting elephant impact on habitat (Coetzee *et al.* 1979). Evidence from the Tsavo National Park, Amboseli National Park and the

Addo Elephant National Park showed that in confined systems, high elephant densities could result in the extirpation of certain plant and animal species (Smit 1997). Megaherbivore populations are slow to respond to environmental changes. Elephants are capable of switching to alternative food items, so tree loss is unlikely to have an immediate effect on elephant numbers (Gadd 1997). However, less competitive animal species are more sensitive to habitat change, and are protected by implementing measures to alleviate excessive elephant utilisation of available food and water (Gadd 1997).

Elephants can subsist in virtually any habitat that provides adequate quantities of food and water but optimum habitat includes both grass and browse as they are mixed feeders (Estes 1991). The diet of elephants consists of grass, forbs, bark, twigs, leaves and fruit. Browsing involves breaking off branches and uprooting shrubs and small trees. Some elephant bulls master the technique in pushing over large mature trees. The elephants' use of browse is related to grass availability and therefore the rate at which trees are depleted is strongly dependent upon any events that alter grass availability (Gadd 1997). It is estimated that an elephant's daily dry matter forage intake is equivalent to 4 to 6% of its body mass. Thus, a mature elephant bull weighing 2800 kg will require 42 kg of forage per day (Trollope *et al.* 1998). The proportion and kind of forage consumed by elephants vary according to the season and availability of food. Elephants tend to show preference for grasses and herbs during the rainy season and for woody plants in the dry season (Trollope *et al.* 1998). According to Buss (1961), grass comprises 88% of the elephant's diet in the dry season in Uganda. In Murchison Falls National Park (Uganda), Field (1971) found that although grass was the main constituent of the diet, the amount of browse eaten ranged from 8 to 45% of the total food intake. In the Tsavo National Park (Kenya), Napier Bax & Sheldrick (1963) found that herbaceous material forms the bulk of the elephant diet, even in normal dry seasons.

In Zimbabwe and South Africa, browse is more important in the dry season than in the wet season, with a rapid increase in the amount of grass eaten soon after the first rains (Anderson & Walker 1974). In a drought, however, damage to woody species reaches a peak as elephant pressure on the woody component increases due to poorer quality of the grass (Gadd 1997).
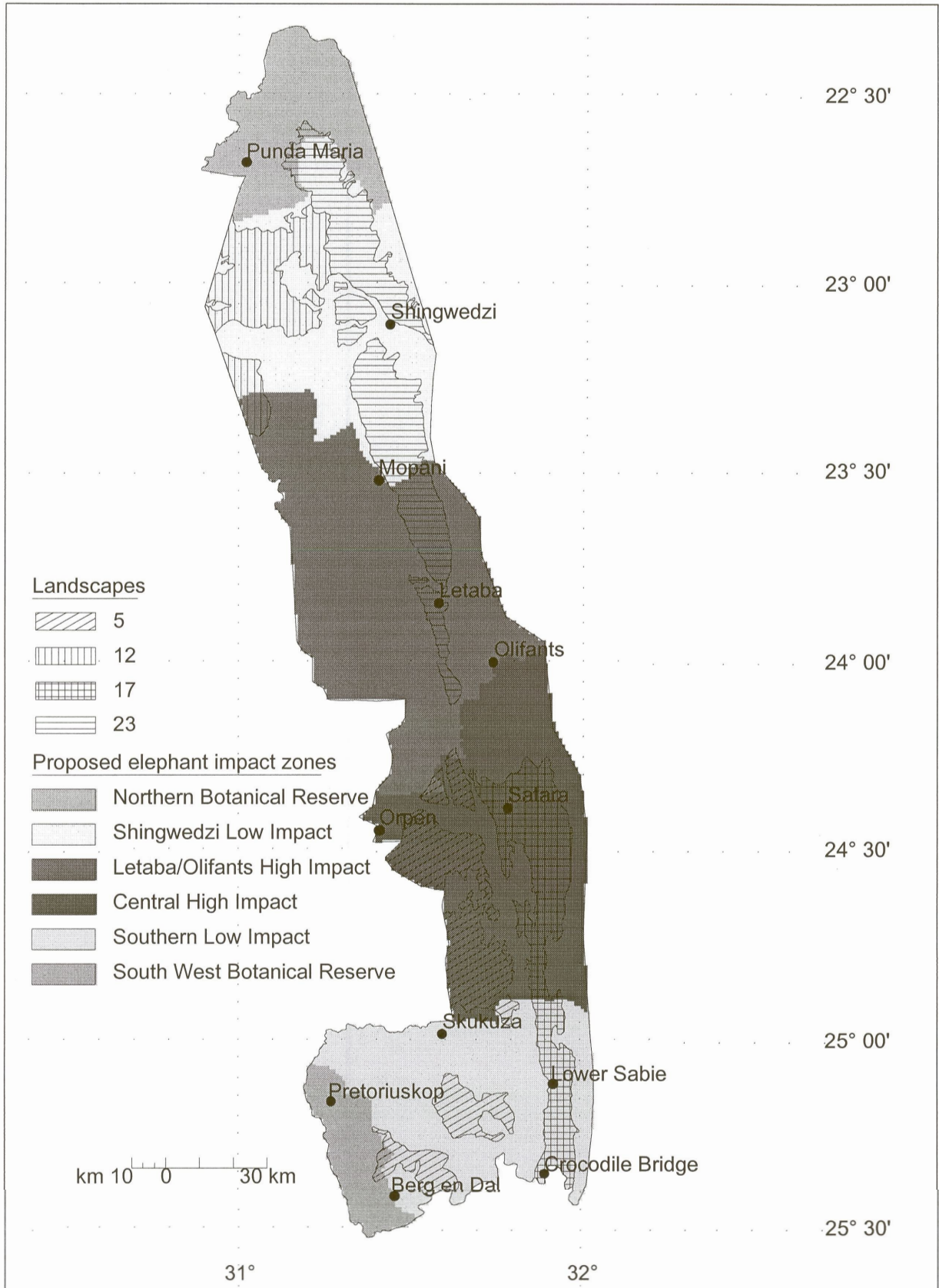
Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 1. The proposed elephant management zones in the Kruger National Park to be used to control the impact of the elephants on the system's biodiversity (Source: Whyte *et al.* 1998).

Generally the proportion of browse in the elephant diet is much higher than in East Africa, having been estimated between 74 and 86% (dry season figures) from stomach contents of elephants in the Chizarira and Mana Pools Game reserves (Anderson & Walker 1974). Van Wyk & Fairall (1969) estimated the proportion of browse to be 50% for elephants in the Kruger National Park, and stated that woody species were far more important in the diet of elephants living in the Kruger National Park than those living in the more open savanna areas of East Africa. Pienaar, Van Wyk & Fairall (1969) found that elephants in the Kruger National Park utilise herbaceous grasses and forbs mainly during the rainy season. During the dry winter months the elephants congregate along the rivers and permanent watering points where they consume reeds, grasses, forbs and the leaves, bark and twigs of riverine trees and shrubs (Trollope *et al.* 1998). Further away from water the elephants browse the dry leaves of preferred trees and shrubs. In areas where fires have occurred that minimized grazing opportunities, they push over and utilise trees that have escaped the fires and retained their leaves. Tree species that are particularly selected for by elephants are *Adansonia digitata* (baobab), marula, *Acacia nigrescens* (knobthorn), *Combretum imerbe* (leadwood) and *Pterocarpus angolensis* (kiaat) (Trollope *et al.* 1998).

Elephant impact on vegetation is known to be selective, though a wide variety of woody plants may be involved. Pellew (1983) found that elephants largely ignore trees <1 m, while Jachmann & Bell (1985) found that elephants feed mostly between the height of 2–3 m. Although elephants rather forage on smaller than larger stems, trees up to the height of 7 m were found to be highly susceptible to elephant damage (Jachmann & Bell 1985; Gadd 1997). The consequences of elephant impact on any particular species depends on the nature of the scars, the ability of the plant to recover, its demography and role in various plant communities and the interrelationships between the latter and other ecosystem components. Many factors, therefore, contribute in a complex manner to determine the effect of elephant impact on any particular plant species and/or plant community and the management of elephant numbers (Coetzee *et al.* 1979). Caughley (1976) found that elephant impact has been preventing recruitment of *Colophospermum mopane* (mopane) into taller size classes, but the impact have been found not to effect the regeneration thereof. Whyte & Wood (1996) found that 159 baobabs died between 1993 and 1996. Whyte, Nel, Steyn & Whyte (1996) expressed their concern over the decline in the baobab population

due to elephant utilisation. Van Wyk & Fairall (1969) reported severe utilisation of marula by elephants especially in the southern region of the Kruger National Park. Joubert (1982) noted severe debarking and uprooting of marula trees by elephant bulls along tourist roads and Owen-Smith (1988) noted that the extent of elephant bark damage and felling of marula trees in the Kruger National Park was a source of concern to park managers.

In a vegetation impact study on elephants in protected areas adjacent to the Kruger National Park, Gadd (1997) reported that a minor part of the elephants' diet (0.14% of all feeding events) comprised woody vegetation with stems smaller than 2 cm in diameter. Seedlings were eaten in extremely small amounts by comparison to their overall availability. Lewis (1987) suggested that the mortality of marula seedlings in the Luangwa Valley should be attributed to browsers other than elephants, in particular impala (*Aepyceros melampus*). Walker, Stone, Henderson & Vernede (1986) found that marula seedlings in particular are highly palatable and may be killed by herbivores when not protected by other vegetation. Whyte (Pers. comm.)[2] has not observed any marula seedlings being utilised by specific elephant bulls over a two-year period during his study on vegetation utilisation by elephants. Gadd (1997) found that 45% of the marula trees (with a stem diameter >10 cm) that were surveyed suffered elephant impact, mainly branch breakage. Gadd (1997) also concluded that marula trees are capable of surviving any branch breakage if less than 75% of the tree is damaged. Branch breakage did not have a significant impact on the marula population surveyed, as most branch breakage was less than 50% to individual trees. Main stem breakage and bark stripping was the major cause for the 2% mortality of the marula population observed (Gadd 1997).

Opposed to the destructive impact that elephants may have on marula trees, Lewis (1987) concluded that elephants may have a positive impact on the marula population in the Luangwa Valley as they play a role in both tree recruitment and the dispersion of marula seeds. Results of this study showed that seeds that passed through an elephant's digestive tract had a much higher germination rate during their first year than those that did not (Lewis 1987).

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[2] N. Whyte. 1999. Department of Zoology, University of Pretoria, Pretoria.

The feeding preference of elephants for certain species can cause a net decline of those species while permitting expansion of less palatable species (Laws 1970). Many studies have been done on elephant browsing on specific tree species (Thomson 1975; Okula & Sise 1986; Jachmann & Croes 199; Leuthold 1996; Whyte *et al.* 1996) out of concern that certain tree species will be lost due to overutilisation by elephants. Leuthold (1996) found that in the Tsavo National Park the original deciduous woodlands dominated by *Commiphora* spp. and *Acacia* spp. were being replaced over large areas by much more open wooded grassland. The major causes were thought to be (1) overutilisation of trees by elephants, which favored the establishment of a fairly continuous grass cover, and (2) fires that were nourished by the grass cover impeded the regrowth of woody vegetation (Leuthold 1996).

**The Fire Factor**

*Past and present burning policies of the Kruger National Park*

The inclusion of the effects and interaction of fire in this study is the general recognition that elephants and fire can have a highly significant impact on the species and structural diversity of tree and shrub vegetation in African savannas (Trollope *et al.* 1998). For a better understanding of the effects of fire on the vegetation of the Kruger National Park, Trollope *et al.* (1998) gave the following overview of the past and present burning policies as they pertain to the Park:

Indiscriminate burning was used between 1926 and 1954 to provide green grazing for wildlife. Since 1954 to 1975 a fixed triennial burning program was applied and the Park was divided into approximately 400 burning blocks generally ranging in size from 2500 to 5000 ha. The blocks were planned to be burnt every three years in spring after 50 mm rain had fallen. Major deficiencies in this burning program were identified. Many burns were scheduled but not carried out due to insufficient time; attempting only spring burns resulted in poor utilisation of grazing; and the frequent absence of rains after burning had deleterious effects on the recovery of the sward (Stocks, Van Wilgen, Trollope, McRae, Weirich & Potgieter 1993). During the application of this burning policy it became apparent that a fixed burning program was impractical to apply over the Park as a whole and did not constitute a natural fire regime. Accordingly in 1975 the program was adapted in the light of research results and field

experience to permit burning during late winter, before and after the spring rains, mid-summer and during autumn. This burning was done on a rotational basis in order to provide short, palatable grazing throughout the growing season (Stocks *et al.* 1993). The frequency of burning was also changed in arid savannas to permit both triennial and quadrennial burning in order to provide different types of grazing habitat for concentrated bulk grazers (Stocks *et al.* 1993; Trollope *et al.* 1998).

A further adaptation was made to the burning program in 1980 to allow for an apparent ten-year quasi rainfall cycle where a decade of below-average rainfall is usually followed by a decade of above average rainfall. The rate of grass fuel accumulation is higher during the wet cycles resulting in a greater frequency of lightning fires, the perceived natural ignition source of vegetation fires. Consequently a variable burning frequency based on rainfall and the level of accumulation of grass fuel was introduced. It was believed that such a burning program would simulate a more natural fire regime where variable climatic conditions are a major driving force. The season of burning was also adapted to simulate fires caused by lightning which are generally limited to occur during mid-summer and high rainfall cycles. The majority of the controlled burns were consequently scheduled before and after the spring rains with mid-summer burns also being applied during above rainfall conditions (Trollope *et al.* 1998).

Finally in 1990 a further innovation was introduced to simulate point ignitions of fires which occur in a natural fire regime where lightning is the major ignition source. This involved combining the 400 burning blocks into 88 burn units, which were further grouped into 23 management units. It was believed that by burning larger areas (up to 30 000 ha) the fire front ignited around the perimeter of the burn unit would fragment into separate fires during the extended duration of the burn. These fragmented fires would then spread through the burn unit as a mosaic of different types of fires in response to change in wind direction, air temperature and relative humidity. This change was made in response to ongoing research being conducted on fire behaviour in the Park where it was recognised that the procedure where the burning blocks were ignited around the perimeter was resulting in the rangeland being burnt mainly by intense headfires. This was concluded to be preventing the recruitment of large trees as a result of the intense fires. Continuous back burns prevented species like marula from developing into large

trees and, therefore, limiting the development of a parkland type of savanna in many areas. This procedure was followed until 1994 when a *Laissez Faire* burning policy was introduced, where only fires ignited by lightning were permitted to burn and all other ignition sources were controlled as far as possible (Trollope *et al.* 1998).

The two main causes of fires occurring in the Kruger National Park are man-induced controlled burns and unintentional fires that are caused by poachers, tourists, arsonists, accidents and lightning. The controlled burns are ignited around the perimeters of the burn blocks and are left to burn towards the centre which results in the formation of a well-developed smoke convection. This burn method is referred to as ringburning. Ringburning has the effect of increasing the intensity of the fire by drawing the fire fronts into the center of the block being burnt, therefore causing a maximum topkill of trees and shrubs (Trollope *et al.* 1998). Ringburning also leads to a disproportionately large area burning as a high-intensity headfire (an effect magnified by the fact that these fires are carried out during the day, and never at night) (Van Wilgen, Biggs & Potgieter 1998a). There is a significant difference between the intensity of controlled fires and wildfires. The latter occur as point ignitions which burn outwards towards the perimeter of the block as a mosaic of different types of fires ranging from intense headfires to less intense backfires and therefore possibly causing a lower topkill of trees and shrubs (Trollope *et al.*1998).

The Kruger National Park has a comprehensive set of fire records spanning over 5 decades and can be analysed spatially to provide information about the historic influence of fire on vegetation patterns and trends in the park. The fire records for different periods were recorded in the following three formats (Van Wilgen *et al.* 1998a):

(1)     Sketch maps of the distribution of fires for each year from 1941 to 1956, available from a previous analysis of rangers' diaries. These were digitised, and overlaid on the boundaries of existing fire blocks to establish the percentage of the block that was burnt in that year. These fires were recorded at a coarse scale (1:500 000), resulting in partially burnt blocks only having a rough estimate of the percentage burned.

(2)     The Board controlling the Park took a decision to institute prescribed burning in fixed blocks on a three-year cycle in 1957. Fire records of these blocks, giving the dates and causes of

fires, and in some cases, an estimate of the percentage of the block that burned, are available for the period 1957 to 1991.These records were extracted from the management files for each block.

(3)     As from 1992, all prescribed burns were stopped. Natural (lightning) fires were allowed to burn in line with a natural fire policy, although other fires did also occur. These fires were mapped and added to the database by allocating a date, percentage burned, and cause of each fire to the existing fire management blocks. Between 1957 and 1988, numerous changes and adjustments were made to the boundaries of the blocks. Van Wilgen, Biggs, Regan, Mare (1998b) re-allocated the fire records to the existing blocks, and estimated the mean fire return period throughout the Kruger National Park (Figure 2).

*The effect of fire on the vegetation of the Kruger National Park*

The effect of fire on vegetation depends upon the combined effects of the different components of the fire regime, being the type and intensity of fire and the season and frequency of burning (Bailey 1988; Trollope *et al.* 1998). Reviewing literature on the role of fire in savanna development, Trollope (1980) concluded that fire favours the development and maintenance of a predominantly grassland vegetation by destroying the juvenile trees and shrubs and preventing the progression of more mature plants to a taller fire-resistant stage. Generally herbaceous plants are favoured over woody plants because of the location of the perennating buds at or below ground level (Bailey 1988). Bailey (1995) further stated that the effect of fire on vegetation is contradictory depending on ecosystems and circumstances. Trollope & Potgieter (1985) recognised the need to obtain more information on the effect of fire behaviour and in particular fire intensity, on the flora of the Kruger National Park.

The Kruger National Park had different fire regimes for different periods in the Park's history, where protection against fire was followed by prescribed burning and then by a "natural" fire policy in 1994. Fires covering 16.79 million ha occurred between 1941 and 1996. The mind shift, away from rigid prescribed burning on a fixed dominantly triennial cycle has been in response to concerns after Trollope *et al.* (1995) concluded that a dominance of grass species characteristic of poorly managed pastures and overgrazing was a result of excessively frequent burning. Van Wilgen *et al.* (1998a) expressed concern over putative trends in woody vegetation
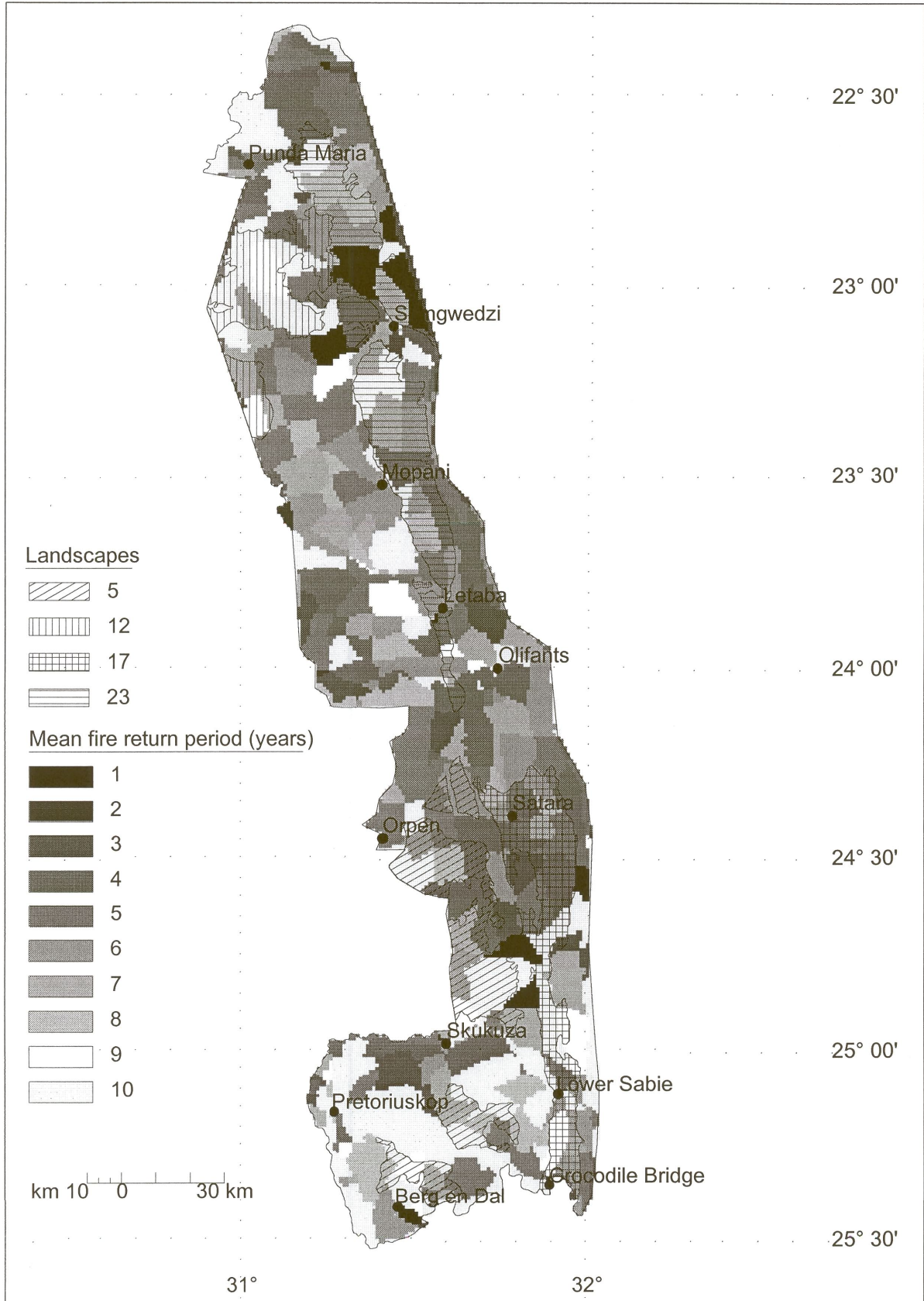
5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 2. Mean fire return periods in the Kruger National Park for the period 1958 to 1996 (Source: Van Wilgen *et al*. 1998b).

structure. It would appear from examining early aerial photographs that large areas have been homogenized, possibly due to the rigid application of a triennial burn policy. Tree densities have declined dramatically for some species, and this decline may be due to the "unnatural" fire regime in combination with other factors, such as browsing by ever-increasing numbers of elephants (Van Wilgen *et al*. 1998a).

In an experimental fire applied in arid savanna areas of the Kruger National Park, surface headfires caused higher topkill of stems and branches compared to backfires (Trollope *et al*. 1995). Trollope (1983) and Trollope *et al*. (1998) found a significant correlation between fire intensity and topkill. Trollope & Potgieter (1985) classified fires into categories according to fire intensity (Table 1). Fire intensity is a measure of energy released in fires, which varies with fuel moisture content, wind and slope conditions under which the fires burn. Fire type will also affect fire intensity. Fire types include headfires (fires burning with the wind or upslope), backfires (fires burning against the wind or downslope) as well as ground fires (fires burning in the organic layers of the soil), surface fires (fires in the lower vegetation strata) and crown fires (fires in the canopies of trees) (Trollope 1983). The most common types of fires in savanna areas as found in the Kruger National Park are surface fires that burn either as head or backfires. Trollope (1983) found that a hot fire of approximately 2500 $kJ.s^{-1}.m^{-1}$ was necessary to cause a significant topkill of bush to a height of 2 m. Results of this study (Trollope 1983) also indicated that the topkill of bush does not increase appreciably when fire intensities are greater than 2500 $kJ.s^{-1}.m^{-1}$. Shrubs and seedlings in the < 0.5 m height class however, suffered a significant topkill of stems and branches, irrespective of the fire intensity (Trollope 1983).

Research in the Kruger National Park showed that the bush became more resistant to fire as the height of the trees and shrubs increased (Figure 3) (Trollope *et al*. 1998). The topkill of bush being 1 m in height is as high as 84.6% opposed to a topkill of 16.3% for bush of 5 m. These results indicate that generally the woody vegetation of the Kruger National Park is not significantly affected by fire alone when the trees and shrubs are taller than 3 m. Woody vegetation of the Kruger National Park is not sensitive to the season of burn (Trollope *et al*. 1995), but the frequency of burning, however, has a significant effect on the physiognomy of tree and shrub communities in savanna areas (Trollope 1983).

Table 1.

Fire categories according to fire intensity (Trollope *et al.* 1995).

| Fire Intensity (kJ.s$^{-1}$.m$^{-1}$) | Description |
|---|---|
| <500 | Very cool fire |
| 501-1000 | Cool fire |
| 1001-2000 | Moderately hot fire |
| 2002-3000 | Hot fire |
| >3000 | Extremely hot fire |

The visual difference in woody phytomass between the experimental control plots that have been protected from fire for 42 years and the annual, biennial and triennial burning treatments show a dramatic decline in the woody phytomass with an increase in the frequency of burning. Trollope *et al.* (1998) found the main effect of fire on the woody vegetation in the Kruger National Park is to cause a topkill of stems and branches, forcing the plants to coppice from the collar region of the stem. Fire in the Kruger National Park seems to have an effect mainly on the structure of the woody vegetation and not on the species diversity (Enslin, Potgieter, Biggs & Biggs 2000).

Bush surveys conducted inside and outside three elephant exclosures in the Kruger National Park that had been subjected to controlled burning for extended periods of time, led to the following conclusions on the effect of fire and the interaction of elephants and fire on the vegetation of the Kruger National Park. (Trollope *et al.* 1998):

- Neither fire nor the interaction of elephants and fire have a significant effect on the overall density of bush

- The interaction of elephants and fire causes a significantly marked reduction in the phytomass of bush in areas with clay soils irrespective of rainfall

- Elephants are having a significant impact on taller trees (>3 m) outside the exclosures. In all cases there was a higher proportion of trees inside than outside the exclosures in the >3 m height class.

## Objectives

The most basic management objective of the Kruger National Park is to conserve all the species, which constitute the park's ecosystem, as well as the ecological processes that sustain these species. Implicit in this, is the fact that no single species should be allowed to threaten the existence of any other species of plant or animal. The Parks Board's policy on controlling elephant numbers as well as implementing a fire management plan rests on this objective of conservation (Hall-Martin 1992a). The current elephant population and fire regime in the Kruger National Park may both be seen as artifacts of man's interference in the system, and the loss of a species such as the marula tree from the ecosystem would clearly constitute a failure to achieve this objective.

**The main objectives of this study were therefore:**

I.  To determine the status and the population structure of the marula (*Sclerocarya birrea* (A. Rich.) Hochst. subp. *caffra* (Sond.) Kokwaro (Kokwaro & Gillet 1980)) in four major landscapes (two on granite and two on basalt) of the Kruger National Park.

II. To determine the impact of the African elephant (*Loxodonta africana*, Blumenbach) on marula (*Sclerocarya birrea* (A.Rich.) Hochst. subsp. *caffra* (Sond.) (Kokwaro) (Kokwaro & Gillet 1980)) trees in the Kruger National Park.

III. To determine the effect of different fire treatments on the population structure and density of the marula (*Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro (Kokwaro & Gillet 1980)) in the Kruger National Park.

**Hypotheses**

To achieve the objectives, the following hypothesis have been compiled:

1.  The population structure of the marula across the different landscapes and hence sub strata is not homogenous, but can be correlated to the elephant densities in the landscapes.

2.  The extent of elephant impact to the marula population is high, but not homogeneous across the different landscapes.

3. Different fire treatments have different effects on the population structure and density of the marula.

4. Fire influences the morphology of the marula, enhancing a multi-stemmed morphology.

5. Fire and herbivory is preventing the young marula individuals (<2 m) from developing into adult trees, while elephants are preventing the establishment of a mature marula structure.
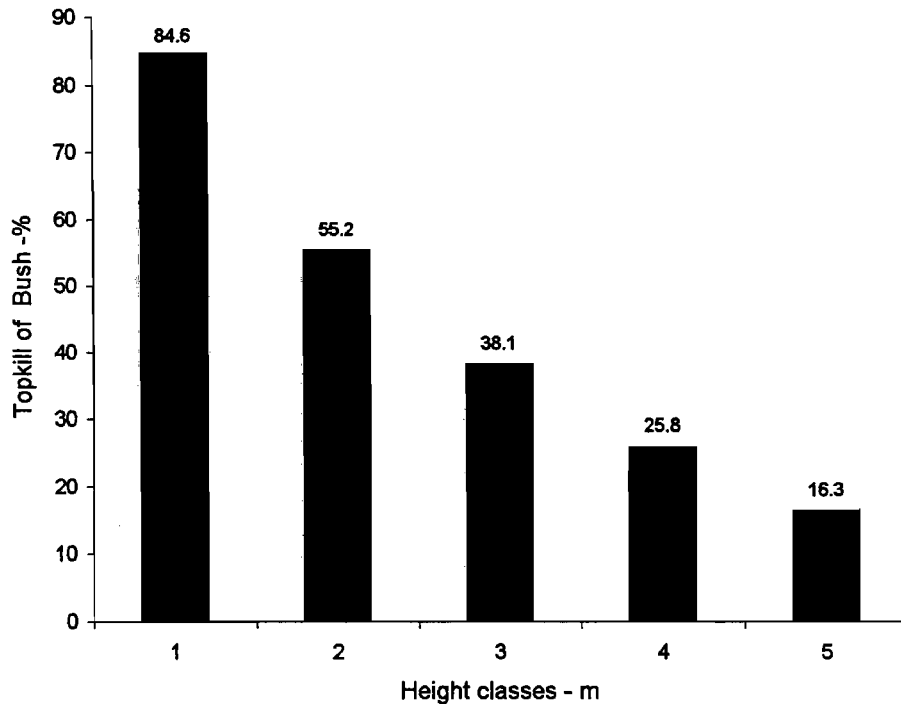


Figure 3. Effect of height on topkill of bush for different height classes subjected to a fire intensity of 3000 kJ. $s^{-1}.m^{-1}$ in the Kruger National Park (Trollope et al.1998).

**Assumptions**

To test the hypotheses, the following assumptions were made:

1. The population structure derived from an elephant exclosure represents the normal population structure for the marula in the rest of the Park should there have been no elephant impact.

2.   All uprooted marula trees and main stem breakage of trees with a circumference >10 cm is ascribed to elephant impact.

3.   Branch breakage does not impact on the marula population structure.

4.   Impact on marula seedlings is mainly ascribed to herbivores other than elephants.

5.   Fire does not have a significant impact on the structure of marula trees >2 m.

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# A DESCRIPTION OF THE STUDY AREA WITH REFERENCE TO THE HABITAT PREFERENCE OF THE MARULA TREE (*SCLEROCARYA BIRREA* (A.RICH.) HOCHST. SUBSP. *CAFFRA* (SOND.) KOKWARO (KOKWARA & GILLET 1980).

## Study Area

The Kruger National Park, which encompasses an area of 18 998 $km^2$ forms part of the Lowveld regions of Mpumalanga and the Northern Province, semi-arid regions of the southern temperate zone (Smuts 1975). The Kruger National Park occupies the area between 22°20' to 25°32' latitude south and 30°52' to 32°2' longitude east. The climate is subtropical with warm wet summers and mild winters seldom experiencing frost. In the Kruger National Park precipitation decreases from south to north, except for the area around Punda Maria which is situated at a higher altitude (Gertenbach 1980). Annual rainfall varies from ±750 mm in the south to ±350 mm in the north, but variations around the mean can be marked from year to year (Tyson & Dyer 1978). December, January and February are on average the wettest months, with July and August the driest (Gertenbach 1980). Figure 4 is a contour map that shows the rainfall pattern of the study area as described by the CCWR (Dent, Lynch & Shulze 1989). The pattern of rainfall over the past century has been characterised by extended wet and dry periods, in which rainfall has tended to be either higher or lower than the long-term mean for about 10 consecutive years (Van Wilgen, Biggs, Regan & Mare 1998b). On average the precipitation in wet and dry cycles in the Kruger National Park is 13% above and below normal (Gertenbach 1980). A variety of geological formations, soil types and climatic conditions support a variety of vegetation types varying from open savanna to dense woodland.

The flora of the Kruger National Park comprises approximately 1903 taxa, including over 400 trees and shrubs, and over 220 grasses. Broadly speaking, there are four dominant vegetation types in the Park. In the southwest, the low nutrient status of the soils results in a relatively low grazing pressure, and grass fuels accumulate during the growing season; rainfall is also higher, and as a result of these factors fires tend to be relatively frequent in these areas (Van Wilgen *et al.* 1998b). The area is well wooded, and important tree species include the red bushwillow (*Combretum apiculatum* subsp. *apiculatum*), knobthorn (*Acacia nigrescens*), tamboti

(*Spirostachys africana*) and marula (*Sclerocarya birrea* subsp. *caffra*). In the southeast, on basalt substrates, grasses are more palatable and tend to be heavily grazed. Important tree species include the knobthorn, leadwood (*Combretum imberbe*) and marula (Van Wilgen, Biggs & Potgieter 1998a). North of the Olifants River, the granite areas in the west are poorly grassed; mopane (*Colophospermum mopane*) and red bushwillow are dominant trees. Multi-stemmed mopane shrubs (1 to 2 m in height) dominate the northeastern areas on basalt (Van Wilgen *et al.* 1998a). The marula tree is recognised in both the southwestern and southeastern areas south of the Olifants River as an important tree species of the Kruger National Park.

Gertenbach (1983) identified 35 landscapes within the Kruger National Park, each with specific geomorphology, climate, soil and vegetation pattern. These landscapes were described as functional management units, and Gertenbach (1983) suggested that management in the Kruger National Park should be based on the zonation of the Park into these landscapes. Trollope, Trollope, Biggs, Pienaar & Potgieter (1998) investigated the changes of large trees with a canopy diameter greater than 5 m in Landscapes 5, 12, 17 and 23. Results of this study showed that a moderate decline in tree density occurred in Landscapes 5 and 12 whereas moderate to marked declines occurred in Landscapes 17 and 23.

It was therefore decided to adopt the same approach as Trollope *et al.* (1998) and restrict the study to the same landscapes of the Kruger National Park as described by Gertenbach (1983): **Landscape 5:** Mixed *Combretum/Terminalia sericea* woodland; **Landscape 12:** *Colophospermum mopane/Acacia nigrescens* savanna; Landscape 17: *Sclerocarya birrea/Acacia nigrescens* savanna; and **Landscape 23:** *Colophospermum mopane* shrubveld (Figure 5). Two exclosures, the Hlangwine exclosure and Roan enclosure (Figure 5), were used to study marula responses to fire, and the population structure of the marula in the absence of herbivory respectively. The experimental burn plot trial in the *Sclerocarya birrea/Acacia nigrescens* savanna was used to determine the effect of different fire treatments on the population structure and density of the marula trees.
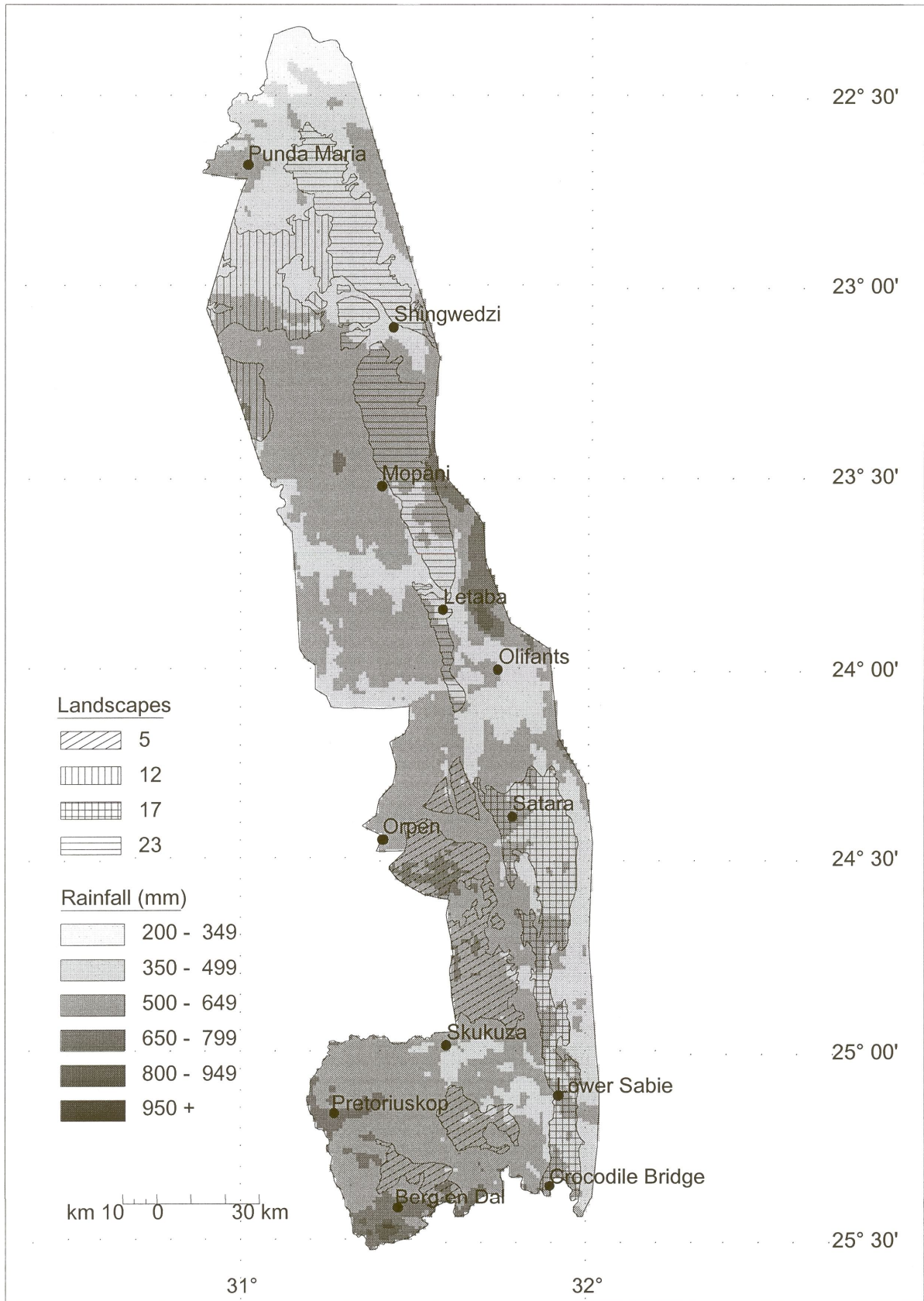
**Landscapes**

| | |
|---|---|
| ▨ | 5 |
| ▥ | 12 |
| ▦ | 17 |
| ▤ | 23 |

**Rainfall (mm)**

| | |
|---|---|
| | 200 - 349 |
| | 350 - 499 |
| | 500 - 649 |
| | 650 - 799 |
| | 800 - 949 |
| | 950 + |

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

Figure 4. A contour map of the average rainfall in the Kruger National Park as described by the CCWR (Source: Dent *et al.* 1989) with the four major landscapes used in this study.
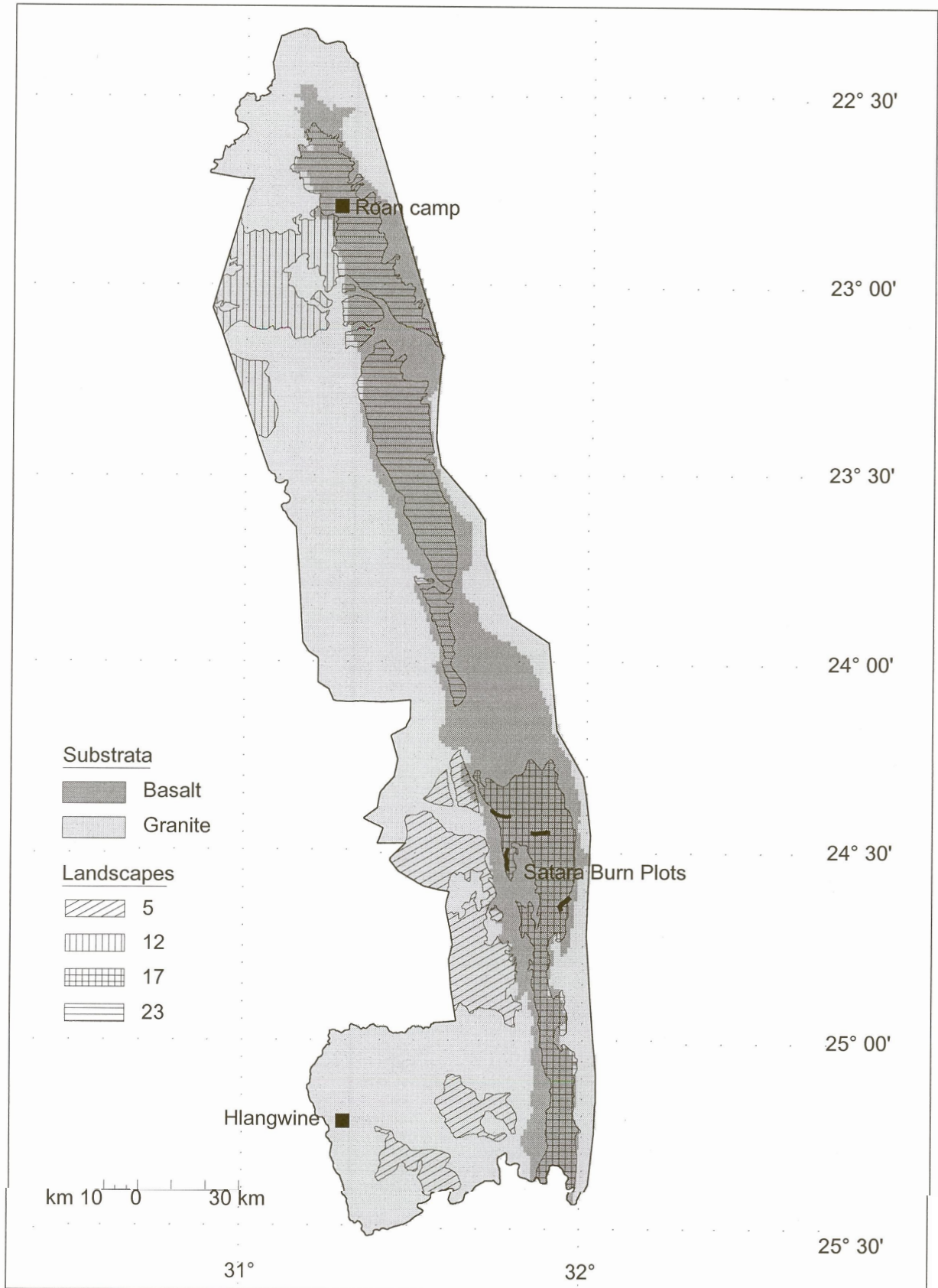
Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 5. The study area consisting of the four major landscapes of the Kruger National Park, Roan enclosure, Hlangwine exclosure and the Satara experimental burn trial.

Associations within these landscapes described by Gertenbach (1983) are (bold where *Sclerocarya birrea* subsp. *caffra* is a dominant species):

**Landscape 5:** Mixed *Combretum/Terminalia sericea* woodland occurring on sandy granite soil (Gertenbach 1983).

1. *Terminalia sericea/Combretum zeyheri/Combretum apiculatum* **subsp.** *apiculatum-***community (Gertenbach 1983)**

2. *Acacia nigrescens/Combretum apiculatum* subsp. *apiculatum* - community (Gertenbach 1983)

**Landscape 12:** *Colophospermum mopane/Acacia nigrescens* savanna occurring on sandy granite soils (Gertenbach 1983)

**Landscape 17:** *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* savanna occurring on clayey basalt derived soils (Gertenbach 1983)

1. *Sclerocarya birrea* **subsp.** *caffra/Dichrostachys cinerea/Pterocarpus rotundifolius/ Themeda triandra* **treeveld (Gertenbach 1983)**

2. *Sclerocarya birrea* **subsp.** *caffra/Acacia nigrescens/Themeda triandra/Bothriochloa radicans* **treeveld (Coetzee 1983; Gertenbach 1983)**

3. *Sclerocarya birrea* **subsp.** *caffra- Acacia nigrescens- Combretum hereroense-Digitaria eriantha- Panicum maximum- Sporobolus fimbriatus* **treeveld (Coetzee 1983)**

4. *Sclerocarya birrea* **subsp.** *caffra- Dichrostachys cinerea* **- shrubby, brushy treeveld and grassveld (Coetzee 1983)**

5. *Sclerocarya birrea* **subsp.** *caffra- Acacia nigrescens- Bothriochloa radicans- Themeda triandra* **treeveld (Coetzee 1983)**

6. *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* - dominated brushveld of wide plateau divides (Coetzee 1983)

7. *Acacia nigrescens - Grewia bicolor* var. *bicolor - Terminalia prunioides - Combretum apiculatum* - brushveld (Coetzee 1983)

8. *Dichrostachys cinerea - Acacia tortilis* subsp. *heteracantha* shrubveld and brushveld (Coetzee 1983)

9.  *Grewia bicolor* var. *bicolor* - *Acacia tortilis* subsp. *heteracantha*- *A. nigrescens* - dominated brushveld (Coetzee 1983)

10. *Dalbergia melanoxylon* - *Combretum imberbe* - *Lannea schweinfurthii* var. *stuhlmannii* treeveld (Coetzee 1983)

11. *Themeda triandra* - *Panicum coloratum* var. *coloratum* grassveld (Coetzee 1983)

12. *Acacia nigrescens* - brushveld (Coetzee 1983)

13. *Euclea divinorum* - *Sporobolus smutsii* - *Trianthema triquetra* - dominated vegetation of sodic bottomlands (Coetzee 1983)

14. Vlei, spruit and river complex (Coetzee 1983)

**Landscape 23:** *Colophospermum mopane* shrubveld occurring on clayey basalt derived soils (Gertenbach 1983).

1.  *Bothriochloa radicans* open shrubveld (Gertenbach 1983)

2.  *Themeda triandra* open shrubveld (Gertenbach 1983)

3.  *Setaria incrassata* open shrubveld (Gertenbach 1983)

**Description of the landscapes and their associations**

**Landscape 5: Mixed *Combretum/Terminalia sericea* woodland (Gertenbach 1983) (Mixed Bushwillow woodland).**

*Location, geomorphology and climate*

This landscape is discontinuous due to the fact that it consists of two areas that are separated by Landscape 4 *viz.* the thickets of the Sabie and Crocodile Rivers. One portion of the landscape occurs in the southern district and the remainder forms the southwestern part of the Central District as far north as the Orpen/Timbavati area (Gertenbach 1983). The geological substrata are granite and gneiss with numerous dolerite intrusions that never exceed 10 m in width. The landscape is undulating with distinct uplands, ecotones and bottomlands. The altitude varies between 350 and 500 m and the landscape occupies 1578 km$^2$ or 8.1% of the Kruger National Park (Gertenbach 1983). This landscape has a relatively temperate climate with the occurrence of sporadic frost confined strictly to the bottomlands. During daytime higher temperatures are

experienced in the bottomlands than on the uplands, but at night it becomes colder in the bottomlands (Gertenbach 1983). The average maximum and minimum monthly temperature for Satara (which is also applicable to this landscape) is 29.5°C and 15.5°C respectively. Rainfall varies between 530 and 600 mm per year (Gertenbach 1983).

*Soil Pattern*

Venter (1990) described the soils of this landscape under the Nhlanguleni, Skukuza and Renosterkoppies land types of the Skukuza land system. Landscape 5 has soils that correspond strongly with position in the topography. The upland soils are sandy with between 6 and 15% clay and the dominant soil forms are Hutton (orthic A over red apedal B) and Clovelly (orthic A over yellow brown apedal B). Where the slopes become steeper Glenrosa soils (orthic A over lithocutanic B) can be expected (Gertenbach 1983). Over a period of time an accumulation of clay has taken place in the bottomlands and therefore the soil in the bottomlands has become clayey with Estcourt (orthic A over an E horizon over prismacutanic B), Sterkspruit (orthic A over prismacutanic B), Swartland (orthic A over pedocutanic B over saprolite) and Valsrivier (orthic A over pedocutanic B over unconsolidated material) as the dominant soil forms (McVicar *et al.* 1991).

*Vegetation*

This landscape is an area with dense bush savanna vegetation on the uplands, open tree savanna in the bottomlands and with dense riverine vegetation on the banks of drainage lines and rivers. The vegetation on the deep sandy soils of the uplands consists of a *Terminalia sericea/Combretum zeyheri/Combretum apiculatum* subsp. *apiculatum*-community (Gertenbach 1983) with a dense low and high shrub layer and few or no trees. Where the slopes become steeper and the soils more shallow, larger trees such as marula, *Albizia harveyi* and *Acacia nigrescens* are found (Gertenbach 1983). The bottomlands of this landscape are covered with open tree savanna with *Combretum apiculatum* subsp. *apiculatum* and *Acacia nigrescens* as dominant tree species. The dominant tree species on the numerous dolerite intrusions that occur in the granite are *Acacia nigrescens* ,marula, *Combretum apiculatum* subsp. *apiculatum* and *Acacia tortilis*.

**Landscape 12:** *Colophospermum mopane/Acacia nigrescens* savanna (Gertenbach 1983) (Mopane/Knobthorn savanna).

*Location, geomorphology and climate*

The major portion of the area between the Bububu and Mphongolo Rivers consists of this landscape. A sub-section of this landscape occurs further south towards the western boundary of the Kruger National Park in the vicinity of Timatoro. The landscape extends northwards up to the Waterberg Sandstone. The underlying geological formations are undifferentiated metamorphic rock and amphibolite from the Swaziland System, as well as granite and gneiss. The terrain is much less dissected than the adjacent granite and small pans are common (Gertenbach 1983). The absence of prominent koppies are characteristic of the area and the altitude varies between 400 and 460 m above sea level. This landscape occupies 1042 km$^2$ or 5.5% of the Kruger National Park (Gertenbach 1983). Rainfall in the vicinity varies between 500 and 600 mm per year. Temperatures are mild and frost seldom occurs.

*Soil Pattern*

Due to relatively flat topography there is little variation in soil types. Dominant soil forms are Hutton (orthic A over red apedal B), Swartland (orthic A over pedocutanic B over saprolite), Glenrosa (orthic A over lithocutanic B) and Shortlands (orthic A over red structured B) and the clay content of the soil exceeds 15% (Gertenbach 1983).

*Vegetation*

The vegetation of this landscape is an open tree savanna with occasional low shrubs. Dominant trees in this landscape are *Colophospermum mopane, Acacia nigrescens, Combretum hereroense* subsp. *hereroense* var. *hereroense* and *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* (Gertenbach 1983).

**Landscape 17:** *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* savanna on basalt (Gertenbach 1983) (Knobthorn/Marula savanna).

*Location, Geomorphology and Climate*

This landscape extends on basalt from the Crocodile River in the south to just north of Satara with the Lebombo Mountains as the eastern and the Karoo sediments as the western boundary. It

is one of the largest landscapes of the Kruger National Park and occupies 1411 km$^2$ or 7.2%. A characteristic of this landscape is that it consists of reasonably flat plains with individual well defined drainage channels. All the large rivers such as the Crocodile, Sabie, Nwaswitsonto, Nwanetsi and Sweni Rivers cut through this landscape. The underlying parent material of this landscape is the Sabi River Basalts with a possibility of dolerite intrusions in the basalt (Gertenbach 1983).

The vegetation composition and structure varies in relation to climate, relief unit, slope, angle, soil type and other associated characters such as soil depth, texture, colour, pH and conductivity, as well as in relation to grazing impact (Coetzee 1983). Coetzee (1983) describes this landscape as gently undulating and clayey, with relatively open woody structure and a variety of field layers. This landscape has a subtropical climate (Gertenbach 1987), and according to Gertenbach (1980) the rainfall of this landscape diminishes from south to north. The long-term average rainfall at Crocodile Bridge is 599 mm while the average for Satara is 548 mm (Gertenbach 1983). The altitude varies from 170 m in the vicinity of Crocodile Bridge to as much as 250 m above sea level, just north of Satara (Gertenbach 1983). The mean monthly maximum and minimum temperature for this landscape is 29.5°C and 15°C respectively.

*Soil patterns*

Venter (1990) described this landscape under the Satara land system. The Satara land system includes the basaltic plains, which are olivine-poor lavas around Satara and southward to Crocodile Bridge. On the flat plains landform, mainly moderately deep to shallow, red and brown, structured and paraduplex clays (Shortlands and Swartland forms) are formed (Venter 1990). The Sabi River Basalts weather to form a black, brown or red clayey soil. These soils are largely non-calcareous with 15 to 35% clay in the A horizons. Table 2 gives a general description of the soils and dominant woody vegetation in the Satara land system. The soil pattern is relatively homogeneous and no great changes in soil types occur over short distances (Gertenbach 1983). The A horizons may be orthic or melanic. An orthic A horizon is a surface horizon that does not qualify as an organic, humic, vertic or melanic topsoil although it may have been darkened by organic matter (McVicar, Bennie, de Villiers, Ellis, Fey, von M. Harmse, Hensley, Lambrechts, Bruce, Dohse, Eloff, Grey, Hartmann, Idema, Laker, Merryweather,

Michael, Schloms, Schonau, Snyman, van Niekerk, Verster, Loxton, Meyer, Paterson, Schoeman, Scotney, Turner, van Rooyen & Yager 1991). The melanic A horizon has a fairly wide range of dark coloured, usually well structured topsoils that develop under semi-arid to sub-humid climates and even under humid climates in geomorphologically youthful and hence not strongly weathered landscapes. Part of this range of dark coloured topsoils is vertic (McVicar *et al.* 1991). B horizon clay content is usually in the 25 to 55% range. Soil depth varies from shallow, with lithocutanic B horizons, to deeper with pedocutanic B horizons. Total depth is usually 300 to 600 mm, but occasionally up to 1 000 mm and more. Most of these soils are of the Mayo, Shortlands, Glenrosa, Bonheim, Milkwood, Valsrivier and Swartland forms (McVicar *et al.* 1991). The Bonheim form (melanic A horizon over a pedocutanic B horizon) is particularly common in bottomlands (Gertenbach 1983).

Calcareous soils are restricted to depressions and valley bottoms in this land type. Deep, red, vertic clay (Arcadia form) is occasionally encountered on footslopes, e.g. west of Muntshe hill. Along the basalt/rhyolite contact at the foot of the Lebombo mountains, very deep calcareous vertic clay is often encountered (Venter 1990). In some bottomlands the Bonheim form grades into the vertic Arcadia form. Vertisols of the Rensburg form also occurs (Coetzee 1983) (Table 2). A relatively high density of dolerite dykes occurs in the area directly north and east of Satara rest camp, resulting in the more frequent occurrence of shallow soils (Glenrosa and Mayo forms) and stony areas. The vegetation reflects this in that *Grewia bicolor* var. *bicolor* occurs more frequently in this area. Although marula trees are found on the midslopes and in the valley bottoms, the highest frequency of marula trees are found on the crests in the Satara land type with a very low frequency on the footslopes of this land type (Figure 6).

*Vegetation*

This landscape is described as a non-vertic, tropical, semi-arid, basaltic lowveld (Coetzee 1983) which includes deep, red vertic clay soils (Arcadia form) on the footslopes and in the valley bottom (Venter 1990) (Table 2). The most important two components of this landscape as described by Coetzee (1983) and Gertenbach (1983) are the *Sclerocarya birrea/Dichrostachys cinerea/Pterocarpus rotundifolius* subsp. *rotundifolius/Themeda triandra* treeveld south of Tshokwane and the *Sclerocarya birrea/Acacia nigrescens/Themeda triandra/Bothriochloa*

*radicans* treeveld north of Tshokwane. This larger division is mainly attributed to the higher rainfall in the southern and the lower rainfall in the northern section of this landscape, with the 500 mm isohyet as the reputed boundary.

On the floodplains along the Sweni spruit in this landscape occurs a unique community consisting of *Hyphaene coriacea*-savanna. The vegetation on the Oakleaf soils on the banks of drainage channels and rivers is a tall tree savanna and includes the following woody species: *Lonchocarpus capassa, Ficus sycomorus* subsp. *sycomorus, Diospyros mespiliformis, Kigelia africana, Trichilia emetica* subsp. *emetica, Croton megalobotrys, Acacia xanthophloea* and *Hyphaene coriacea. Phoenix reclinata* and *Cyperus sexangularis* occur in the streambeds, together with *Phragmites australis*. Marula trees are absent in this plant community.

Where soils become shallow the following species occur more commonly: *Combretum apiculatum* subsp. *apiculatum, Acacia exuvialis, Terminalia prunioides, Grewia bicolor* var. *bicolor, Digitaria eriantha, Aristida congesta* subsp. *barbicollis* and *Heteropogon contortus*. In the vicinity of Rietpan/Mlondozi, *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* and *Pterocarpus rotundifolius* subsp. *rotundifolius* are dominant. marula is almost absent in these areas. In certain low lying parts, species such as *Acacia tortilis, Combretum imberbe, Lannea schweinfurthii* var. *stuhlmannii, Dalbergia melanoxylon* and *Lonchocarpus capassa* are more common. Where soils are very clayey and show vertic characteristics, stunted *Acacia nigrescens* with *Setaria incrassata*-stands occur.

**Plant communities in the *Sclerocarya birrea/Acacia nigrescens* savanna on basalt with marula as the dominant tree species:**
Of the 14 plant communities recognised by Coetzee (1983) and Gertenbach (1983), five closely-related tree veld plant communities are dominated by marula. These plant communities occur on relatively lightly grazed slopes and summits of undulating terrain. Their Central District distribution is from the Gudzane-Mbatsane region in the north to the Sabie River in the south. Major interruptions are in the two main grazing regions associated with the Nwanetsi-Sweni and Nwaswitsonto river systems and the flat *Acacia gerrardii* subsp. *gerrardii*. var. *gerrardii* -

dominated plateaux. The ecotopes were recognised as the net effect of topography, soil patterns, vegetation and related grazing patterns. The five ecotopes differ in respect of terrain form, rainfall and sandstone influence and associated differences in soil moisture and leaching.

Table 2.

General description of the soils and dominant woody vegetation in the Satara land system (Venter 1990).

| Land unit | Soil | Woody vegetation |
|---|---|---|
| Crest | Moderately deep to shallow red and brown structured and paraduplex clay. **Dominant soil forms:** Shortlands Swartland Glenrosa Bonheim | Open *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* tree savanna. **Dominant woody species:** *Acacia nigrescens* *Sclerocarya birrea* subsp. *caffra* *Dichrostachys cinerea* |
| Midslope | Shallow red and brown orthic and melanic loam and clay. **Dominant soil forms:** Glenrosa Mayo Shortlands | Moderately dense *Acacia nigrescens/Dichrostachys cinerea* bush savanna. **Dominant woody species:** *Acacia nigrescens* *Grewia bicolor* var. *bicolor* *Dichrostachys cinerea* |
| Footslope | Deep to moderately deep black and brown vertic and pedocutanic frequently calcareous clay. **Dominant soil forms:** Arcadia Bonheim Swartland | Grassland to moderately dense *Combretum hereroense/Euclea divinorum* bush savanna. **Dominant woody species:** *Combretum hereroense* *Euclea divinorum* *Acacia nigrescens* |
| Valley bottom | A complex association of black and brown calcareous alluvial clay and loam in various stages of profile Development. **Dominant soil forms:** Arcadia Oakleaf Rensburg Bonheim | Dense heterogeneous riverine forest. **Dominant woody species:** *Lonchocarpus capassa* *Gymnosporia senegalensis* *Combretum hereroense* *Euclea divinorum* |

| SATARA LAND TYPE | Extensive plains | | | |
|---|---|---|---|---|
| | Olivine-poor basalt | | | |
| Land Unit | 1 | 3 | 4 | 5 |
| Hillslope Unit | Crest | Midslope | Footslope | Valley Bottom |
| % of LT | 74 | 8 | 10 | 8 |
| Slope (%) | 0-4 | 1-5 | 0-4 | 0-5 |
| Length (m) | 299-2367 | 0-430 | 0-551 | 26-345 |
| Shape | STR/CV | CV | CC/STR | CC/IR |
| Frequency(%) of dominant soil forms in Land Type per Land Unit | | | | |
| Frequency(%) of dominant woody plant species in Land Type per Land Unit | | | | |
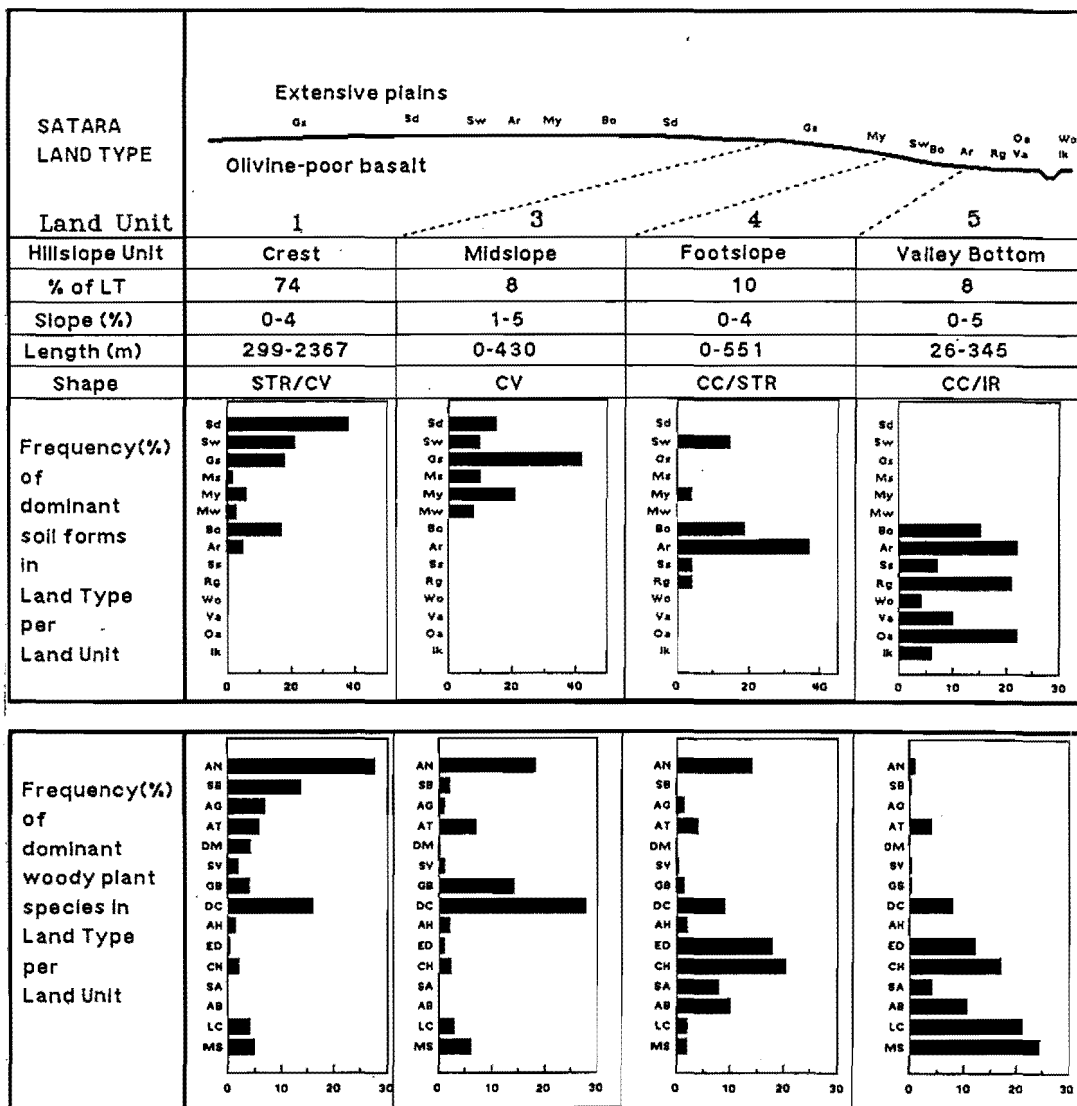
**Soil Forms**

| | |
|---|---|
| Ar | - Arcadia |
| Bo | - Bonheim |
| Du | - Dundee |
| Gs | - Glenrosa |
| Ik | - Inhoek |
| Ms | - Mispah |
| Mw | - Milkwood |
| My | - Mayo |
| Oa | - Oakleaf |
| Rg | - Rensburg |
| Sd | - Shortlands |
| Ss | - Sterkspruit |
| Sw | - Swartland |
| Va | - Valsrivier |
| Wo | - Willowbrook |

**Woody Species**

| | |
|---|---|
| AB | - *Acacia sp.* |
| AG | - *Acacia gerrardii* subsp. *gerrardii* |
| AN | - *Acacia nigrescens* |
| AT | - *Acacia tortilis* |
| AH | - *Albizia harveyi* |
| CH | - *Combretum hereroense* subsp. *hereroense* |
| DC | - *Dichrostachys cinerea* subsp. *africana* |
| DM | - *Dalbergia melanoxylon* |
| ED | - *Euclea divinorum* |
| GB | - *Grewia bicolor* var. *bicolor* |
| LC | - *Lonchocarpus capassa* |
| MS | - *Gymnosporia senegalensis* |
| SA | - *Spirostachys africana* |
| SB | - *Sclerocarya birrea* subsp. *caffra* |
| SV | - *Flueggea virosa* subsp. *virosa* |

Figure 6. Frequency (%) of dominant soil forms and dominant woody species on olivine poor basalt in the Satara land type per land unit (Source: Venter 1990).

a)      The *Sclerocarya birrea* subsp. *caffra/Dichrostachys cinerea/Pterocarpus rotundifolius* subsp. *rotundifolius/Themeda triandra*-treeveld (Coetzee 1983).

This ecotope is also recognised by Gertenbach (1983), and occurs in the relatively high rainfall region south of Tshokwane. It is an open tree savanna with a moderate shrub layer, but with a dense field layer, and occurs on the lightly grazed undulating and gently sloping (< 2°) basaltic terrain. The soils are largely non-margalitic and with distinctly lower pH and conductivity than in similar terrain of the lower rainfall region north of Tshokwane (Coetzee 1983). The soils in the south are typically of the Glenrosa form, i.e. an orthic A horizon with 15 to 35% clay and coarse sand and a non-calcareous B lithocutanic horizon; and of the non-calcareous Swartland form; i.e. an orthic A horizon and a pedocutanic B horizon on saprolite. Soil A- and B horizon pH in this ecotope are typically less than 6.0 (Coetzee 1983).

The vegetation structure here is sparsely to moderately shrubby, sparse treeveld and similar shrubveld and brushveld with scattered trees (Coetzee 1983). Dominant trees in this variation are marula, *Acacia nigrescens, Lannea schweinfurthii* var. *stuhlmannii* and *Lonchocarpus capassa*. Species in the shrub layer are *Dichrostachys cinerea* subsp. *africana, Pterocarpus rotundifolius* subsp. *rotundifolius, Acacia nilotica* subsp. *kraussiana, Acacia gerrardii* subsp. *gerrardii* var. *gerrardii, Albizia harveyi, Gymnosporia senegalensis, Gymnosporia heterophylla* var. *heterophylla, Ozoroa engleri, Ximenia caffra* var. *caffra, Dalbergia melanoxylon* and *Cissus cornifolia*. The presence or absence of *Gymnosporia senegalensis* best distinguishes the two variations of the veld. The field layer is dense and the sequence of dominance is *Themeda triandra, Panicum coloratum* var. *coloratum, Digitaria eriantha, Bothriochloa radicans, Panicum maximum, Heteropogon contortus* and *Urochloa mosambicensis* (Gertenbach 1983).

b)      The *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens/Themeda triandra/ Bothriochloa radicans*-treeveld (Coetzee 1983 & Gertenbach 1983).

This veld occurs in the relatively low rainfall region north of Tshokwane, and consists of an open tree savanna with a moderate to sparse shrub layer and a dense field layer. Soils of this lightly grazed, gently undulating and gently sloping (0 to 1°) terrain are commonly margalitic. The margalitic soils are of: (a) the Bonheim form with a melanic A horizon with 15 to 35% clay and a non-calcareous, non-red, pedocutanic B horizon; (b) the Mayo form with a melanic A horizon

with 15 to 35% clay and a non-calcareous lithocutanic B horizon; and (c) the Milkwood form with a non-calcareous, melanic A horizon with 15 to 35% clay, on hard rock. Non-margalitic soils are, however, also common in this ecotope. These are of the Glenrosa and Swartland forms. Soil A- and B horizon pH here exceed 6.0 (Coetzee 1983).

The vegetation structure is typically sparse treeveld with scattered to moderate shrub cover and scattered to sparse brush cover (Coetzee 1983). The dominant trees are marula, *Acacia nigrescens, Lannea schweinfurthii* var. *stuhlmannii* and *Combretum imberbe*. The shrub layer is sparse to moderate and *Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Albizia harveyi, Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* , *Acacia tortilis, Grewia bicolor* var. *bicolor, Dalbergia melanoxylon, Flueggea virosa* subsp. *virosa, Combretum hereroense* subsp. *hereroense, Ziziphus mucronata* subsp. *mucronata, Ormocarpum trichocarpum, Maerua parvifolia* and *Ehretia rigida* are usually present. The main difference between the two variations lies in the composition of the field layer. The field layer of the latter variations is also dense but the sequence of dominance is *Themeda triandra, Bothriochloa radicans, Aristida congesta* subsp. *barbicollis* and *Eragrostis superba*. Other species that occur regularly are *Enneapogon cenchroides, Schmidtia pappophoroides, Panicum maximum, Heteropogon contortus* and *Sporobolus fimbriatus*.

Forbs which commonly occur in both the variations of the *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* savanna are *Vernonia oligocephala, Rhyncosia minima, Chascanum hederaceum, Heliotropium steudneri, Crotalaria virgulata, Tephrosia polystachya, Rhyncosia densiflora* subsp. *chrysadenia* and *Chamaecrista mimosoides*. A characteristic of this landscape is that forbs are fairly rare in the stable, relatively undisturbed veld. Under conditions of moderate to heavy grazing the forbs show a marked increase and species such as *Solanum panduriforme, Sericorema remotiflora, Pavonia burchellii, Ipomoea obscura* var. *fragilis, Justicia flava, Hermbstaedtia odorata, Corchorus asplenifolius, Barleria prionitis* and *Phyllanthus asperulatus* increase considerably.

c)     The *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens/Combretum hereroense/ Digitaria eriantha/Panicum maximum/Sporobolus fimbriatus* treeveld (Coetzee 1983).

This ecotope is a lightly grazed shrubby, brushy, treeveld of gently undulating terrain, with a strong sandstone influence and less than 15% clay in the A horizon. Sandstone influence is often present in the predominantly basaltic region, near the boundaries of the latter with Karoo Sediment Landscapes 4 and 5. This influence is noticeable as comparatively low soil clay content, high percentage medium to fine sand and relatively low percentages coarse sand, and in some examples sandstone is actually present as stones in the soil profile or as bedrock. Where the sandstone influence is particularly strong the Mispah form, with an orthic A horizon containing less than 15% clay, on sandstone occurs. Where the sandstone influence is moderately strong, the A horizon's clay content is approximately 20%. Soils of the Glenrosa and Swartland forms also occur in this plant community (Coetzee 1983).

Woody dominants are tall marula in the tree layer, small *Acacia nigrescens* trees at the brush level and *Combretum hereroense* subsp. *hereroense* brush at the shrub level. *Digitaria eriantha, Panicum maximum* and *Sporobolus fimbriatus* are the field layer dominants (Coetzee 1983).

d)     The *Sclerocarya birrea* subsp. *caffra/Dichrostachys cinerea* – shrubby treeveld and grassveld (Coetzee 1983).

This ecotope has *Dichrostachys cinerea* - dominated shrub and brush; with *Themeda triandra - Panicum coloratum* var. *coloratum - Bothriochloa radicans - Digitaria eriantha* - dominated field layers; and with relatively xeric indicator species (e.g. *Acacia nigrescens, Acacia tortilis, Flueggea virosa* subsp. *virosa, Chloris virgata, Heliotropium steudneri and Boerhavia diffusa*). It is a lightly grazed, gently undulating terrain with a moderate sandstone influence and 15 to 20% clay in the A horizon. The soils are very similar to the aforementioned ecotope.

The vegetation structure is grassveld with scattered shrub and brush, or sparsely to moderately shrubby, sparse treeveld. Marula is the dominant tree and *Dichrostachys cinerea* the dominant shrub. Field layer dominants include the grasses *Themeda triandra, Panicum coloratum* var. *coloratum, Bothriochloa radicans* and *Digitaria eriantha*.

e)      The *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens/Bothriochloa radicans/ Themeda triandra* treeveld (Coetzee 1983)

This landscape is a treeveld of the relatively strongly undulating, non-rocky, basaltic terrain around Satara. The soils of this ecotope belong to (a) the Mayo form with a melanic A horizon with 15 to 35% clay, over a non-calcareous, lithocutanic B horizon; and (b) the Glenrosa form with an orthic A horizon with 15 to 35% clay and fine sand, over a non-calcareous, lithocutanic B horizon. The A horizon pH is 6.0, and the B horizon pH varies from 6.1 to 6.8 (Coetzee 1983).

The vegetation structure is sparse to moderate treeveld with scattered shrub and brush. Marula is the dominant tree, while *Acacia nigrescens* is the dominant shrub and brush. *Combretum apiculatum* subsp. *apiculatum* and/or *Acacia exuvialis* shrubs and brush are typically present. Occasionally at relatively low clay percentage (less than 20% in A horizon), *Combretum apiculatum* subsp. *apiculatum* can be the dominant shrub. *Bothriochloa radicans* and *Themeda triandra* are the dominant grasses. Common subdominant grasses include *Digitaria eriantha* and *Panicum coloratum* var. *coloratum*.

**Ecotopes in the *Sclerocarya birrea* subsp. *caffra/Acacia nigrescens* savanna (Coetzee 1983) where marula are characteristically absent or not dominant:**

a)      The *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* - dominated brushveld of wide plateau divides (Coetzee 1983).

The lightly grazed Nkongwana Spruit region of the Lindanda Plains and the basaltic, Klein-Mlondozi Spruit region of the Rietpan plains, belong to this ecotope. The terrain is level to gently sloping (less than 1 °).

The soils of the Rietpan Plains are typically of the Mayo form with a melanic A horizon and a non-calcareous lithocutanic B horizon. Recorded A horizon pH range from 5.7 to 6.2. Soils, which adjoin the Karoo Sediment landscape, are of the Glenrosa and Bonheim forms. The melanic A horizon of the typical plateau-associated soils of this southern divide, are distinct from the orthic A horizon of the next ecotope on surrounding slopes, where soils are typically of the

Glenrosa and Swartland forms. Soil A horizons of the divide are also distinctly clayey, with approximately 30% clay (Coetzee 1983).

Soils of the Nkongwana Plains are of the Mayo and Glenrosa forms, with 15 to 35% clay. The orthic A horizons consist of fine to course sand while the B horizons are non-calcareous. Recorded pH values for A horizons are 5.7 and 5.8.

The vegetation structure on these flat plains is typically sparse to moderate brushveld with scattered to sparse shrub cover. *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* is the dominant tree and often also the dominant shrub species. Occasionally prominent woody species of the shrub level include *Acacia nigrescens, Dichrostachys cinerea, Pterocarpus rotundifolius* subsp. *rotundifolius* and *Acacia harveyi*. The most common grass is *Panicum coloratum* var. *coloratum*. *Heteropogon contortus* is often also among the subdominants.

b)      The *Acacia nigrescens - Grewia bicolor* var. *bicolor - Terminalia prunioides - Combretum apiculatum* - brushveld (Coetzee 1983).

This ecotope is common between the upper reaches of the Nwanetsi River in the Satara vicinity and in well-drained parts of the Nwanetsi vicinity, where the Nwanetsi-Gudzane and the Sweni-Makongolweni drainage channels converge. The vegetation indicates an aridness of habitat, largely ascribed to the quick drying of shallow soils, as well as to high water runoff in the strongly undulating terrain with its numerous abrupt incisions by drainage channels.

Soils are of the following forms: (a) Mayo, with a melanic A horizon with 15 to 35% clay over a non-calcareous lithocutanic B horizon; (b) Glenrosa, with an orthic A horizon with 15 to 35% clay over a non-calcareous B horizon; (c) Milkwood, with a non-calcareous, melanic A horizon with 15 to 35% clay over hard rock; (d) Mispah, with an orthic A horizon. Soil pH of A and B horizons are between 6.0 and 6.9 (Coetzee 1983).

The vegetation of this landscape unit is transitional to the vegetation of the more arid Tropical Basaltic Lowveld of the Olifants River Valley. The structure of the vegetation is sparsely to moderately shrubby, scattered to sparsely brushy, shrub- and brushveld, dominated mainly by

various combinations of *Acacia nigrescens*, *Grewia bicolor* var. *bicolor*, *Combretum apiculatum* subsp. *apiculatum* and *Terminalia prunioides*. The grass *Bothriochloa radicans* is usually dominant in the field layer (Coetzee 1983).

**c)** **The *Dichrostachys cinerea* - *Acacia tortilis* subsp. *heteracantha* shrubveld and brushveld (Coetzee 1983)**

This distinct landscape consists primarily of the heavily grazed and trampled Lindanda Plains. It occurs on the same soil forms as the adjoining *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* - dominated brushveld. Clay percentages and soil depths are essentially similar too. However, the conductivities of the soils, particularly of the B horizons, are significantly higher on the heavily grazed parts, indicating higher base-status and therefore higher nutrient content.

The vegetation belongs to the same variation as the less heavily grazed *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* - dominated brushveld, though it differs floristically at subcommunity level (Coetzee 1983). The vegetation structure on the heavily grazed Lindanda Plains is sparsely to moderately shrubby, sparse shrub- and brushveld with scattered brush. The dominant woody species are *Dichrostachys cinerea* subsp. *africana* and *Acacia tortilis* subsp. *heteracantha*. Both these species become relatively abundant with heavy grazing. A combination of *Bothriochloa radicans*, *Panicum coloratum* var. *coloratum* and *Aristida congesta* subsp. *barbicollis* is usually dominant in the field layer (Coetzee 1983).

**d)** **The *Grewia bicolor* var. *bicolor* - *Acacia tortilis* subsp. *heteracantha*- *Acacia nigrescens* - dominated brushveld (Coetzee 1983).**

This ecotope occurs in the heavily grazed low areas (bottomland) of the major river systems. The most extensive examples are in the Sweni - Makongolweni - Guweni - Nungwini area, in the Tshokwane region of the Nwaswitsonto River and in the immediate vicinity of the Sabie River. Prominent patches also occur near Gudzane Dam along the lower Nwanetsi River. Slope angles vary from 0 to 2°. Clay content of the A horizon of 23 to 35% is similar to that of some of the surrounding less intensively grazed basaltic areas, but the pH of 6.1 to 6.6 is comparatively high.

The soils are typically of the following forms: (a) Bonheim, with 15 to 35% clay in the melanic A horizon and a non-calcareous B horizon; (b) Mayo, with 15 to 35% clay in the melanic A horizon and a non-calcareous B horizon; (c) Swartland, with an orthic A horizon and 15% clay in the non-calcareous B horizons; (d) Glenrosa, with an orthic A horizon with 15 to 35% clay and a non-calcareous B horizons.

The vegetation structure is typically a sparsely to moderately shrubby, sparse brushveld, occasionally with scattered *Acacia nigrescens* trees. *Acacia tortilis* subsp. *heteracantha* and a mixture of *Acacia nigrescens, Grewia bicolor* var. *bicolor* and *Dichrostachys cinerea* dominate the shrub and brush layers. *Dichrostachys cinerea* is abundant on soils with relatively deep A horizons with a low pH.

**e)** **The *Dalbergia melanoxylon - Combretum imberbe - Lannea schweinfurthii* var. *stuhlmannii* treeveld (Coetzee 1983)**

This is lightly grazed, non-vertic, non-sodic bottomlands which is moderately dry with relatively high soil conductivity and relatively low pH. This landscape occurs on the low basaltic plains along the upper reaches of the Mbatsane and Shinkelengane spruits, against the Lebombo Mountains. Soil A horizons have 24 to 35% clay with a pH of 5.1 to 6.4. The B horizon clay percentage is between 46 and 49 with a pH between 5.1 and 5.5 (Coetzee 1983).

The vegetation structure can be a sparse shrub- or brushveld. One or more of *Dalbergia melanoxylon, Combretum imberbe* and *Lannea schweinfurthii* var. *stuhlmannii* are characteristically among the dominant woody plants. The field layer is dominated by a combination of the grasses *Themeda triandra, Bothriochloa radicans, Digitaria eriantha* and *Panicum coloratum* var. *coloratum* (Coetzee 1983).

**f) The *Themeda triandra - Panicum coloratum* var. *coloratum* grassveld (Coetzee 1983)**

This ecotope occurs on the lightly grazed bottomland plains south and west of the Lindanda Plains. The soils are of the non-calcareous Bonheim, Mayo, Swartland and Glenrosa form. The A horizons have 25 to 43% clay with a pH of 5.5 to 6.3, while the B horizons have 33 to 56% clay with a pH of 5.7 to 8.0 (Coetzee 1983).

The vegetation structure can be grassveld, or sparse shrub- or brushveld. *Albizia harveyi* and/or *Dichrostachys cinerea* are the typical dominant woody species in the shrubveld and brushveld. *Themeda triandra* and *Panicum coloratum* var. *coloratum* are the typical dominant field layer species (Coetzee 1983).

**g)**     ***Acacia nigrescens* - brushveld (Coetzee 1983)**

*Acacia nigrescens* dominated brushveld occurs on lower slopes along rivers and in other low areas on vertic and near vertic bottomlands, and is particularly common in the lower Nwanetsi-Gudzane Catchment. Comparatively large patches also occur near Tshokwane in the Nwaswitsonto Catchment. The soils of this landscape unit are of the following forms: (a) Bonheim, with a melanic A horizon with 15 to 35% clay over a calcareous, non-red, pedocutanic B horizon; (b) Arcadia, with a calcareous or non-calcareous, red vertic A horizon with a self-mulching or weakly crusting surface.

The vegetation structure of a typical *Acacia nigrescens*-dominated brushveld is sparsely to moderately shrubby, sparse to moderate brushveld, with or without scattered trees. All woody levels are dominated by *Acacia nigrescens*. Field layer dominants are *Bothriochloa radicans* or *Panicum maximum*.

**h)**     **The *Euclea divinorum* - *Sporobolus smutsii* - *Trianthema triquetra* - dominated vegetation of sodic bottomlands (Coetzee 1983)**

A distinct sodic influence is indicated by patches of vegetation in bottomlands that are adjoined by granophyric or rhyolitic slopes. *Euclea divinorum*-dominated shrub and brush are typical of relatively large patches. Occasional woody species in such shrubby and brushy sodic areas include *Euclea undulata*, *Carissa bispinosa* and *Rhus gueinzii*. The grass *Sporobolus smutsii* is a common field layer dominant in the shrubby and brushy areas or in local patches of grassveld (Coetzee 1983).

**i)**     **Vlei, spruit and river complex (Coetzee 1983)**

The basaltic region lacks the consistent levees with which the typical riparian bush in the granitic region is associated. River-associated trees are therefore less common in the basaltic region and

occur as irregularly scattered individuals of fragmentary stands of riparian bush. Marula is not associated with riparian vegetation.

## Landscape 23: *Colophospermum mopane* shrubveld (Mopane shrubveld).

*Location, geomorphology and climate*

The Olifants, Letaba and Shingwedzi Rivers intersect this landscape which extends northwards from the Timbavati River. It broadens to include the plains of Tsende and Dzombo, and extends further north to Klopperfontein.

The geological rock formations upon which this landscape developed is basalt (Gertenbach 1983). The mopane shrubveld is situated between 300 and 400 m above sea level and is the largest and most homogeneous landscape. It covers 1 993 km² or 10.3% of the Kruger National Park. The rainfall of this landscape varies between 450 and 500 mm per annum (Gertenbach 1983). The summers are very hot and as a result of the flat topography there is relatively little differences in microclimate. The mean monthly maximum and minimum temperature for Shingwedzi is 30°C and 15°C respectively.

*Soil pattern*

The soils that occur in this landscape are darker in colour (melanic) and usually have high clay contents (20 - 50% clay). In some cases the A horizons are thin (300 mm) and overlay a thick layer of lime concentrations. Such soils belong to the Milkwood (melanic A over hard rock), Mayo (melanic A over lithocutanic B) and Mispah (orthic A over hard rock) forms. These types of soil occur mainly on the middle- and footslopes. On the higher middleslopes the colour of the soils is usually red and the dominant soil forms are Bonheim (melanic A over pedocutanic B), Swartland (orthic A over pedocutanic B over saprolite) and Mayo (melanic A over lithocutanic B). Where the topography is flat or even concave, darker coloured soils with vertic characteristics occur. These soils belong to the Bonheim (melanic A over pedocutanic B), Arcadia (vertic A) and Rensburg (vertic A over G-horison) forms (Gertenbach 1983).

*Vegetation*

Multi-stemmed mopane shrubs being 1 to 2 m in height dominate the woody vegetation of this landscape. The absolute dominance of *Colophospermum mopane* results in other woody species being relatively rare.

**Description of the elephant exclosures**

*The Hlangwine Exclosure*

A separate study was conducted in the Hlangwine exclosure to examine the response of marula individuals to fire in the absence of herbivory. The Hlangwine exclosure is located in Landscape 1, the Lowveld Sour Bushveld in the southern moist savanna near Pretoriuskop. This landscape, as described by Gertenbach (1983), covers approximately 2.8% of the Kruger National Park and has an annual rainfall that varies between 600 and 1000 mm. The high soil moisture causes the grass to sprout even during winter. Soils of this landscape are sandy, mainly of the Hutton and Clovelly forms. The vegetation structure of the uplands is an open tree savanna with relatively low shrubs. *Terminalia sericea* and *Dichrostachys cinerea* subsp. *nyassana* dominate the woody component (Gertenbach 1983). The field layer is tall (1 to 2 m) and is dominated by sour grass species such as *Hyperthelia dissoluta*, *Elionurus muticus* and *Hyparrhenia hirta*. The bottomlands in the landscape are narrow and consist of an open savanna with single trees and sparse shrubs with a denser grass cover (Gertenbach 1983). Marula is noted as an important tree species associated with this landscape.

The Hlangwine exclosure, which is divided into six blocks, was established in 1973 and comprises 269 ha. Each block is approximately 700 x 500 m. The dominant woody species in the Hlangwine exclosure are *Terminalia sericea* and *Dichrostachys cinerea* subsp. *africana* while *Hyperthelia dissoluta*, *Pogonarthria squarrosa*, *Loudetia simplex* and *Aristida congesta* dominate the grass layer.

*The Roan enclosure*

The Roan enclosure was used as a control site to monitor the population structure of marula, since this area was protected from elephants since 1967. It is located in Landscape 23 on basalt, in the northern arid savannas near Shingwedzi and comprises 309 ha. This exclosure (which is

divided into four blocks) have not been subjected to a fixed burning program, and the different blocks were burned on a random basis throughout the years with a mean fire return period between 2 and 3 years. The dominant woody species inside the camp are *Colophospermum mopane*, *Ormocarpum trichocarpum* and *Dalbergia melanoxylon*. No exclosure sites occur in Landscapes 5 or 12 on the granitic soils or in Landscape 17 on basalt. The animal population within the camp consists mainly of about 30 roan antelope (*Hippotragus equinis*), while smaller species such as steenbok also occur. The diet of the roan antelope primarily consist of grass, although they also browse to a certain extent the green leaves and young shoots of shrubs and favoured trees (*Dalbergia melanoxylon* and *Lonchocarpus capassa*) during excessively dry periods (Joubert 1970).

**Characteristics of *Sclerocarya birrea* subsp. *caffra***

*General*

*Sclerocarya birrea* subsp. *caffra* (marula) is a member of the Anacardiaceae (mango family) and is found throughout the eastern low altitude regions of southern Africa. The marula tree - as a subtropical plant - has a high optimum germination temperature between 27°C and 37°C (Lewis 1987). The maximum mean monthly temperature of the landscapes used during this study falls in this range being 29.5°C and 30°C respectively. Marula is a medium-sized tree up to 10 m in height, but it may reach 15 m under favourable conditions (Palgrave 1983). The growth form consists of a single straight trunk which branches high up into a few, bare branches that grow slightly upwards and horisontally to form a moderate dense, round to semi-circular canopy. Male and female flowers are borne on separate trees (Jacana & Twisisa 1997). From March to June, large fruits up to 3.5 cm in diameter and approximately 42 g in weight, ripen and fall to the ground with as many as 8000 fruits per tree (Lewis 1987). Various studies showed marula populations to be highly clumped (Walker, Stone, Henderson & Vernede 1986, Lewis 1987 and Gadd 1997).

The marula is amongst the most highly valued of indigenous trees as they provide valuable food and shade (Coates Palgrave 1977), and is a favourite food plant of the elephant. Their leaves are browsed by game, the bark stripped by elephants and the abundant crops of fruit which are high

in vitamin C, are eaten by game animals, monkeys and baboons (Pooley 1993). The marula also plays a distinct role in the cultural rite of various black tribes. They utilise the seed and especially the fruit extensively and the leaves and bark are used for medicinal purposes (Von Teichman, Small & Robertse 1986). As the largest gene pool of wild marula variants are found in the Kruger National Park, a research project was initiated to ennoble the wild African Marula. Holtzhausen (1996) has ennobled the marula, orchards have been established and several products of the fruit are commercially obtainable.

Results of Walker *et al.* (1986) showed that the use of growth rings were not a reliable method to determine the age of marula. Some of the growth rings of the marula trees sampled turned out to be rows of fiber, which have been laid down in response to stress. Walker *et al.* (1986) further suggested that the analysis of population structure and dynamics should be based on the sizes of marula trees. Haig (1999) used the number of growth rings of recently felled marula trees to estimate the approximate age of the trees by fitting the following regression: $y = 0.765x - 1.47$, with $r^2 = 0.967$ and $p < 0.001$, i.e. basal circumference on age (Figure 7). The regression of Haig (1999) was therefore, only used to determine the approximate age of marula trees throughout this study, when necessary.
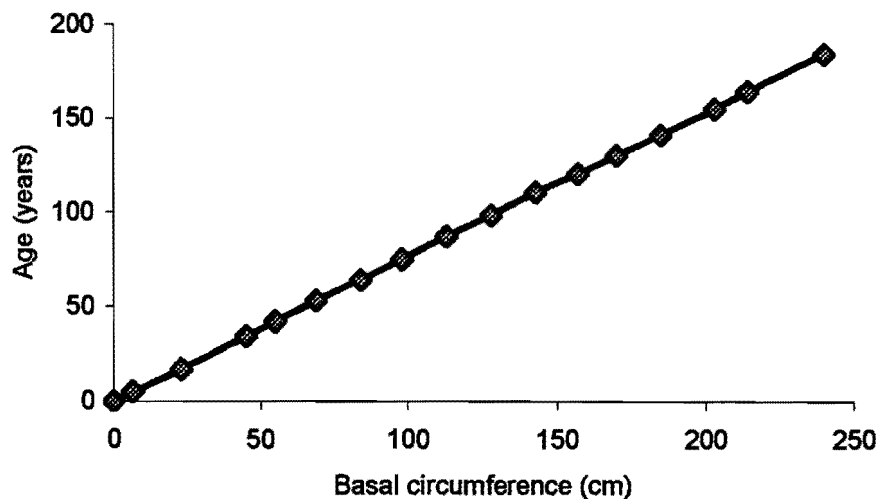


Figure 7. Graphical representation of age derived from basal circumference for *Sclerocarya birrea* trees (Source: Haig 1999).

*Habitat preference*

In the Kruger National Park marula occurs widely on sandy granitic soils but on the drier, clayey basaltic soils it is largely restricted to moister climates with annual rainfall exceeding 500 mm (Coetzee, Engelbrecht, Joubert & Retief 1979) and well drained soils. Trollope *et al.* (1998) found in the Kruger National Park that the sandy soils of granitic origin are more favourable for the growth of trees than the clay soils of basaltic origin. The sandy soils retain less moisture in the upper soil layers but permit the infiltration of moisture down to greater depths in the soil profile than the clay soils thus favouring the deeper rooted woody vegetation more than the shallow rooted grass sward. Marula typically occupy the convex upper parts of the gently undulating basalt plains, where soils are leached with comparatively low clay content.

This is in concordance with the study done by Lewis (1987) in the Luangwa Valley, Zambia. Lewis (1987) found that the spatial distribution of marula was correlated with physical soil characteristics and may have contributed to the highly aggregated pattern of the sample population. Of the marula trees sampled by Lewis (1987), 75% were found on well-drained soils (sandy clay loamy soils over sandy soils, loamy sandy soils, sandy clay to clay soils, stony clay soils and sandy clay loamy soils to clay soils). Soils that are both deep and well drained (sandy clay loamy soils over sandy soils, loamy sandy soils and sandy clay loamy soils to clay soils) accounted for 60% of the trees. Poorly drained soils (sandy clay to clay or heavy clay soils) had only 19% of the tree population sampled by Lewis (1987). In the Kruger National Park on both the granite and basalt substrata, marula trees are mostly restricted to the crests, midslopes and dolerite intrusions.

In landscapes 5 and 12 on granite, marula trees are mostly found on the crests and midslopes where the soils are shallow with Glenrosa, Hutton and Swartland as the dominant soil forms. Marula is a dominant tree species on the numerous dolerite intrusions that occur in Landscape 5. In olivine-poor basalt substrata, the frequency of marula trees decreases as the soil forms with high clay content become more dominant (Table 3). In landscape 17 on basalt, marula trees are one of the dominant tree species on the crests and occur on the midslopes where Shortlands, Glenrosa and Mayo are the dominant soil forms (Figure 6). The marula tree is not dominant on the clayey melanic soils on the footslopes, in the valley bottoms and on the open plains where

Arcadia, Bonheim and Mispah are the dominant soil forms (Figure 6). Table 2 is a summary of the soil forms in which marula is dominant and absent/not abundant, while Table 3 is a summary of the prominent tree species that occur in the presence where marula dominates the woody vegetation.

Some plant communities that were identified by Coetzee (1983) on basalt and where marula trees typically occur are:

(a)     Stunted *Acacia nigrescens* communities on plateaux and low terrain with much montmorillonite clay (Coetzee *et al*. 1979).

(b)     Spiny Arid Bushveld on the dry, shallow, calcareous soils near major drainage lines towards the 500 mm rainfall isohyet (Coetzee *et al*. 1979).

(c)     *Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* - dominated communities of poorly drained topography above the 600 mm isohyet (Coetzee *et al*. 1979).

Table 2.

The different soil forms in the *Sclerocarya birrea/Acacia nigrescens* savanna, and the presence/absence of *Sclerocarya birrea* subsp. *caffra* on these soils.

| Soil forms on which *Sclerocarya birrea* subsp. *caffra* trees are present | Soil forms on which *Sclerocarya birrea* subsp. *caffra* trees are absent or not abundant |
|---|---|
| Bonheim | Arcadia |
| Glenrosa | Milkwood |
| Shortlands | Mispah |
| Mayo | |
| Swartland | |

Table 3.

Prominent tree species on granite and basalt that occur where *Sclerocarya birrea* subsp. *caffra* has been identified as one of the dominant species.

| Species on granite | Species on basalt |
|---|---|
| *Albizia harveyi* | *Acacia nigrescens* |
| *Acacia nigrescens* | *Lannea schweinfurthii* var. *stuhlmannii* |
| *Combretum apiculatum* subsp. *apiculatum* | *Lonchocarpus capassa* |
| *Acacia tortilis* | *Combretum imberbe* |
| | *Combretum hereroense* |
| | *Dichrostachys cinerea* |

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

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## Abstract

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

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

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## Introduction

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

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

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

*al.* 1979). This is in accord with Lewis (1987) who found the tree population decreased with increased clay content. The granitic landscapes in the Kruger National Park are therefore more suitable for the establishment of the marula tree population.

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

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

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

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

## Study area

The Kruger National Park encompasses an area of 18 998 $km^2$ and forms part of the Lowveld regions of Mpumalanga and the Northern Province, semi-arid regions of the southern temperate zone (Smuts 1975). The climate is subtropical with warm, wet summers and mild winters seldom experiencing frost. In the Kruger National Park precipitation decreases from south to north, except for the area around Punda Maria which is situated at a higher altitude (Gertenbach 1980). The pattern of rainfall over the past century has been characterised by extended wet and dry periods with cycles of about 10 years. This study was conducted in four major landscapes of the Kruger National Park as described by Gertenbach (1983), i.e. the mixed *Combretum/Terminalia sericea* woodland (Landscape 5), the *Colophospermum mopane/Acacia nigrescens* savanna (Landscape 12), the *Sclerocarya birrea/Acacia nigrescens* savanna (Landscape 17) and the *Colophospermum mopane* shrubveld (Landscape 23) (Figure 8). Table 4 is a summary of the main characteristics of these landscapes. When examining the rainfall pattern of the four landscapes as described by the CCWR (Dent, Lynch & Shulze 1989), Landscape 5 yields a higher annual rainfall than the rest of the landscapes. The annual rainfall in Landscape 5 varies between 500 and 800 mm as opposed to 350 and 700 mm in the other landscapes.
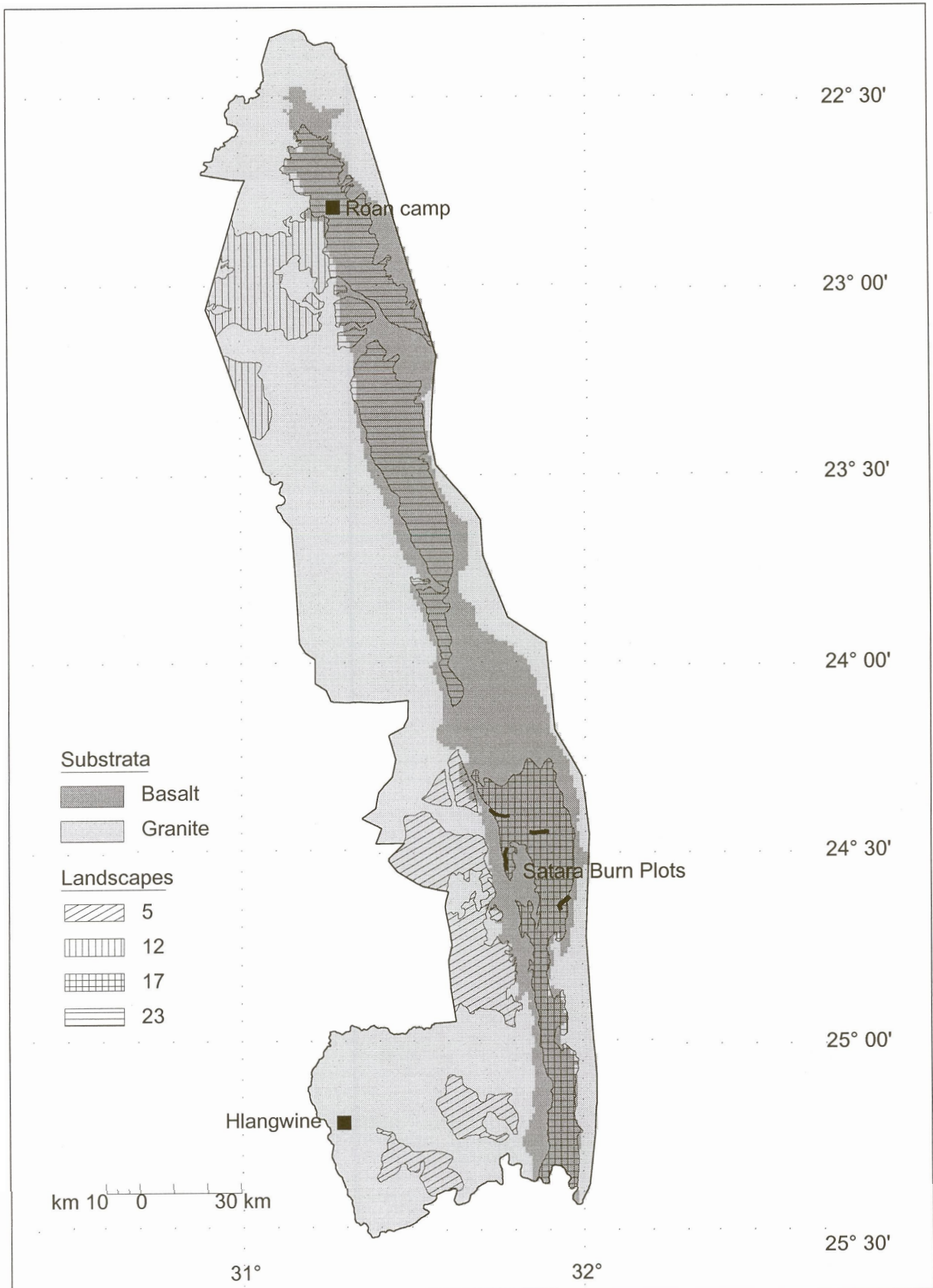
Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

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

Table 4

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

| Aspects | Landscape 5 (mixed *Combretum/ Terminalia sericea* woodland) | Landscape 12 (*Colophospermum mopane/Acacia nigrescens* savanna) | Landscape 17 (*Sclerocarya birrea/ Acacia nigrescens* savanna) | Landscape 23 (*Colophospermum mopane* shrubveld) |
|---|---|---|---|---|
| Size | 1587 km$^2$ | 1042 km$^2$ | 1411 km$^2$ | 1993 km$^2$ |
| Geology | Granite | Granite and gneiss | Basalt | Basalt |
| Dominant soils | Sandy | Sandy | Clay | Clay |
| Soil clay Content | 6 – 15% | 15% and more | 15% to 35% | 20% to 50% |
| Rainfall (annual mean) | 500 to 800 mm | 500 to 600 mm | 550 to 600 mm | 450 to 500 mm |
| Vegetation diversity | Dense bush savanna Open tree savanna Dense riverine vegetation | Open tree savanna dominated by mopane trees | Dense bush savanna Open tree savanna Grassland Dense riverine vegetation | Mopane dominated shrubveld Other species rare |
| Impala Densities/km$^2$ (1983 – 1997) | 215 | 118 | 171 | 115 |
| Elephant densities/km$^2$ (1985 - 1997) | 4.3 | 5.7 | 2.7 | 2.6 |

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

## Methods

### Data collection

To examine the population structure of a single tree species such as the marula, it is necessary to record as many trees as possible in the study area that will be representative of the population in each landscape. Thus the survey transects were selected by stratified sampling of habitats, in such a way as to cover the major marula tree clumps in each of the landscapes. Thirty possible transects were mapped in each landscape, of which 20 were selected at random to provide a good coverage of the structural composition of the marula tree population. The location of transects were restricted by the availability of vehicle tracks such as firebreaks.

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

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

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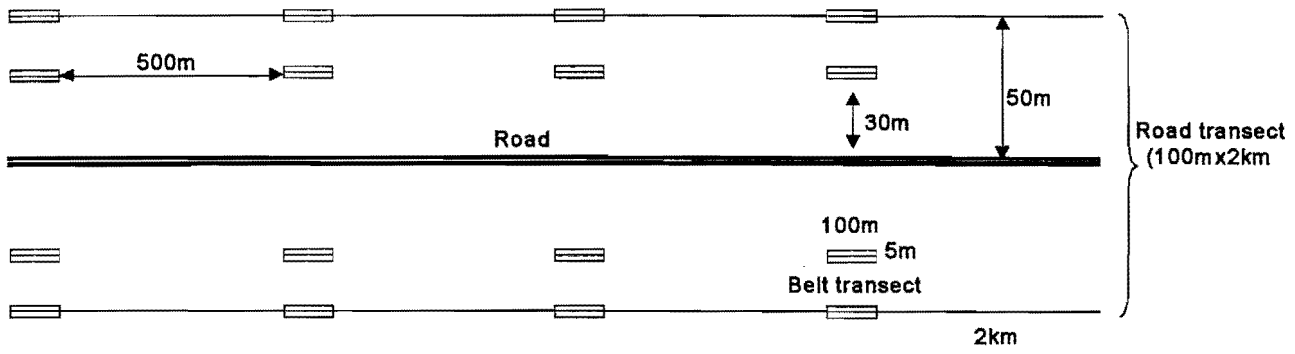
(a)
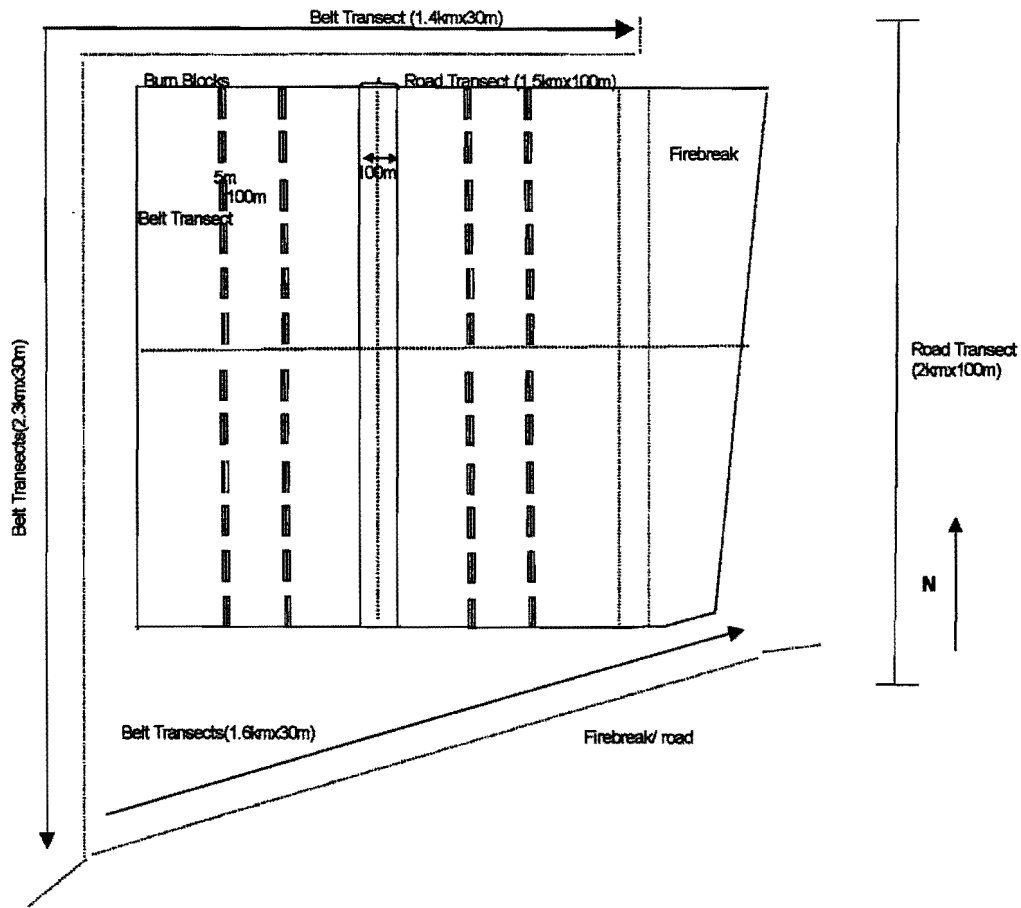


(b)

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

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

## Data analysis

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

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

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

# Results

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

## Lower canopy

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

## Mature trees

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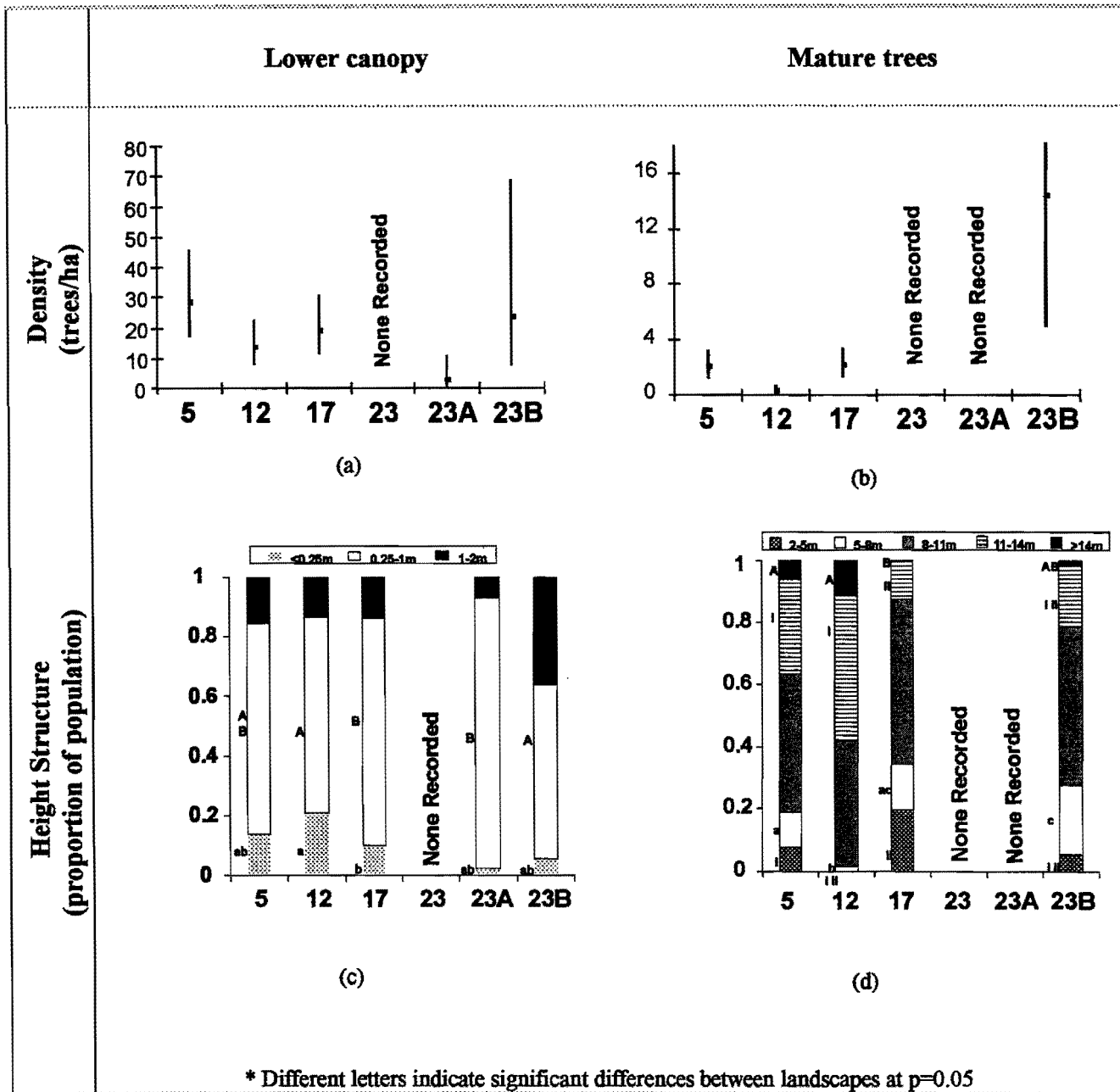
**Lower canopy**          **Mature trees**

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

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

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

Table 5.

Landscape effects on lower canopy and mature marula trees.

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

$r^2$=0.10714, p<0.00005          $r^2$=0.27296, p=0.00007

(a)                              (b)

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

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

p=0.0005                         p=0.0001

(a)                              (b)

Figure 12.  Exclosure effects on (a) the height and (b) the crown diameter of marulas in the lower canopy.
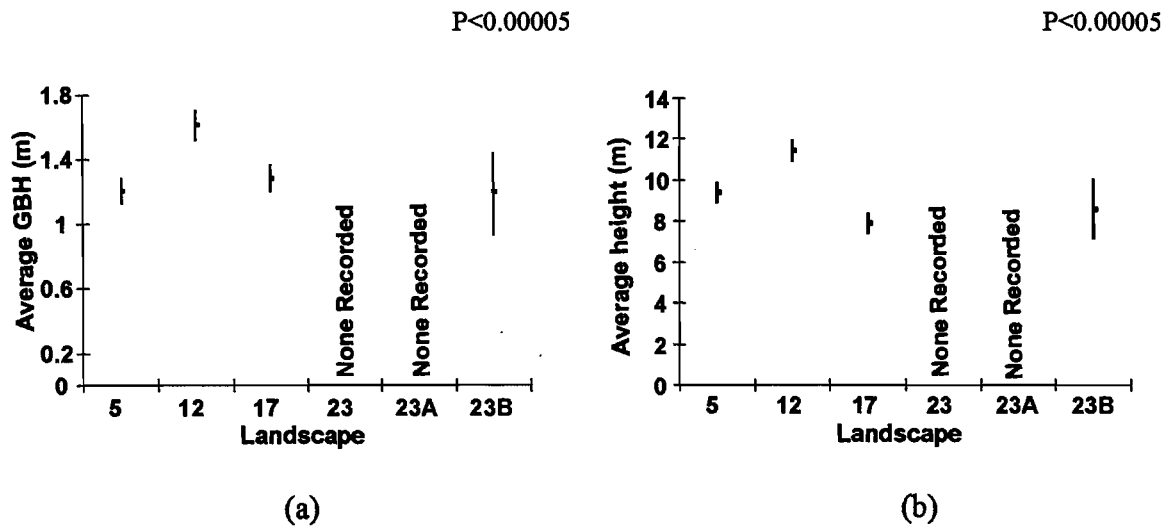
P<0.00005                                         P<0.00005



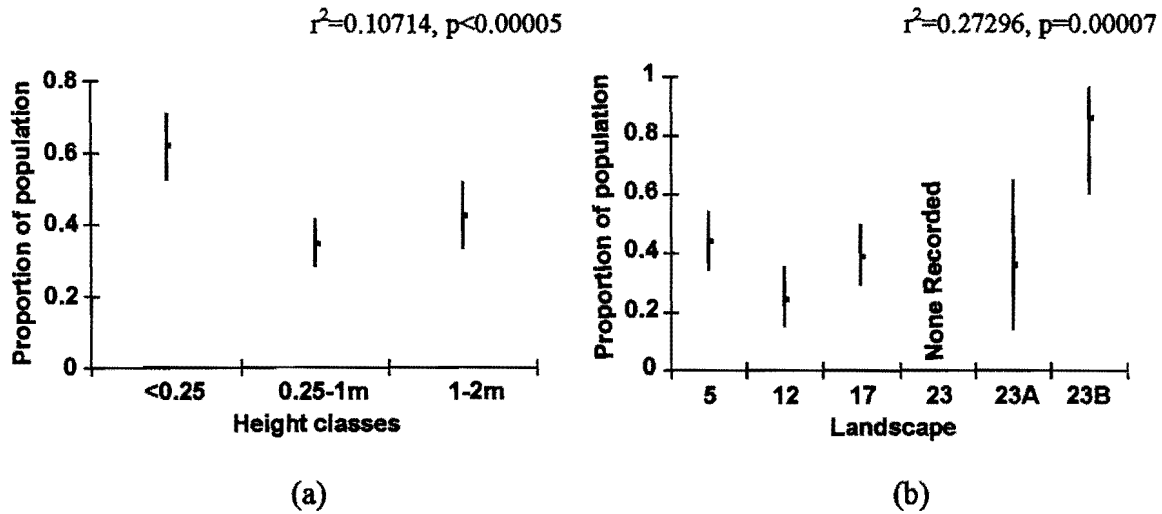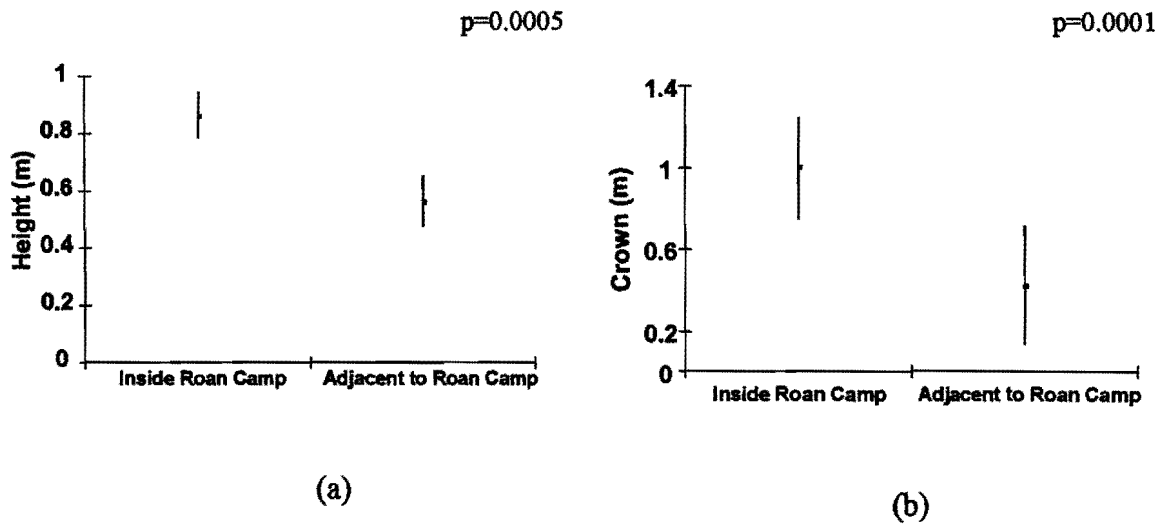(a)                                                (b)

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

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

## Discussion

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

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

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

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

*Density*

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

The fact that mature marula tree densities did not differ significantly between Landscapes 5 and 17 (where Landscape 5 yielded a higher annual rainfall than Landscape 17), and that the density in the roan enclosure was significantly higher than in all other landscapes (Figure 10b), indicates that the density of mature marulas respond to factors other than rainfall and geology. The significantly higher density of trees in the roan enclosure can be explained by the fact that the enclosure was constructed in 1967, and the vegetation was therefore protected from elephant impact for most of the time since the dramatic increase in elephant numbers that occurred during the 1960's. The

lower density of trees in Landscape 12 can probably be ascribed to increased herbivory pressure as a result of less diverse vegetation, since soils are similar to Landscape 5, which has more mature marulas (Figure 10b). This supports the result of Lewis (1987) who found increased browsing pressure for seedlings in areas with lower species diversity, hence resulting in less recruitment into the upper canopy. Anderson & Walker (1974) found that elephants will forage on a favoured species until food becomes less available, when they will move on to the next favoured species. The lower marula seedling density directly adjacent to the roan enclosure could be attributed to a lack of seed producing trees in this area. The mature marula trees within the roan camp (specifically those closest to the fence) are most probably the source of these seedlings.

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

*Population structure*

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

When examining the overall structure of individuals in the lower canopy, the general indication is that new regeneration occurs continuously. The only significant difference in class A was found between Landscapes 12 and 17, where Landscape 12 yielded a higher proportion of new seedlings (Figure 10c). The average elephant density between 1985 and 1997 in Landscape 12 (5.7 elephants/km$^2$) is much higher than the density in Landscape 17 (2.7 elephants/km$^2$), and the higher number of elephants may promote the germination as well as seed dispersion of marula trees (Lewis 1987). The undulating terrain of the granites also contributes towards the

establishment of seedlings, as they are more protected from fire and herbivory than on the open plains of the basalts. The slightly higher proportion of new seedlings in Landscape 12 when compared to Landscape 5 could be due to less competition from vegetation in a landscape with less diverse plant species composition. The greater proportion of individuals in class C in the roan enclosure indicates that low herbivory impact provides the opportunity for marula individuals in the lower canopy to grow beyond the fire sensitive height of 1.5 m as determined by O.S. Jacobs & R. Biggs (In prep. 2000). As opposed to these seedlings, the lower canopy adjacent to the roan enclosure has a high proportion of individuals in class B due to exposure to annual burning in combination with herbivory. This supports O.S. Jacobs & R. Biggs (In prep. 2000) who found the combination of annual burning and herbivory prevents marula trees in the lower canopy from developing into the upper canopy. The larger structure (height and crown) of marulas in the lower canopy within the roan enclosure compared to those encountered directly adjacent to the roan enclosure (Figure 12) further reflects the impacts of increased herbivory and fire frequency on individuals adjacent to the roan enclosure.

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

that trees higher than the preferred feeding level (>7 m) were in general harder to break or push over by elephants.

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

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

*Single vs. multi-stemmed individuals*
The high proportion of single-stemmed individuals in the lowest height class (A) is due to the fact that they are mainly new seedlings. Once the seedlings grow beyond 0.25 m, the stem morphology

becomes predominantly multi-stemmed due to fire and herbivory impacts (Figure 11a). The higher proportion of single-stemmed individuals in the roan enclosure than in any of the other landscapes (Figure 11b) can be attributed to protection against herbivory. The proportion of single-stemmed individuals in Landscape 12 was significantly lower than in Landscape 5 (both on granite) and is probably due to increased herbivore pressure as result of the less diverse vegetation within Landscape 12.

## Conclusion

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

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

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

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

## Acknowledgements

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

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## Abstract

Previous vegetation studies in the Kruger National Park have showed a dramatic decline in the density of large trees in four major vegetation units of the Park. An assessment of the damage status of *Sclerocarya birrea* (marula), identified as one of the most important tree species in the Kruger National Park, was conducted across three major landscapes of the Park. Previous studies indicated that marula were most utilised by elephants, resulting in weak regeneration and recruitment, with consequent changes to the population structure of the species. Furthermore, results indicated that the marula populations in two major landscapes of the Kruger National Park were threatened. The objective of this study was to generate a data set, which can be used in conjunction with future monitoring, to quantify the elephant damage to the marula population in the Kruger National Park. Results indicated that almost half the surveyed population suffered from damage due to elephant activity, predominantly in the form of bark stripping and felling. Felling resulted in a large proportion of marula trees being reduced to a height of less than 5 m. Main stem breakage by elephant was the main cause of the 7% mortality observed in the marula population.

**Key words:** damage, population structure, savanna, utilisation

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## Introduction

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

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

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

coppicing from the remaining stump and new trunks emerging from the partially uprooted trees (Coetzee *et al.* 1979).

The feeding methods of elephants vary according to the size-classes of woody plants (Vancuylenberg 1977). In a study of *Acacia tortilis* at Lake Manyara, Tanzania, Mwalyosi (1987) reported that smaller trees were less susceptible to being killed by elephants than larger trees. Lewis (1987) and Gadd (1997) found stems smaller than 2 cm in diameter to be a minor part of the elephant's diet, while Pellew (1983) found that elephants did not eat or destroy stems less than 1 m in height. Since the lower canopy (<2 m) is browsed by other mammals, it is often difficult to attribute the little damage present with any degree of certainty solely to elephant activity (Ishwaran 1983). In particular, Lewis (1987) and Gadd (1997) found marula seedlings to be consumed by other browsers, especially *Aepyceros melampus* (impala). Jachmann & Croes (1991) found the preferred feeding levels of elephants to be between 2 – 3 m, while Jachmann & Bell (1985) found that trees above this height were regularly pushed over. Guy (1976) suggested that the pushing over and uprooting of trees by elephants are more a social display than a feeding necessity, although, Coetzee *et al.* (1979) found that marula trees were utilised after being pushed over in the Kruger National Park. Coetzee *et al.* (1979) concluded that a zone of high elephant impact on vegetation extends to 10 m on either side of the road, followed by a zone of intermediate impact between 10 and 50 m and relatively low impact beyond 50 m from the road. O.S. Jacobs & R. Biggs (In prep.2000 b) found no significant differences in the density of marula seedlings (<2 m tall) between 30 and 50 m from the road.

The dramatic increase in elephant density in the Kruger National Park from 1100 in 1960 to over 8500 in 1970 (Whyte & Wood 1995) led to the implementation of a population control programme in 1976, with the aim of keeping the elephant population constant at about 7500 individuals (Hall-Martin 1992). In 1996 a moratorium was placed on elephant culling and the population has since increased to 8896 in 1998 (I.J. Whyte, In prep. 2000). Concerns about the potential impact elephants have on marula trees in the Kruger National Park gave rise to a study of the population structure of the marula in four landscapes of the Kruger National Park. Results of this study showed the height structure of mature marula trees in the mixed

*Combretum/Terminalia sericea* woodland (Landscape 5) and *Sclerocarya birrea/Acacia nigrescens* savanna (Landscape 17) not to be significantly different, whereas a skewed height structure in the *Colophospermum mopane/Acacia nigrescens* savanna (Landscape 12) differed significantly from the other landscapes (O.S. Jacobs & R. Biggs, In prep. 2000 b) (Figure 14). O.S. Jacobs & R. Biggs (In prep. 2000 b) suggested that the virtual disappearance of marula trees from the *Colophospermum mopane* shrubveld in the Kruger National Park could be attributed to increased elephant populations in combination with triennial fires. The objective of this study was therefore to generate a data set, which can be used in conjunction with future monitoring, to assess the role played by elephant in the observed population structure of the marula in the Kruger National Park, and hence contribute to the adaptive management strategy of the Park.
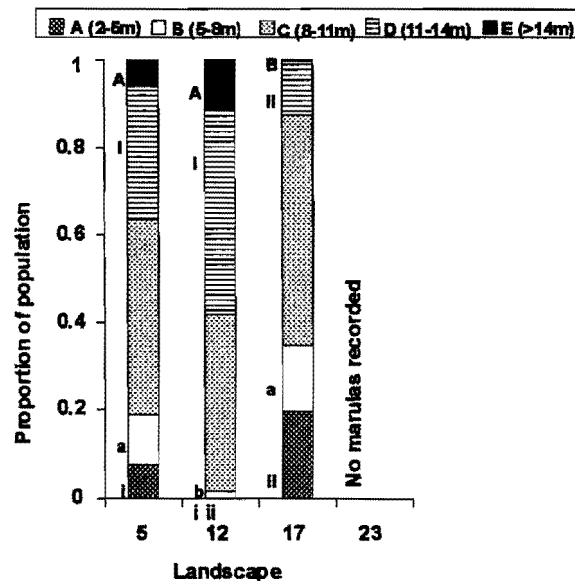


Landscape 5  = Mixed *Combretum/Terminalia sericea* woodland
Landscape 12 = *Colophospermum mopane/Acacia nigrescens* savanna
Landscape 17 = *Sclerocarya birrea/Acacia nigrescens* savanna
Landscape 23 = *Colophospermum mopane* shrubveld

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

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

## Study area

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

## Methods

### Data collection

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

Dead trees were recorded as standing, uprooted or felled. Contrary to the method used by Okula & Sise (1986), uprooted trees with roots still in the soil were considered dead because of the high risk of subsequent destruction by fire. Trees, of which the main stem was broken and no coppicing had occurred, were classified as felled trees. Uprooted and felled trees were assumed

to have died as a result of elephant damage. Causes of mortality for standing dead trees include death due to old age, boring insect activity and ring-barking by elephants.

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

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

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

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

## Data analysis

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

The fire parameter was not analysed as too few observations were recorded (only 23 living trees with fire scars were observed). In order to investigate the tree damage in relation to elephant densities, the annual elephant census results for the period 1985 to 1998 (I.J. Whyte 1998) [1]were used to determine the mean elephant densities (elephants/km$^2$) in the three landscapes.

## Results

Tables 6 to 8 summarise the results of this study. The mean elephant densities per landscape for the period 1985 to 1998 were estimated as: Landscape 5 = 4.3 elephants/km$^2$; Landscape 12 = 5.7 elephants/ km$^2$; Landscape 17 = 2.6 elephants/km$^2$.

*Dead trees*

Approximately 7% of the sampled marula population in the Kruger National Park consisted of dead trees. The majority of these trees had been felled and thus elephant damage seems to be the major cause of tree mortality. The proportion, as well as the nature of dead trees did not differ between marula populations in the different landscapes (Table 7; A).

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

## Table 6.
## Summary of results.

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

\* $r^2$ refers to proportion of total deviance explained by model   \*\* p-values adjusted for multiple testing according to the Bonferoni Theorem

Internal contrasts in proportions of dead trees, degrees of damage, agents responsible for damage and types of bark damage across landscapes, height and damage classes.
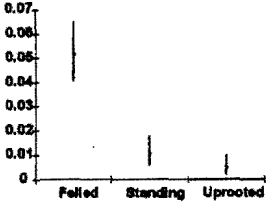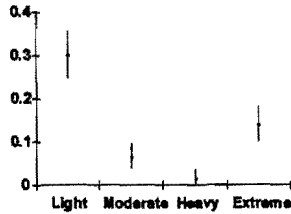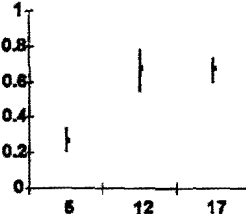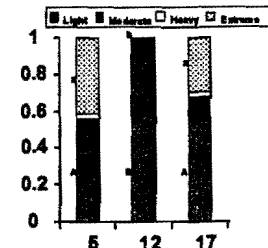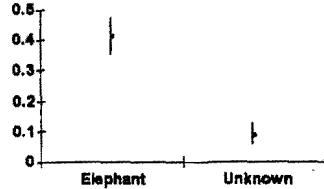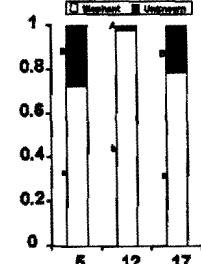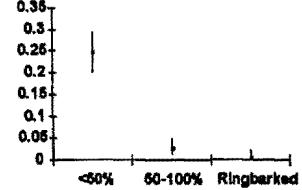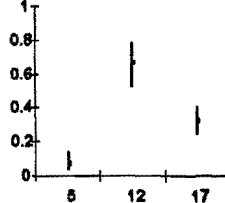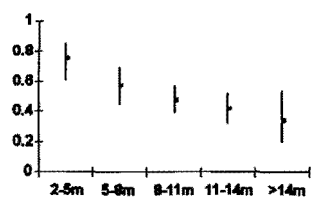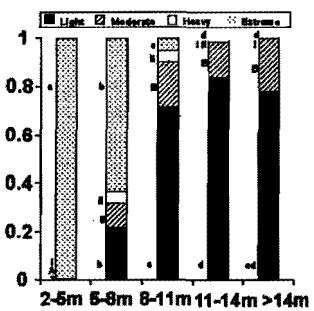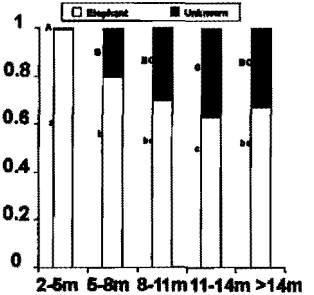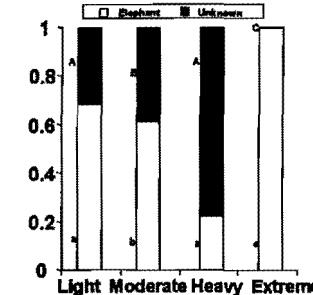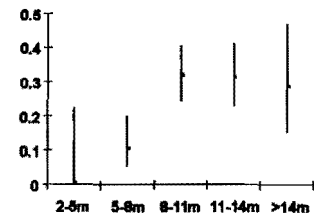
| Parameter | Composition of parameter (Proportion of total sample) | Landscape ** (Proportion of sample per landscape) | Composition across Landscapes ** (Proportion of affected sample) |
|---|---|---|---|
| A Dead Trees |  | NS Average = 6.94% | NS |
| B Damage Class |  |  |  |
| C Damage Agent |  | - |  |
| D Bark Damage |  |  | NS |

**Table 7 continued** .....................

# Table 7 continued

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

\* Common letters indicate parameters not differing significantly

\*\* Landscapes: **5** = Mixed *Combretum/Terminalia sericea* woodland; **12** = *Colophospermum mopane/Acacia nigrescens* savanna; **17** = *Sclerocarya birrea/Acacia nigrescens* savanna

\*\*\* Damage classes: **Light** = tusk marks, <50% bark removed; **Moderate** = <50% bark removed, secondary and smaller branches broken; **Heavy** = >50% bark removed, primary branches broken; **Extremely heavy** = ringbarked or main stem broken

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Table 8

Proportion of sample suffering branch and main stem breakage impacts across landscapes, height and damage classes
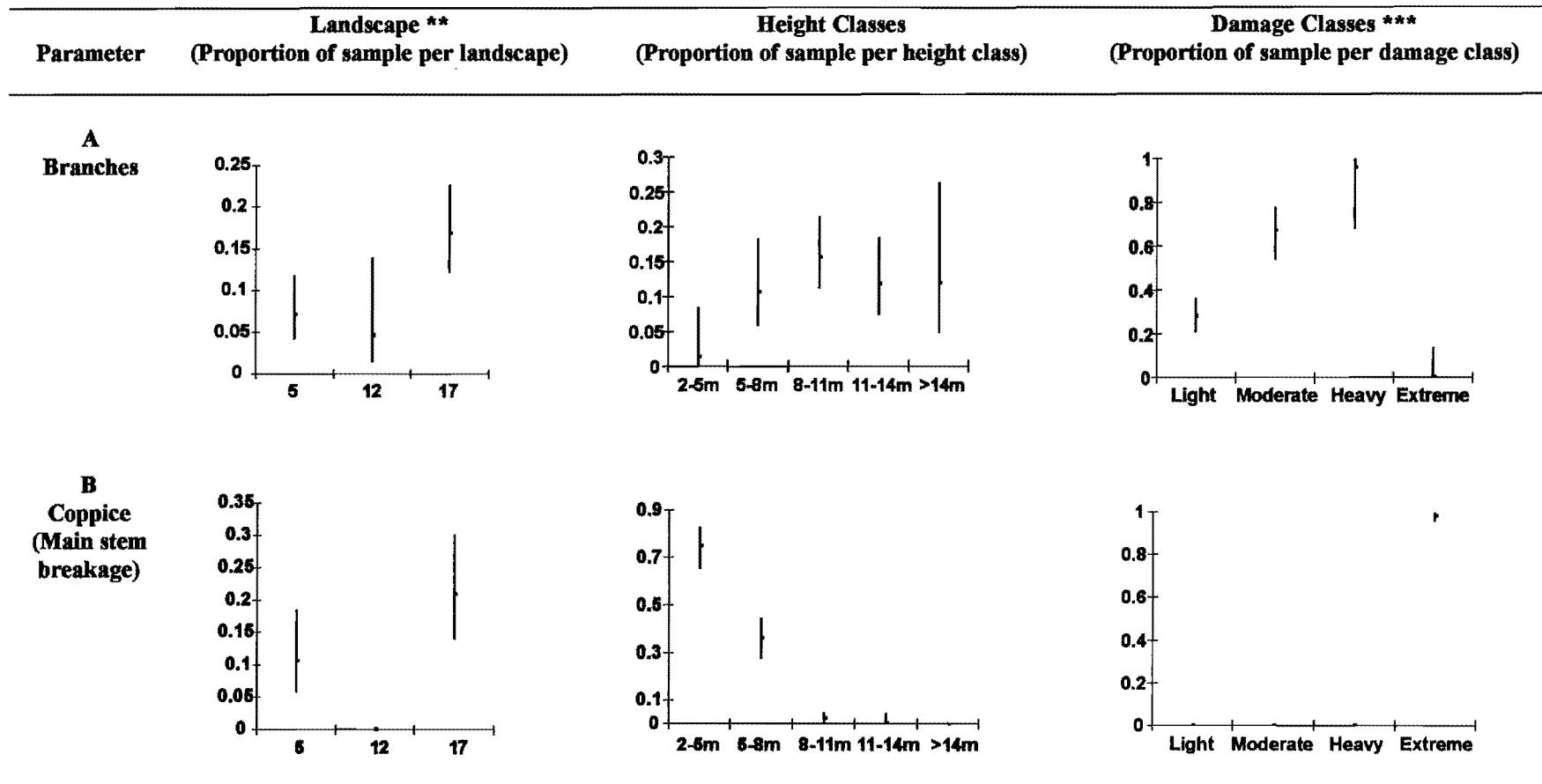
| Parameter | Landscape ** (Proportion of sample per landscape) | Height Classes (Proportion of sample per height class) | Damage Classes *** (Proportion of sample per damage class) |
|---|---|---|---|



**A Branches**



**B Coppice (Main stem breakage)**

**    Landscapes: **5** = Mixed *Combretum/Terminalia sericea* woodland; **12** = *Colophospermum mopane/Acacia nigrescens* savanna; **17** = *Sclerocarya birrea/Acacia nigrescens* savanna

***   Damage classes: **Light** = tusk marks, <50% bark removed; **Moderate** = <50% bark removed, secondary and smaller branches broken; **Heavy** = >50% bark removed, primary branches broken; **Extremely heavy** = ringbarked or main stem broken

*Living trees*

Landscape differences

Approximately 70% of trees in Landscapes 12 and 17 showed signs of damage compared to only 25% in Landscape 5. However, most damage in Landscape 12 was light, whereas a high proportion of extreme damage was recorded in Landscapes 5 and 17 (Table 7; B). A higher proportion of the damage in Landscape 12 was attributable to elephant (Table 7; C). Landscape 12 showed mainly bark damage (Table 7; D), whereas damage in Landscapes 5 and 17 also consisted of a significant proportion of broken branches and main stem breakages (coppicing trees) (Table. 8; A & B).

Height class differences

Examining the damage across height classes, there seems to be a gradual decline with shorter trees suffering more damage than taller marula trees. Trees in the 2–8 m classes showed a significantly higher proportion of extreme damage compared to the predominantly light damage throughout the 8-14 m classes (Table 7; B). The damage across all height classes was mainly ascribed to elephant impacts (Table 7; C). Trees in the 8-14 m height classes had predominantly bark damage (Table 7; D) and broken branches, while damage to shorter trees consisted predominantly of main stem breakages resulting in coppicing (Table 8; A & B). Bark damage to all height classes was predominantly light (<50% bark removed from trunk circumference) (Table 7; D).

Damage class differences

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

**Discussion**

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

*Dead trees*

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

*Living trees*

Structural changes

Approximately 55% of the surveyed marula population had suffered damage of some kind, with about 15% of all recorded damage being extremely heavy. Extreme damage entails mainly broken main stems, from which the marula trees would probably not be able to recover (Barnes 1982), thus changing the population structure towards the shrub category (<3m). Of the sample in the 2 – 5 m height class, 78% trees were coppicing. This indicates that a number of bigger trees had suffered main stem breakage (and hence height reduction) as a result of severe browsing. Anderson & Walker (1974) found that elephant damage in the form of broken stems and branches could reduce the height structure of selected trees, and that severe reduction in height causes a proportion of trees previously not affected by fire, to be susceptible to fire impacts. O.S. Jacobs & R. Biggs (In prep. 2000 a) found that the empirical fire escape height for marulas is between 2.5 and 3 m. This supports Jachmann & Croes (1991) who stated that elephant damage to mature trees which results in smaller, coppicing stems, increases the individuals' vulnerability to fire. They further found that the combined effects of foraging and fire resulted in the loss of a high percentage of woody stems. Although Haig (1999) found that mature trees are mostly resilient to elephant damage and that they coppice readily, it appears as though the interaction between

elephant impact and fire might have a significant impact on the height structure of the marula population in the Kruger National Park.

Damage class differences

The greater proportion of damage in the damage classes were ascribed to elephant damage, except in the case of the high damage class where damage was mainly recorded as unknown. The largest proportion of heavy damage was recorded on trees between 5 – 11 m, which could be ascribed to branch breakage due to elephant, giraffe or wind. However, branch breakage appears to be a minor form of damage as only 10% of the surveyed population had broken branches. Gadd (1997) found that marula trees could survive any branch breakage if less than 75% of damage occurred to an individual tree. Results further support Tchamba & Seme (1993) who found that ringbarking of trees, uprooting and bark stripping constitute a minor part of the elephants' feeding activity. Although bark stripping was found to be the main type of bark damage, a large proportion of the affected sample would probably recover due to the self-healing process (Coetzee *et al.* 1979). Trees, however, are susceptible to boring insects once the sapwood is exposed, and elephant damage to trees most probably contributed to the 1% mortality rate of dead but standing trees (Table 7; A). Haig (1999) found that 35% of the marula population sampled with bark damage yielded borer infection, indicating that elephant impact due to bark damage is not as minimal as suggested by Coetzee *et al.* 1997).

Height class differences

Damage to the shorter trees (class A) was significantly higher than the damage experienced by the taller trees (classes C, D & E), suggesting that elephant select the smaller trees in preference to the larger ones, as found by Van Wyk & Fairall (1969) and Anderson & Walker (1974). Approximately 99% of the population sampled in class A yielded extreme elephant damage, mostly due to main stem breakage. This class includes the preferred level of elephant feeding, estimated between 2 – 3 m (Jachmann & Croes 1991). Jachmann & Bell (1985) found that trees, higher than the preferred feeding level, were pushed over or felled. This can explain the high proportion of extreme elephant damage in class B (5 – 8 m). Elephant impact seems to decrease with increase in height, where classes C, D and E showed virtually no signs of heavy or extreme

damage, and experienced mainly light damage due to bark stripping. Results therefore indicate that trees >8 m are not as severely impacted on by elephants as those <8 m. This supports Jachmann & Bell (1985) who found that trees >7 m were more difficult to fell or uproot, depending on the root system. Van Wyk & Fairall (1969) found that marula trees were, in comparison with other trees with shallow root systems, less often completely uprooted and destroyed. The classes <8 m are therefore probably more uprooted and foraged upon, and this could explain the smaller proportion of trees <8 m throughout the different landscapes as found by O.S. Jacobs & R. Biggs (In prep. 2000 b).

Landscape differences

The significantly lower incidence of elephant damage in Landscape 5 as opposed to Landscape 12 (both on granite), may indicate that marulas in less diverse vegetation are more prone to suffer elephant damage. Landscape 12 is an open tree savanna dominated by mopane trees, where a study on the population structure of the marula (O.S. Jacobs & R. Biggs, In prep. 2000 b) showed a highly skewed structure (Figure 14). A higher elephant density may further exaggerate elephant impact in Landscape 12. The high elephant damage encountered in Landscape 17 (on basalt), however, may indicate that marulas are more selected for on the basalt substrata, independent of other available browse and elephant densities. It further appears as if the extent of elephant damage depends on the composition of the marula population structure. O.S. Jacobs & R. Biggs (In prep. 2000 b) found the marula populations in Landscape 5 and 17 to have a good distribution of individuals throughout the different height classes (Figure 14). The nature of the elephant impact in these landscapes did not differ significantly (Table 7; B) where both yielded predominantly light and extreme damage. The population structure in Landscape 12, however, comprises mainly of trees >8 m (Figure 14) and yielded light bark damage (<50%) with no heavy or extreme damage. Thus, it appears as though the higher proportion of extreme damage in Landscapes 5 and 17 correspond to the higher proportions of small trees (2 –5 m) encountered in these landscapes. When examining damage to the different height classes, it is clear that extreme damage dominates the 2 – 8 m height class. The damage recorded in Landscape 12, however, might be an underestimation of the total elephant damage throughout this landscape, as O.S. Jacobs & R. Biggs (In prep. 2000 b) suggested that the low vegetation diversity probably

enhanced the impact on the 2 – 8 m classes, yielding a lack of immature marula trees. The significantly higher bark damage recorded in Landscape 12 could possibly also be ascribed to less diverse vegetation and hence browsing material in this landscape. This supports Buechner & Dawkins (1961) who stated that access to an abundant supply and great variety of browse may alleviate the need, or desire for feeding on the bark of trees. Barnes (1982) found that bark was stripped in the late dry season, just before the trees started to produce leaves, and Guy (1976) suggested that more bark was eaten in the late dry season because of the increased translocation of water from the roots towards the new leaves.

O.S. Jacobs & R. Biggs (In prep. 2000 b) further stated that Landscapes 5 and 17 appear to have healthy populations. However, results of this study indicates that more than 60% of the trees in classes A and B are suffering extreme elephant damage, and therefore the impact on marula populations in Landscapes 5 and 17 might cause a decline in the health of these populations.


## Conclusion

The combined effects of elephants and fire are documented to result in the loss of woodlands (Laws, Parker & Johnstone 1975; Barnes 1983; Ben-Shahar 1996). Beuchner & Dawkins (1961) stated that all woody vegetation is undergoing a process of conversion to grassland under the combined influence of elephants and fire. Results of Trollope et al. (1998), who found a dramatic decrease in large tree densities, indicate that this might be happening in the Kruger National Park. This study highlighted the role played by elephant in this process with regards to the marula population in the Kruger National Park.

More than half the marula trees sampled in this study are suffering elephant damage at present, with elephants being the main cause of the 7% mortality recorded. Marula individuals with bark damage are likely to be affected by fire damage to exposed tissues by the actions of animals gouging, peeling and ripping the bark while foraging and rubbing on the boles of the trees (Beuchner & Dawkins 1961). Bark damages also increase marula trees susceptibility to borer activity.

Elephants appeared to alter the structure of marula trees, resulting in a significant number of trees coppicing between 2 – 5 m, hence increasing the number of trees susceptible to fire and decreasing the number of trees in the 5 – 8 m height class. Anderson & Walker (1974) found that elephants move on to the next favoured species when food becomes less available, and the process will repeat itself. The amount of elephant damage in Landscape 12, reviewed in conjunction with the population structure, poses a serious concern as it appears that successful recruitment into the upper canopy is not occurring (O.S. Jacobs & R. Biggs, In prep. 2000 b), while most of the older trees suffer bark damage, increasing their susceptibility to boring insects and fire. It further appears that the healthy population structure in Landscapes 5 and 17 (O.S. Jacobs & R. Biggs, In prep. 2000 b) is threatened since the majority of the trees in the 2 – 5 m class appear to have been bigger trees which have suffered main stem breakage, and are now coppicing. These findings support Trollope *et al.* (1998) who stated that the changes in woody vegetation involve a change in structural diversity where the woody vegetation of the Kruger National Park is being transformed into a short woodland community interspersed with a low density of large trees.

## Acknowledgements

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# THE EFFECT OF DIFFERENT FIRE TREATMENTS ON THE POPULATION STRUCTURE AND DENSITY OF THE MARULA (*SCLEROCARYA BIRREA* SUBSP. *CAFFRA*) IN THE KRUGER NATIONAL PARK.

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## Abstract

To determine the influence of frequency and season of burn on the growth structure and density of *Sclerocarya birrea* (A. Rich) Hochst. subsp. *caffra* (Sond. Kokwaro), six replicated fire treatments of the experimental burning plot trial were surveyed in the *Sclerocarya birrea/Acacia nigrescens* savanna of the central Kruger National Park. Studies were also conducted in an exclosure to determine the success of recruitment of *Sclerocarya birrea* (marula) individuals across a range of fire intensities in the absence of herbivory. The results indicated that the lower canopy structure (individuals <2 m) was greatly affected by fire, whereas density was unaffected. The lower canopy generally responded to the interaction between frequency and season, and not to the main effects of season or frequency. August triennial burns had the greatest impact on the total seedling structure, with higher fire intensities resulting in the development of a multi-stemmed morphology.

**Keywords:** fire frequency, fire intensity, fire season, management fire, prescribed fire, savanna.

## Introduction

The visual appearance of the woody vegetation over much of the Kruger National Park confirms that there has been a significant decline in the density of large trees in the Kruger National Park (Viljoen 1988). Preliminary examination of certain scenes from the fixed- point- photo series suggests that, particularly on basaltic soils, a marked decline of mature marula tree numbers has occurred over the past eighteen years and that recruitment is not taking place. This is possibly due to an interaction between fire and elephants. It is hypothesised that elephants are killing the mature marula trees by debarking or pushing them over, while fire is preventing young trees from establishing. Norton-Griffiths (1979) found that fire could hold woody plant recruitment rates well below mortality rates even at burning rates that were considered conservative. As part of an investigation into the population structure of the marula trees in the Kruger National Park, the effect of season and frequency of burning, as well as fire intensity, on this tree species was studied. The main objective of this study was to determine the effect of fire management on the structure and density of the marula population of the Kruger National Park, and to determine the success of recruitment of marula individuals in the absence of herbivory. Studies on marula populations were conducted on the experimental burn plot trial in the *Acacia nigrescens/Sclerocarya birrea* savanna and in the Hlangwine exclosure at Pretoriuskop in the Kruger National Park.

Trollope (1980) concluded that fire favours the development and maintenance of a predominantly grassland vegetation by suppressing the development of juvenile trees and shrubs, and preventing the development of more mature plants to a taller fire-resistant stage. The response of vegetation to fire, heavily depends upon fire frequency, seasonality and intensity (Bailey 1988). During a trial to study the effects of different burning frequencies on the density and composition of the woody vegetation in semi-arid savanna in eastern Botswana, Sweet (1982) found that growth of woody plant species and coppice was suppressed by frequent burning.

Fire intensity is a measure of energy released in fires, which varies with fuel moisture content, wind and slope conditions under which the fires burn. The different fire types (headfires, backfires and ground fires) will also affect fire intensity (Trollope 1983). There is a highly significant correlation between fire intensity and topkill (Trollope 1983; Trollope, Trollope, Biggs, Pienaar &

Potgieter 1998b). The main effect of fire on the woody component is to cause topkill of stems and branches, forcing the plants to coppice from the collar region of the stem (Trollope, Potgieter & Zimbatis 1995b). Trollope (1983) found that a hot fire of approximately 2500 kJ. $s^{-1}.m^{-1}$ was necessary to cause a significant topkill of bush to a height of 2 m, and that the topkill of bush does not increase appreciably when fire intensities are greater than 2500 kJ.$s^{-1}.m^{-1}$. Shrubs and seedlings in the <0.5 m height class, however, suffered a significant topkill of stems and branches, irrespective of the fire intensity (Trollope 1983). Trollope *et al.* (1995b) found the threshold height for woody vegetation within the Kruger National Park to be 3 m.

Trollope *et al.* (1995b) further showed that the woody vegetation of the Kruger National Park was not sensitive to season of burning, but that burning frequency seems to have dramatic effects on woody plant phytomass (Trollope *et al.* 1998b). Trollope *et al.* (1998b) stated that the physiological state of the plants rather than the time of year determines the reaction of plants to fire. The average mortality of 14 of the most common bush species in the Kruger National Park that were subjected to fire intensities ranging from 110 to 6704 kJ.$s^{-1}.m^{-1}$ was only 1.3 % (Trollope *et al.* 1995b). The mortality rate of the marula was 0.53% after being subjected to fire intensities >2000 kJ.$s^{-1}.m^{-1}$. Fire therefore, might not necessarily have an impact on the species diversity, but could alter the structure of the woody component (Trollope, Biggs, Potgieter & Zimbatis 1995a).

Van der Schijff (1957) initiated an experimental program of fire research in the Kruger National Park in 1954, where the objectives of this program were to determine the effects of season and frequency of burning on the four major landscapes of the Kruger National Park (Brynard 1972; Van Wyk 1972). The cumulative effect of up to 46 years of different combinations of seasons and frequencies of burning provides a unique opportunity to determine the long-term effects of these treatments on the vegetation of the Kruger National Park, and on the reaction of specific species to different fire treatments (Trollope, Potgieter & Trollope 1998a). Van Wilgen (1987) expressed the need for autecological studies on key plant species on these experimental plots in order to interpret the results of the various treatments.

## Study area and experimental design

The Kruger National Park is situated in the Lowveld regions of Mpumalanga and the Northern Province of South Africa bordering on Mozambique. It covers an area of 18 998 km$^2$. The climate is subtropical with warm wet summers and mild winters, seldom experiencing frost. Annual rainfall varies from 750 mm in the south to 350 mm in the north. The pattern of rainfall over the past century has been characterised by extended wet and dry periods with cycles of about 10 years. A variety of formations, soil types and climatic conditions support a diversity of vegetation types, varying from open savanna to dense woodland. These climatic factors have marked effects on the dynamics of the ecosystem, and on the occurrence of fires (Van Wilgen, Biggs & Potgieter 1998).

Data were collected on certain treatments of the experimental burn plots (Satara, Nwanetsi, Marheya and Lindanda replications) located in the *Sclerocarya birrea/Acacia nigrescens* savanna landscape (Figure 15), which is one of the largest landscapes of the Kruger National Park, covering approximately 7.2 % of the total area. This landscape is described as a semi-arid, basaltic lowveld (Coetzee 1983) with deep, red vertic clay soils (Arcadia form) on the footslopes and in the valley bottom (Venter 1990). The long-term (n = 35 years) average rainfall at Satara is 548 mm (Gertenbach 1983). See Appendix I for a list of the dominant woody species on each of the treatments of these replicates used in this study.

### Experimental Burn Plots

The experimental burn plot trial was initiated in 1954 in four of the major landscapes of the Kruger National Park. Four replicates of this experiment were laid out in each of the following landscapes of Gertenbach (1983): the Lowveld Sour Bushveld of Pretoriuskop; the *Combretum spp/Terminalia sericea* woodland; the *Sclerocarya birrea/Acacia nigrescens* savanna; and the *Colophospermum mopane* shrub. Each replicate consists of 14 contiguous experimental plots, with each plot being approximately seven ha in size and subjected to different burning treatments. Treatments were randomly assigned within the replicate, such that the spatial layout of treatments within each replicate was different (Trollope *et al.* 1998a). The plots are protected from fire by a double width firebreak. Treatments comprise resting the veld (fire exclosure), and burning in autumn, winter, spring and summer on an annual, biennial, triennial, quadrennial and sexennial

basis (Trollope & Potgieter 1985). The quadrennial and sexennial October treatments were initiated in 1979 by dividing the biennial and triennial February plots respectively in half. The plots of these four treatments are therefore half the size (3.5 ha) of the others.

Unpublished data (Trollope 1998)[1], also analysed in this study, were collected from 43 plots that were chosen from the replicates of the experimental burn plot trial located in three of the major vegetation types in the Kruger National Park, namely the Lowveld Sour Bushveld of Pretoriuskop, the *Combretum collinum/Combretum zeyheri* woodland near Skukuza and the *Sclerocarya birrea/Acacia nigrescens* savanna.

**Hlangwine Exclosure**

A separate study was conducted in the Hlangwine exclosure located in Landscape 1, the Lowveld Sour Bushveld in the southern moist savanna near Pretoriuskop. This landscape, as described by Gertenbach (1983), covers approximately 2.8 % of the Kruger National Park and has an annual rainfall that varies between 600 and 1000 mm. The high soil moisture causes the grass to sprout even during winter. Soils of this landscape are sandy, mainly of the Hutton and Clovelly forms. The vegetation structure of the uplands is an open tree savanna with relatively low shrubs. *Terminalia sericea* and *Dichrostachys cinerea* subsp. *africana* dominate the woody component (Gertenbach 1983). The field layer is tall (1-2 m) and is dominated by sour grass species such as *Hyperthelia dissoluta, Elionurus muticus* and *Hyparrhenia hirta*. The bottomlands in the landscape are narrow and consist of an open savanna with single trees and sparse shrubs with a denser grass cover (Gertenbach 1983). The marula is noted as an important tree species associated with this landscape.

The Hlangwine exclosure (Figure 15), which is divided into six blocks, was established in 1973 and comprises 269 ha. Each block is approximately 700 m x 500 m. The dominant woody species in the Hlangwine exclosure are *Terminalia sericea* and *Dichrostachys cinerea* subsp. *africana*.

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[1] TROLLOPE, W.S.W. 1998. Unpublished data from post-burn surveys conducted in the Kruger National Park during 1987. Dept. Livestock and Pasture Science, University of Fort Hare, Alice.
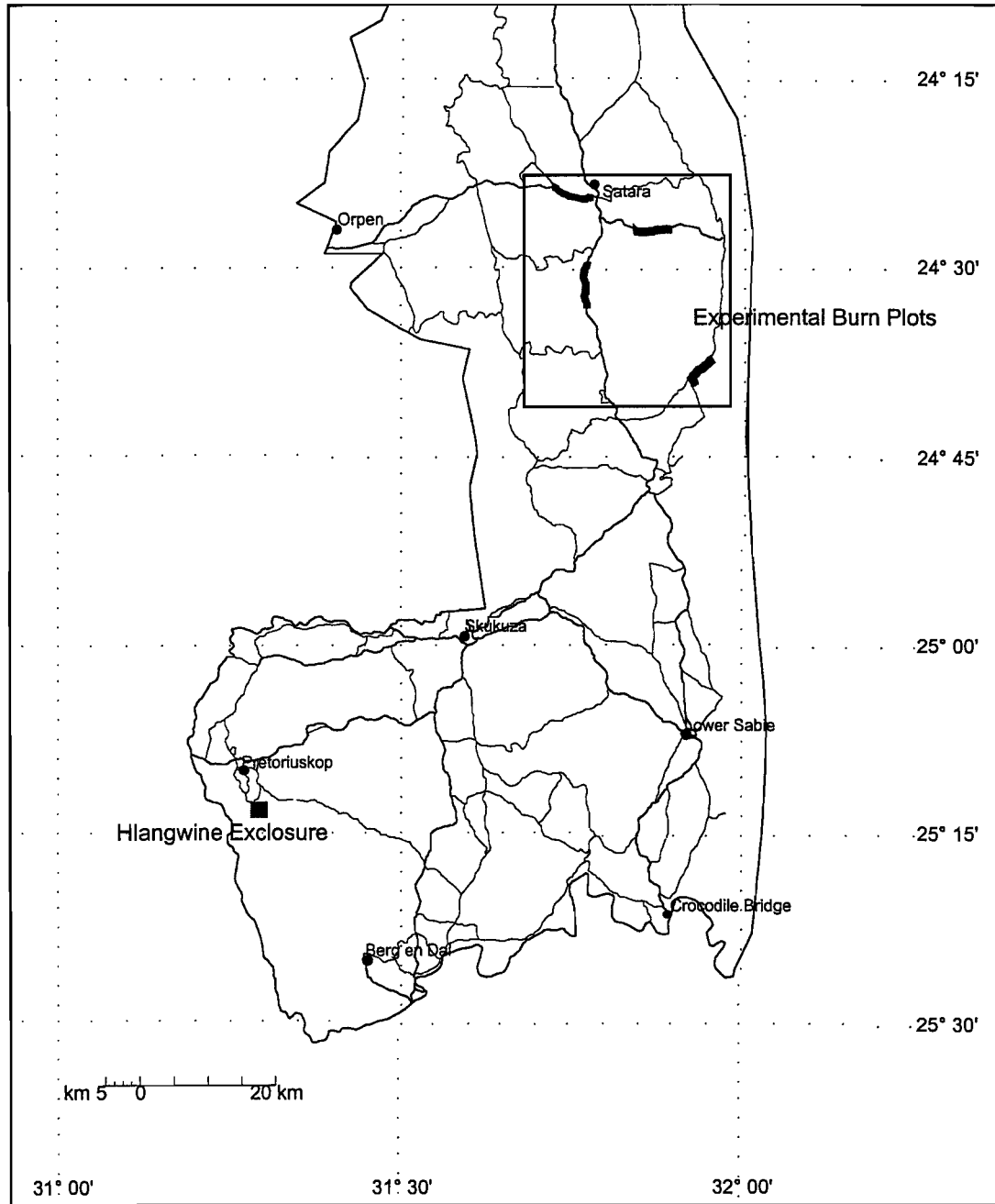
Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 15.     Location of the experimental burn plots (Satara, Nwanetsi, Marheya and Lindanda replications) and the Hlangwine exclosure in the Kruger National Park.

# Methods

## Data collection

### Experimental Burn Plot trial

To study the effect of the different components of the fire regime on the structure and density of marula individuals, data were collected from the following replicated treatments of the experimental burning plot trial:

- August (A1)    -    annual burn
- August (A2)    -    biennial burn
- August (A3)    -    triennial burn
- February (F2)  -    biennial burn
- February (F3)  -    triennial burn
- October (O6)   -    sexennial burn
- Fire exclosure (XC) -  no burn

The treatments used were chosen mainly to include those that are applied when the vegetation is usually physiologically dormant and physiologically active, i.e. those treatments that are applied in the middle of summer and winter respectively. A sexennial treatment was also included to determine the effect of infrequent but intense fires on the structure of marula.

The number of marula individuals in the lower canopy (trees and shrubs <2 m in height) were recorded in eight belt transects with a width of 10 m over the length of each plot. To ascertain the effect of fire on the structure of marula trees in the lower canopy, the height, crown and basal diameters of these individuals were recorded. Where multi-stemmed individuals were encountered, the widest part of the basal diameter was recorded. The stem status of the individuals in the lower canopy, being either multi- (M) or single- (S) stemmed, was also noted to determine the number of coppicing marula trees as opposed to single-stemmed individuals.

The mature marula trees (woody plants >2 m with one or a few definite trunks branching above ground level, as defined by Edwards (1983)) in the above treatments were also recorded. The girth at breast height (GBH) and the height of each tree were measured. If the girth could not be measured because of elephant damage, or because the trunk forked below breast height, the girth at ground level was measured. The regression fitted by Haig (1999) with $r^2 = 0.967$ ($p<0.001$) of

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age on basal circumference of marula was used to derive the approximate age of the trees occurring on the experimental burn plots. The marula growth form is such that there is not a great difference between the basal circumference and the circumference at breast height, thus it can be assumed that the derived age to be accurate when substituting basal diameter with GBH.

Unpublished field data gathered annually by Potgieter (1999)[2] were used to estimate mean fire intensities that occurred on the different treatments during the period 1987 to 1998. Fire intensity has only been recorded since 1987, and due to missing data, only values recorded for 1987 to 1992 and 1995 to 1998 were used to predict fire intensities to which the treatment blocks were subjected. Average fire intensities were estimated for each block, and classified into one of the categories proposed by Trollope & Potgieter (1985). The following fire behaviour model (Trollope 1999) was used to predict fire intensities to which the treatment blocks were subjected:

$$FI = 2729 + (0.8684\ x_1) - (530\ \sqrt{x_2}) - (0.1907\ x_3{}^2) - (596\ 1/x_4)$$

Where:
$FI$ = fire intensity $(kJ.s^{-1}.m^{-1})$
$x_1$ = fuel load $(kg.ha^{-1})$
$x_2$ = fuel moisture (%)
$x_3$ = relative humidity (%)
$x_4$ = wind speed $(m.s^{-1})$

Unpublished data (Trollope 1998)[1] were used to determine the height reduction response (100% (1 – height after burn/height before burn)) of marula trees across all height classes to different fire intensities, ranging from 110 $kJ.s^{-1}.m^{-1}$ to 6704 $kJ.s^{-1}.m^{-1}$. The fires applied to these blocks comprised the annual and biennial treatments during August and October 1989, and the biennial and triennial burning treatments applied during February 1987 (Trollope et al. 1995b). The responses of the various woody species were recorded in two transects laid down the center of each half of the plot, and approximately 20 survey points in each transect were taken. At each survey point the species, height and response of the nearest established tree or shrub were recorded in each quadrant (Trollope et al. 1995b).

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[2] POTGIETER, A.L.F. 1999. Unpublished fire data recorded for the controlled burns applied on the Experimental Burn Plots in the *Sclerocarya birrea/ Acacia nigrescens* savanna in the Kruger National Park. Scientific Services, Kruger National Park, Skukuza.

*Hlangwine Exclosure*

Three blocks in the Hlangwine exclosure (permanently labeled C, B and E) were used to study the reaction of marula individuals to different burning treatments in the absence of herbivory. The burning treatments comprised burning in the middle of summer (C), late winter (E) and autumn (B). Before burning, 50 marula individuals (independent of height) were marked with metal markers, in each of these blocks. Variable numbers of belt transects of 10 m x 50 m were laid out in the different blocks until a total of 50 individuals had been recorded. The height, crown diameter and stem status (multi or single-stemmed) of these individuals were recorded before and after applying the controlled burns. The blocks had not been subjected to any specific burning treatments in the past, and therefore only the fire intensities of the different fires applied in this study were used in the analysis of the data (Table 9). The transects in block E burnt as a back fire, while those in blocks B and C burnt as head fires. Blocks B and E were re-sampled 6 months after the respective fire treatments (shortly after the vegetation started to coppice), while block C was re-sampled 2 months after the fire (as soon as the woody vegetation started to coppice).

The following parameters were recorded before and during the application of the burning treatments in the Hlangwine exclosure: fuel moisture, fuel load, size of burn, wind speed, air temperature and relative humidity, flame height and rate of spread. Values of 16 890 $kJ.kg^{-1}$ and 17781 $kJ.kg^{-1}$ were assumed as the heat yields for grass fuels burning as head and back fires, respectively. These data were used to estimate the intensity of the fires using the following equation (Trollope & Potgieter 1985): $I_H = y\,l\,r$

Where:    $I_H$     = fire intensity $(kJ.s^{-1}.m^{-1})$
          $y$      = heat yield $(kJ.kg^{-1})$
          $l$      = fuel load $(kg.m^{-2})$
          $r$      = rate of spread $(m.s^{-1})$

## Data analysis

*Experimental Burn Plots.*

Analysis of variance was used to examine the data that were normally distributed, i.e. the height, crown, log-transformed basal measurements and GBH measurements. The densities of marula trees in the lower canopy were found to be negative binomially distributed and were thus analysed

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using a negative binomial regression. The proportion of single-stemmed individuals in the lower canopy were examined using logistic regression analysis with over-dispersion corrected using the Williams procedure. Each response was initially examined across all treatments (A1, A2, A3, F2, F3 and XC) and then across a subset of the data (A2, A3 and F2, F3) for separate season and frequency effects. Extremely low counts on the Lindanda replicate and on certain treatments meant that the replicate by treatment interaction could not be estimated.

Table 9

Fire intensity category and fire type of the fire treatments applied to three study blocks in the Hlangwine exclosure.

| Block | Season | Resample period | Fire type | Fire Intensity KJ.s$^{-1}$.m$^{-1}$ | Fire Category |
|-------|--------|----------|-----------|---------------|---------------|
| B | Autumn | 6 months | Head | 4851 | Extremely hot |
| C | Mid-summer | 2 months | Head | 1381 | Moderate |
| E | Late winter | 6 months | Back | 210 | Very cool |

Analysis of variance was further used to investigate the variation in fire intensity on the experimental burn plots. Non-linear regression analysis were used to determine the relationship between reduction and fire intensity as well as between reduction and height of marula individuals.

*Hlangwine exclosure.*

The data collected in the three blocks in the Hlangwine exclosure were pooled and an escape height determined. Changes in height and crown diameter after the lower canopy was exposed to different fire intensities were examined by means of analysis of variance. There was no option but to pseudo-replicate the experiment as the ecology and fire behaviour could not be replicated in the limited exclosures available. Linear regression analysis was used to determine the relationship between height and crown diameter for marula individuals in the lower canopy. A saturated

logistic regression was used to determine the proportion of single-stemmed individuals that changed to multi-stemmed individuals after application of the burn treatments.

# Results

## Experimental Burn Plots

A summary of the observed responses of marula to fires is given in Figures 16 and 17, and each vegetation parameter discussed below. None significant effects are indicated as no response.

*Lower canopy.*

Height response.

Height differs significantly across replicates (p<0.001) and treatments (Figure 16a). Individuals in the lower canopy on Marheya were significantly taller (0.678 m; ± 3.896) than on the other replicates while those on Satara were significantly shorter (0.259 m; ± 9.260). Although the main effect of both season and frequency were not significant, the season by frequency interaction was significant (Figure 16a). Very few marula individuals between 1.5 m and 2 m were present, while the heights below 1.5 m were well represented.

Crown response.

Crown diameter differed significantly across replicates (p<0.001) and treatments (Figure 16b). Only the interaction between frequency and season was significant (Figure 16b). Biennial and triennial February burns yielded very similar crown diameters, whereas biennial August burns yielded significantly wider crown diameters than the August triennial burns.

| | TREATMENT | SEASON | FREQUENCY | INTERACTION |
|---|---|---|---|---|
| **a** Lower Canopy Height (cm) | P<0.001 | No response | No response | P<0.001 |
| **b** Lower canopy crown (cm) | P<0.001 | No response | No response | P=0.0454 |
| **c** Lower canopy log(basal diameter) (cm) | P<0.001 | No response | No response | No response |
| **d** Proportion of single- stem individuals in the lower canopy | P=0.0187 | P=0.00003 | No response | P=0.03215 |
| **e** Tree density of lower canopy (trees/ha) | No response | No response | No response | No response |

A1 – annual August burn    A3 – triennial August burn    F3 – triennial February burn    XC – Fire exclosure
A2 – biennial August burn   F2 – biennial February burn    O6 – sexennial October burn
• No response = not significant at p=0.05 * Bars represent 95% confidence intervals

Figure 16.    Responses of *Sclerocarya birrea* individuals <2.75 m on the experimental burn plot trial in the *Sclerocarya birrea/Acacia nigrescens* savanna.

| | TREATMENT | SEASON | FREQUENCY | INTERACTION |
|---|---|---|---|---|
| **a** Adult GBH (m) | No response | No response | P=0.0107 | No response |
| **b** Adult height (m) | No response | No response | No response | P=0.0294 |
| **c** Fire Intensities (kJ/s⁻¹/m⁻¹) | P<0.001 | P=0.0095 | No response | No response |

Fire Intensities $(kJ/s^{-1}/m^{-1})$

A1 – annual August burn
A2 – biennial August burn
A3 – triennial August burn
F2 – biennial February burn
F3 – triennial February burn
O6 – sexennial October burn
XC – Fire exclosure
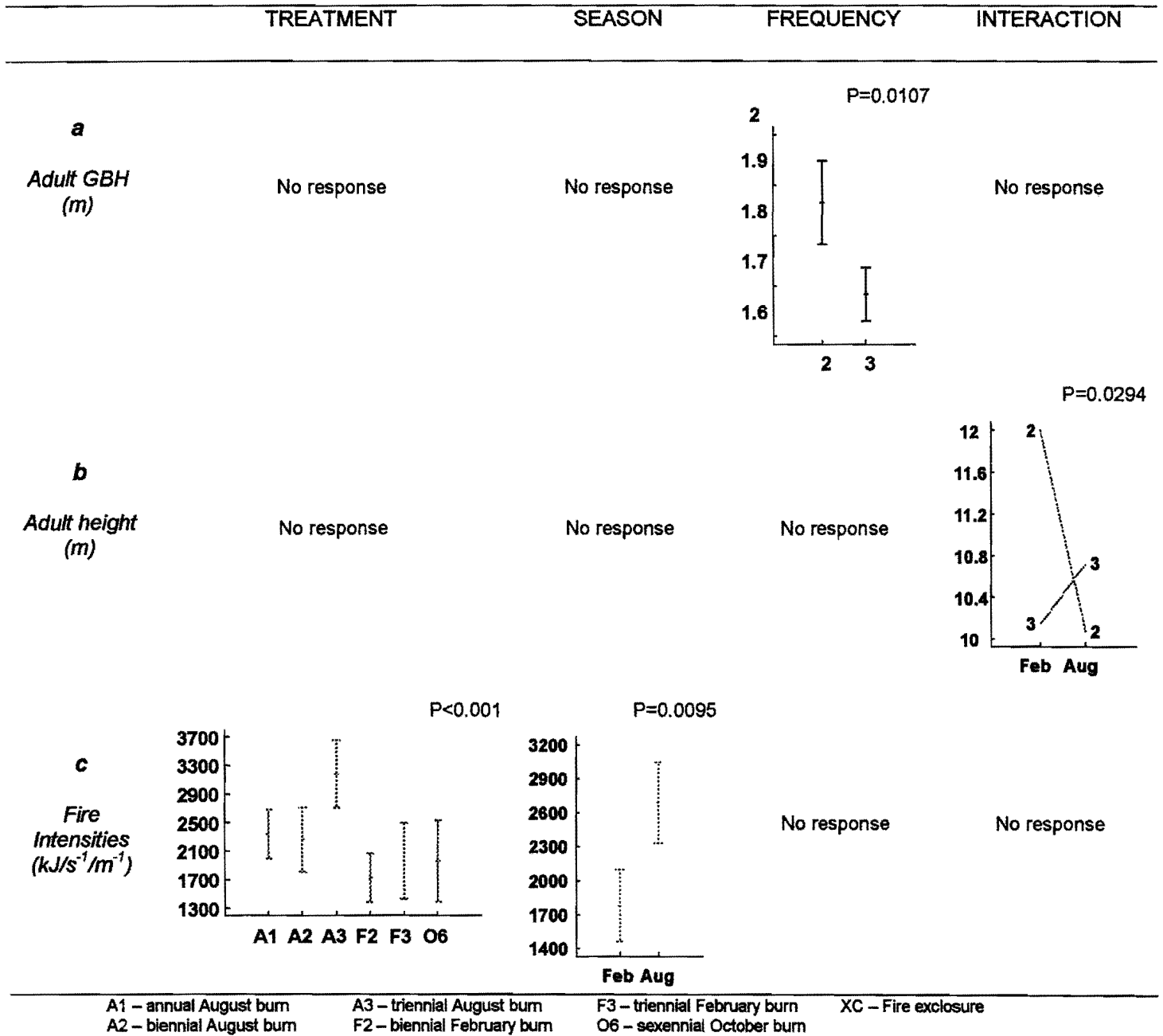
* No response = not significant at p=0.05 * Bars represent 95% confidence intervals

Figure 17. Responses of *Sclerocarya birrea* individuals >2.75 m on the experimental burn plot trial in the *Sclerocarya birrea/Acacia nigrescens* savanna and fire intensities.

Basal diameter response.

The log-transformed basal diameter of individuals in the lower canopy differed significantly across replicates (p<0.001) and treatments (Figure 16c). The August annual burn yielded a wider basal diameter (8.16 cm) than all treatments except the August biennial burn, from which it did not differ significantly. The basal diameter of seedlings did not respond significantly to the main effects of season and frequency of burn, or to their interaction.

Proportion of single-stemmed individuals.

Internal contrast tests show that the fire exclosure (71%) had a significantly higher proportion of single-stemmed individuals than the August treatments, but did not differ significantly from the February and sexennial October treatments. Significant differences in the proportion of single-stemmed individuals were observed across treatments, but not replicates (Figure 16d). Examined for separate season and frequency effects revealed a significant season effect, as well as interactions between replicate and frequency, and between frequency and season (Figure 16d).

Tree density of lower canopy.

A negative binomial regression analysis showed that there were no significant differences in density between treatments, replicates or their interaction. The minimum adequate model was constant plus treatment which explained 35.26% of the total deviance. Examined for separate season and frequency effects also yielded no significant differences between seasons, frequencies, replicates or the interactions of these parameters (Figure 16e).

*Mature Trees.*

Girth response.

The girth at breast height did not differ significantly across treatments (p = 0.0799) or replicates. The main effect of frequency was significant (Figure 17a).

Height response.

The effects of treatment and replicate on mature tree height were not significant, whereas the season by frequency interaction was significant (Figure 17b). The regression for height on GBH did not have a good fit ($r^2$ = 0.1307 and p<0.001). No mature trees between 2 m and 7 m tall

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were found on any of the treatments, including the fire exclosure. However, all the heights between 7 m and 14 m were well represented.

*Fire intensities.*

With year as a covariate (p<0.001), it is clear that fire intensities differed significantly across the different treatments, but not across replicates (Figure 17c). The main effect of season is significant (Figure 17c). Table 10 shows the fire intensities of the different treatments.

Table 10

The fire intensities ($kJ.s^{-1}.m^{-1}$) of the different treatments of the experimental burn plots used in this study.

| Treatment | Mean | Maximum | Standard deviance | Fire category |
|-----------|------|---------|-------------------|---------------|
| August 1 | 2305 | 4203 | 289.24 | Hot |
| August 2 | 2228 | 4606 | 1356.78 | Hot |
| August 3 | 3144 | 4282 | 935.65 | Extremely hot |
| February 2 | 1723 | 5302 | 1439.67 | Moderate |
| February 3 | 1993 | 4370 | 1560.66 | Moderate |
| October 6 | 2185 | 3729 | 827.34 | Hot |

*Reduction Response*

A scatter plot of reduction plotted against fire intensity revealed no relationship between these parameters, and none of a wide range of curves could be fitted successfully to the data. A non-linear generalized logistic regression shows a very clear relationship between height and fire reduction (p = <0.001, $r^2$ = 99.4%) (Figure 16). The following empirical equation can be used to predict reduction of *S. birrea* from height:

$$\text{Reduction (\%)} = 2.78 + \frac{97.24}{\{1 + 19 \exp [43.77 (\text{height} -1.505)]\}^{1/19}} \quad \text{(m)}$$

**The Hlangwine Exclosure**

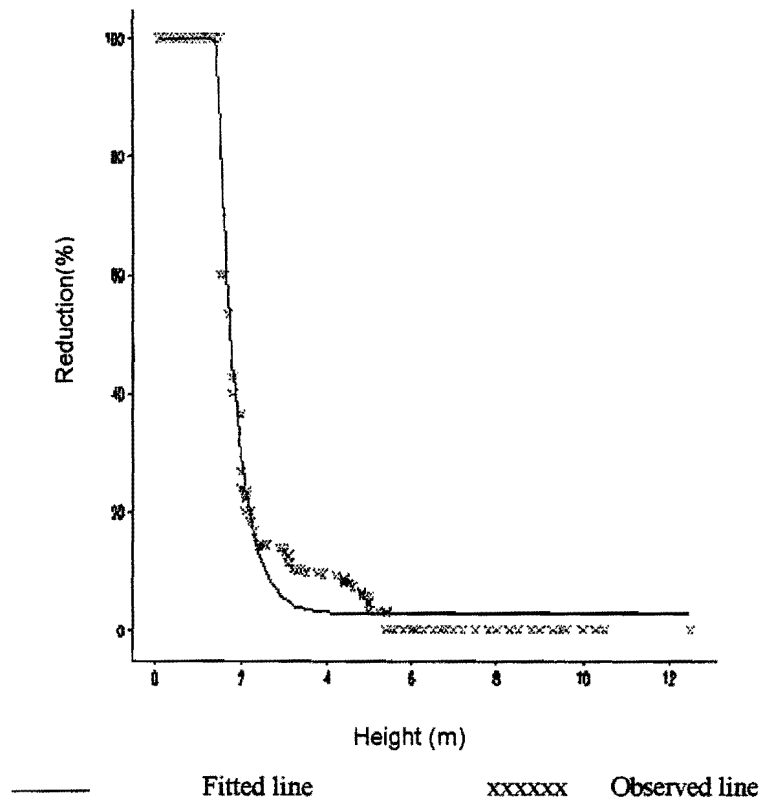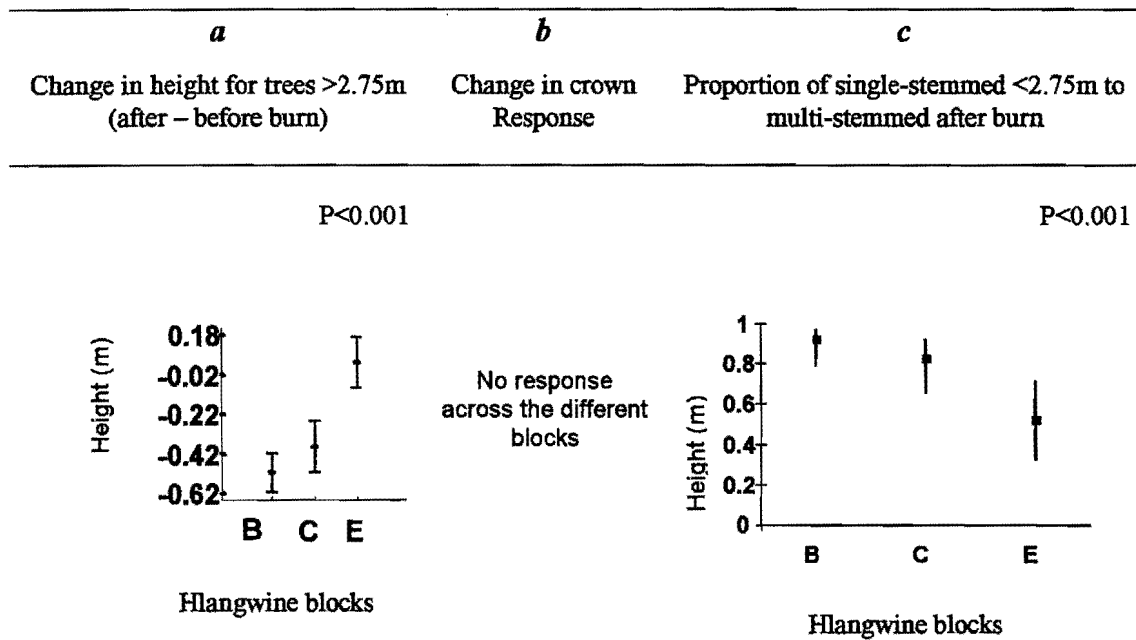The responses of *Sclerocarya birrea* to fire in the Hlangwine exclosure are depicted in Figure 18 and Figure 19.



———————  Fitted line          xxxxxx   Observed line

Figure 18.   Fitted versus observed relationship between height and reduction of *Sclerocarya birrea*.

| *a* | *b* | *c* |
|---|---|---|
| Change in height for trees >2.75m (after – before burn) | Change in crown Response | Proportion of single-stemmed <2.75m to multi-stemmed after burn |



* No response = not significant at p=0.05          * Bars represent 95% Confidence Intervals

Figure 19.      Responses of *Sclerocarya birrea* to fire in the Hlangwine exclosure.

Mortality response.

No marula individuals in the data set experienced mortality across the range of fire intensities recorded on the three blocks. The smallest marula seedling recorded (20 cm on block B) survived the extremely hot fire application by coppicing from the basal region.

Height response.

The tallest tree affected by fire was found to be 2.70 m (Figure 18). Only trees below the empirical fire escape height of 2.75 m were therefore, used to investigate the effect of fire on the structure of marula trees in the Hlangwine camp. The empirical escape heights of the three blocks did not differ significantly.

The change in height (height after burn – height before burn) differs significantly across different fire intensities (Figure 19a). The maximum reductions in height were B = - 2.2 m, C = - 1.9 m and

E = - 0.43 m. The maximum regrowth measured for the different blocks were B = 0.15 m, C = 0.3 m and E = 0.6 m.

Crown response.

Although the change in crown diameter did not differ significantly across the different blocks, a t-test used on the pooled data revealed an overall average decrease of 10.89 cm (p = 0.003) on the three blocks.

A linear regression analysis shows a positive correlation between height and crown diameter (p<0.001, $r^2$ = 59.1%). The relationship between height and crown remained very similar before and after the burn; the relationship before the burn being given by the equation: crown = 0.1778 + 0.16163 x (height <2.75).

Single versus Multi-stemmed.

The proportion of single-stemmed individuals which changed to multi-stemmed after fire application, differed significantly across the three blocks (Figure 19c), and block E differed significantly from blocks B and C.

## Discussion

### The Experimental Burn Plots

*Lower canopy.*

Height and crown response.

Height and crown diameter of the lower canopy was significantly affected by the interaction between season and frequency, but not by the main effects of these parameters (Figure 16a & b). This corresponds with results of Trollope *et al.* (1998b) who found that vegetation in the Kruger National Park is not sensitive to the season of burn. However, these results contradict Trollope *et al.* (1998b) who suggested that the frequency of fire has a highly significant impact on woody phytomass.

Height and crown responses displayed similar trends (Figure 16a & b). Individuals in the lower canopy on the biennial August treatments were taller than those on the other August treatments, suggesting favourable conditions for reaching a fire escape height. Compared to those on the annual August treatments, they have a one-year longer fire return period in which to grow taller. By the August triennial treatments, fuel accumulation results in extremely hot fires, which negate further gains in height. Although annual August fires have significantly lower fire intensities (hot) than August triennial burns, the annual fire return period prevents the individuals in the lower canopy from developing into taller ones. Annual burns also attract increased herbivory, especially from *Aepyceros melampus* (impala) and *Equus burchellii* (zebra) (E.D. Salvesen & M.A.J. Eschenlohr, In prep. 2000), and this may result in increased browsing on woody vegetation. The triennial February burns have a combination of a longer fire return period and moderate fire intensity, resulting in a taller marula structure (Figure 16a). As expected, the exclusion of fire on the fire exclosure plots yielded tall seedlings due to the lack of topkill (Figure 16a). However, the height of individuals in the lower canopy on the fire exclosure is probably suppressed by competition from the herbaceous layer that has not burnt since 1954, resulting in the average height not being much higher than on the other treatments.

Individuals in the lower canopy exposed to the biennial August burns appear to have a bigger structure (height and crown) than seedlings on the biennial February treatments (Figure 16a & b). This is most probably due to the physiological state of the seedlings when exposed to frequent summer burns as opposed to frequent winter burns. The fact that seedlings on the Marheya replicate have the largest structure in terms of height, crown and basal diameter, whereas those on the Satara replicate have the smallest structure (height and crown), can probably be ascribed to finer scale variation in soils and herbivory pressure within the *Sclerocarya birrea/Acacia nigrescens* landscape.

It is interesting to note that the individuals in the lower canopy of the triennial February burn (half of which became the sexennial October treatment in 1979) differed significantly in height and crown diameter from the sexennial October burn, even though the sexennial October burn has only been subjected to three burns since initiation (Figure 16a & b). Due to this relatively short treatment period, the sexennial October treatment may not be a true reflection of long term

marula response to sexennial summer burns. Only individuals in the lower canopy on the sexennial October treatment differed significantly from the fire exclosure in both height and crown diameter, suggesting that this treatment may result in dramatic long-term structural changes.

The differences in the mean basal diameter of individuals in the lower canopy across treatments (Figure 16c) and replicates correspond with the differences in the mean basal diameter of all woody vegetation as found by Enslin *et al.* (2000). As expected, the mean basal diameter of the fire exclosure was significantly smaller than that of all other treatments. Once marula individuals in the lower canopy are exposed to fire (independent of treatment), they coppice from the collar region at the base of the plants, resulting in a significant increase in the basal diameter as well as the proportion of multi-stemmed individuals (Figure 16c & d). This corresponds with results of Trollope *et al.* (1995b), who found that 63% of all woody vegetation sampled, coppiced from the collar region after being subjected to a range of fire intensities.

The higher proportion of single-stemmed individuals in the February treatments and fire exclosure as opposed to the August treatments (Figure 16d), can be explained by the significantly higher fire intensities in August, which result in greater basal coppicing. Higher herbivory pressure on the annual August burns probably contributed to the low proportion of single-stemmed individuals. The presence of multi-stemmed individuals on the fire exclosure plots can only be attributed to herbivory effects.

Examining the density results of the lower canopy across treatments, it is clear that fire does not have a significant impact on the density of marula individuals (Figure 16e). This corresponds with results of Enslin *et al.* (2000), who found that the total woody species diversity and composition on the experimental burn plots did not change between 1954 and 1998, and specifically found no significant marula tree density changes in this landscape. The results also support Trollope *et al.* (1998a) who stated that the frequency of burning does not have a significant effect on the density of woody plants.

*Mature trees.*

By deriving the age of mature trees from GBH measurements (Haig 1999), it appears that all surveyed trees are at least 80 years old. These results, indicate that no mature trees have become established on the experimental burn plots during the past 80 years. This could possibly be ascribed to unfavourable conditions for recruitment of lower canopy marula individuals into the mature population during the 34 years prior to the start of the trial, or perhaps thereafter. Should favourable conditions for marula recruitment have arisen since the start of the trial, the effects of fire and herbivory on the surveyed plots during the past 46 years may have prevented marula individuals from reaching the fire escape height, and could possibly have resulted in the mortality of trees which were just above the empirical escape height at the time the trial was initiated.

Examining the GBH of these adult marula individuals, it seems that longer fire return periods (triennial burns) resulted in smaller GBH than shorter fire return periods (biennial burns), which cause more frequent topkill (Figure 17a). It appears as if the height of mature trees is not much affected by fire, which can be expected as such individuals have outgrown the fire sensitive height (2.5 to 3 m). However, there is a height response to the season by frequency interaction. The conclusion of the GBH and height results indicate that long-term fire treatments can perhaps have an effect on adult marula trees.

*Reduction Response*

Examining the height reduction response of marula, there is no relationship between reduction and fire intensity. This contradicts the results found for individuals in the lower canopy on the experimental burn plot trial, but can be explained by the fact that the lower canopy as well as adult trees, which differ in their response to fire, were included in this reduction study.

The highly significant regression of fire reduction on height is evidence of the overriding influence of height on susceptibility of plants to fire (Figure 20). These results further provide an independent verification of an empirical escape height between 2.5 and 3.0 m for marula. The threshold at 1.5 m suggests that marula seedlings are particularly susceptible to fire, as this height is substantially greater than the height of 0.5 m determined by Trollope (1983) as being the height below which shrubs and seedlings in general suffer significant topkill, irrespective of fire intensity.
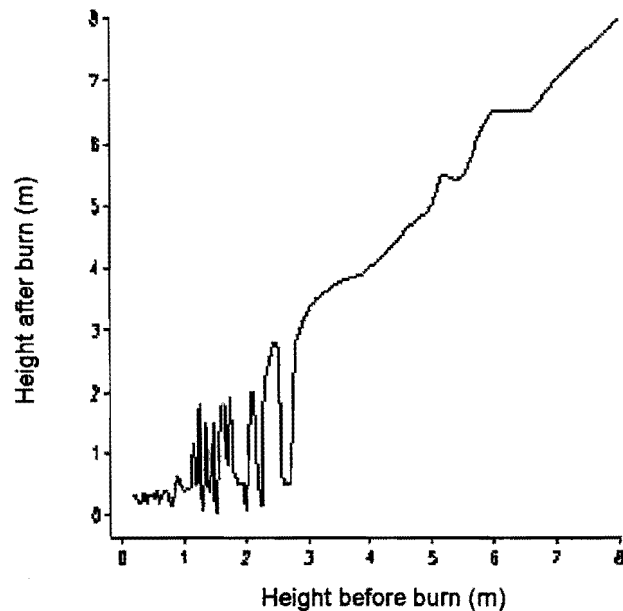
Figure 20.    Line plot of height after burn against height before burn for *Sclerocarya birrea* individuals in the Hlangwine exclosure.

**The Hlangwine Exclosure**

No mortality and hence no density changes occurred in the study conducted in the Hlangwine exclosure. This supports the results obtained from the experimental burn plot trial in this study as well as Enslin *et al.* (2000).

Examining the response of height and crown diameter of marula individuals <2.75 m tall, it appears that differing fire intensities only have significantly different effects on the height structure. Although burning results in a decrease in crown diameter, this decrease does not differ significantly for different fire intensities. Very cool fires do not have a significant impact on height, whereas moderate to extremely hot fires result in significant decreases in height. This corresponds with Trollope *et al.* (1998b), who found that a 2 500 kJ. $s^{-1}.m^{-1}$ fire intensity has a significant effect on height structure, as it results in 53.2% topkill of bush.

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Examining the height regrowth response, the least regrowth was found to appear on the extremely hot April burn (block B). This corresponds with Enslin *et al.* (2000) who found that the woody layer is at a physiologically sensitive state (at a growth peak) at this time of year, and is therefore more vulnerable to coppicing and hence regrowth. Marula individuals <2.75 m appear to recover to their initial height and crown structure within six months of being subjected to a very cool fire in late winter. Although the reduction in height between blocks B (extremely hot) and C (moderate) is not significantly different, the marula individuals of block C have recovered much faster as coppicing already took place two months after being burnt. The regrowth at this time was already twice as much as on block B that was re-measured 6 months after the burn. This supports Trollope *et al.* (1998b), who suggested that fires should be applied when vegetation is normally physiologically dormant (mid winter) and physiologically active (mid summer), and not during their sensitive physiological state (autumn and spring).

Similar trends to the experimental burn plot results were found when examining the proportion of single-stemmed, where all three blocks yielded a significant change to a multi-stemmed morphology after being burnt. It appears that there is a correlation between fire intensity and change in morphology, where increased fire intensities yield a greater change to the multi-stemmed morphology.

## Conclusions

The variance in seasonality and frequency resulted in different effects of fire on marula. Bailey (1995) also found the effect of fire to be variable and contradictory depending on rangeland ecosystem and circumstances. Results of this study further support Bailey (1988) in stating that response of vegetation to fire depends upon frequency, seasonality and intensity, but showed that the interaction between the main effects of season and frequency was the incremental factor. The changes in the woody vegetation in response to fire did not involve a decrease in species diversity, but rather a change in vegetation structure and morphology, and support those of Trollope *et al.* (1995b), Enslin *et al.* (2000) and Bailey (1988) who stated that repeated burning often increases

the species diversity. Results also support Sweet (1982) who found that fire did not significantly affect the density of trees or shrubs, but it affected the structure of the woody vegetation.

Marula seedlings up to a height of 1.5 m are particularly susceptible to fire, and they generally respond to the frequency by season interaction, and not to the main effects of season or frequency. However, results support Trollope *et al.* (1998b) in suggesting that management fires are best applied during mid-summer or mid-winter. Fire enhances the change in the structure of marula seedlings to multi-stemmed, where increased fire intensity results in increased proportions of multi-stemmed individuals. As opposed to the individuals in the lower canopy, adult trees do not respond to fire. Results show the empirical escape height for marulas to be between 2.5 and 3.0 m.

The triennial August burns appear to have the greatest impact on the marula seedlings, probably due to the extremely high fire intensities resulting in increased topkill. The annual August treatments seem to attract increased herbivory, resulting in this treatment having height and basal diameter responses similar to the triennial August treatment. The February treatments and biennial August burn seems to have the least impact on the structure of marula seedlings, indicating favourable conditions for reaching a fire escape height.

Between 1954 and 1992 the fire management policy of the Kruger National Park was to apply triennial burns during late winter on a rotational basis to the fire management blocks of the park (Trollope *et al.* 1998b). The extremely high fire intensities, with the resultant low heights and crown diameters recorded on the August triennial treatments in this study, strongly suggest that this burning policy has hampered the establishment and development of marula seedlings in the park. This may largely explain the observed lack of marula recruitment in the park over the past eighteen years. This supports the results of Enslin *et al.* (2000) who found that the woody vegetation is being transformed into a lower woodland community interspersed with a low density of large trees, together with significant changes in the proportion of single-stemmed individuals. This phenomenon should, however, not be viewed in isolation, as fire/herbivory interactions most probably contributed towards change in habitat.

The current *laissez faire* burning policy was introduced in 1994 where only fires ignited by lightning are permitted to burn and all other ignition sources are controlled as far as possible (Trollope *et al.* 1995a). Lightning ignited fires usually occur in summer with a shorter fire return period. Thus, the current policy may provide more favourable conditions under which marulas can reach less vulnerable heights (taller than 1.5 m). This change in fire policy may result in a turnaround in the observed adult marula decline in the Kruger National Park.

It is believed that some of the parameters and responses determined in this study can be useful for the modeling and understanding of savanna tree responses to fire. Areas of future research and monitoring highlighted by this study centre around the recruitment of lower canopy individuals into the adult population to ascertain whether the current fire policy provides favourable conditions for the establishment of adult marula trees. Although this study shows that fire does play a role in hampering recruitment, it is necessary to examine the population structure of marula in the rest of the *Sclerocarya birrea/Acacia nigrescens* savanna, in order to understand the role of fire in contrast to recruitment events.

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Appendix I: List of the dominant shrub and tree species recorded on the Marheya, Satara, Lindanda and Nwanetsi replications of the experimental burn plots in the Kruger National Park (Enslin 1999[3])

| Replicate | Plot | Dominant vegetation species (decline in dominance from left to right) |
|---|---|---|
| **Satara** | F2 | *Dichrostachys cinerea* subsp. *africana, Ormocarpum trichocarpum, Flueggea virosa* subsp. *virosa* |
| | F3 | *Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Flueggea virosa* subsp. *virosa* |
| | A1 | *Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Flueggea virosa* subsp. *virosa* |
| | A2 | *Flueggea virosa* subsp. *virosa, Dichrostachys cinerea* subsp. *africana, Grewia villosa* var. *villosa* |
| | A3 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Flueggea virosa* subsp. *virosa* |
| | O6 | *Acacia nigrescens, Flueggea virosa* subsp. *virosa, Combretum imberbe* |
| | C | *Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Flueggea virosa* subsp. *virosa* |
| **Nwanetsi** | F2 | *Dichrostachys cinerea* subsp. *africana, Ormocarpum trichocarpum, Cassia abreviata* |
| | F3 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Ehretia obtusifolia* |
| | A1 | *Dichrostachys cinerea* subsp. *africana, Ormocarpum trichocarpum, Combretum africana* |
| | A2 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Ehretia obtusifolia* |
| | A3 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Ehretia obtusifolia* |
| | O6 | *Acacia nigrescens, Combretum africana, Dichrostachys cinerea* subsp. *africana* |
| | C | *Acacia nigrescens, Flueggea virosa* subsp. *virosa, Dichrostachys cinerea* subsp. *africana* |
| **Lindanda** | F2 | *Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Grewia bicolor* var. *bicolor* |
| | F3 | *Ehretia obtusifolia, Dichrostachys cinerea* subsp. *africana, Maerua parvifolia* |
| | A1 | *Dichrostachys cinerea* subsp. *africana, Ormocarpum trichocarpum, Maerua parvifolia* |
| | A2 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Ehretia obtusifolia* |
| | A3 | *Dichrostachys cinerea* subsp. *africana, Ehretia obtusifolia, Ormocarpum trichocarpum* |
| | O6 | *Ehretia obtusifolia, Ormocarpum trichocarpum, Dichrostachys cinerea* subsp. *africana* |
| | C | *Maerua parvifolia, Grewia bicolor* var. *bicolor, Ormocarpum trichocarpum* |
| **Marheya** | F2 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Ehretia obtusifolia* |
| | F3 | *Commiphora schimperi, Dichrostachys cinerea* subsp. *africana, Ormocarpum trichocarpum* |
| | A1 | *Dichrostachys cinerea* subsp. *africana, Acacia nigrescens, Acacia tortilis* |
| | A2 | *Dichrostachys cinerea* subsp. *africana, Ehretia obtusifolia, Flueggea virosa* subsp. *virosa* |
| | A3 | *Dichrostachys cinerea* subsp. *africana, Ehretia obtusifolia, Commiphora schimperi* |
| | O6 | *Dichrostachys cinerea* subsp. *africana, Maerua parvifolia, Ormocarpum trichocarpum* |
| | C | *Commiphora schimperi, Ehretia obtusifolia, Acacia nigrescens* |

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[3] Enslin, B. 1999. Unpublished data from surveys conducted on the Satara experimental burn plots of the Kruger National Park, Department of Research, Kruger National Park, Skukuza.

# CONCLUSION

The combined effects of elephants and fire are documented to result in the loss of woodlands (Ben-Shahar 1996 and Barnes 1983). Beuchner & Dawkins (1961) stated that all woody vegetation is undergoing a process of conversion to grassland under the combined influence of elephants and fire. Major decline in tree densities in certain landscapes of the Kruger National Park were recorded by Trollope, Trollope, Biggs, Pienaar & Potgieter (1998) and Viljoen (1988). In both cases the decline occurred after the Kruger National Park experienced a highly significant increase in elephant densities and fire during the period 1960 to 1986/89 (Trollope *et al.* 1998). Viljoen (1988) speculated that the change in vegetation in the *Sclerocarya birrea/Acacia nigrescens* savanna between 1944 and 1981 could be ascribed to the intense drought during the 1960's in combination with frequent burning and elephant impact.

Tree loss is undesirable as they are of aesthetic, economic and ecological importance (Barnes 1983). Trees provide shade, fruits, browse, and fallen leaves for herbivorous and detrivorous organisms, and play an essential role in the flow of nutrients within the system (Gadd 1997). The marula is one of the best known and most highly valued indigenous fruit trees and has been declared as a protective tree species (Coates Palgrave 1983). In the eastern lowveld of South Africa, the marula tree is regarded as a crucial element of the scenery, and game farm managers are hesitant to acquire more elephants if they jeopardise the abundance of these trees (Gadd 1997). In the Kruger National Park, existing TPC's for rare plants are based on the decline in numbers and recruitment of an order (taking into account the probable biology of the species) that would cause conservation concern, and obvious evidence of "non-natural" threats which constitute persuasive proof on a scale likely to be leading to such declines.

**The current status of the marula population in the landscapes under review is as follows:**

*Landscape 23:* It appears as though marula trees were historically present in this landscape, but that management practices such as increased elephant populations and a fixed fire policy have contributed to the removal of marulas from this landscape.

*Landscape 12:* An unstable population structure for the marula exists. Existing adult trees are mainly older trees at the end of their life cycle, and their death may in time lead to the extinction of the population as the seed source disappears. This process, which is believed to have led to the virtual extinction of marula trees in Landscape 23, may currently be taking place in Landscape 12. The amount of elephant damage in Landscape 12, reviewed in conjunction with the population structure, poses a serious concern as it appears that successful recruitment into the upper canopy is not occurring (O.S. Jacobs & R. Biggs In prep. 2000), while most of the older trees suffer bark damage, increasing their susceptibility to boring insects and fire.

*Landscape 5 & 17:* Although the population structures in Landscape 5 & 17 appear to be healthy, with a good distribution of individuals throughout the different height classes, results of this study further reveals that more than 60% of the trees in the 2 – 8 m height classes are suffering extreme elephant damage. It therefore appears as if the population structures of these landscapes are highly affected by elephant impact, and that they are not as healthy as suggested.

Results of this study indicate that sufficient regeneration of the marula is taking place in the Kruger National Park, but that a combination of factors is preventing successful recruitment into the upper canopy. Geology and rainfall appears not to be the dominant factors contributing to the differences in the population structure between the different landscapes. Results further indicate that seedling mortality can not be related to increased herbivory by small browsers such as impala, but that a combination of browsing pressure and fire influence the structure of the lower canopy. The main impact on the adult marula trees could be related to elephant densities as well as the vegetation diversity. The marula population in less diverse landscapes in the Kruger National Park appears to be more susceptible to herbivory impact. More than half of the marula trees sampled in the Kruger National Park are suffering elephant damage at the current stage, with elephants being the main cause of the 7% mortality recorded. Elephants appeared to alter the tree structure of marulas, resulting in a significant amount of trees coppicing between 2 – 5 m, hence increasing the amount of trees susceptible to fire and decreasing the amount of trees in the 5 – 8 m height class.

The inclusion of the effects and interaction of fire in this study is the general recognition that elephants and fire can have a highly significant impact on the species and structural diversity of tree and shrub vegetation. Results of this study support Bailey (1988) in stating that response of vegetation to fire depends upon frequency, seasonality and intensity, but showed that the interaction between the main effects of season and frequency was the incremental factor. The changes in the woody vegetation in response to fire did not involve a decrease in species diversity, but rather a change in vegetation structure and morphology. The triennial August burns appear to have the greatest impact on the marula seedlings, probably due to the extremely high fire intensities resulting in increased topkill. Between 1954 and 1992 the fire management policy of the Kruger National Park was to apply triennial burns during late winter on a rotational basis to the fire management blocks of the park (Trollope *et al.* 1998). The extremely high fire intensities, with the resultant low heights and crown diameters recorded on the August triennial treatments in this study, strongly suggest that this burning policy has hampered the establishment and development of marula seedlings in the park. This may largely explain the observed lack of marula recruitment in the park over the past eighteen years. This supports the results of Enslin, Potgieter, Biggs & Biggs (2000) who found that the woody vegetation is being transformed into a lower woodland community interspersed with a low density of large trees, together with significant changes in the proportion of single-stemmed individuals.

Overall results of this study therefore strongly supports the hypothesis that elephants are influencing the population structure by impacting on the adult marula trees, while fire is preventing recruitment of the trees into the upper canopy. It further appears as if the problem is more complex, where these factors, in combination with species diversity, global climate change and increased browsing pressure may be contributing to the change in the marula population of the Kruger National Park. The current *laissez faire* burning policy was introduced in 1994 where only fires ignited by lightning are permitted to burn and all other ignition sources are controlled as far as possible (Trollope, Biggs, Potgieter & Zimbatis 1995). This change in fire policy, together with the implementation of the elephant impact zones, may result in a turnaround in the observed marula population decline in the Kruger National Park.

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