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

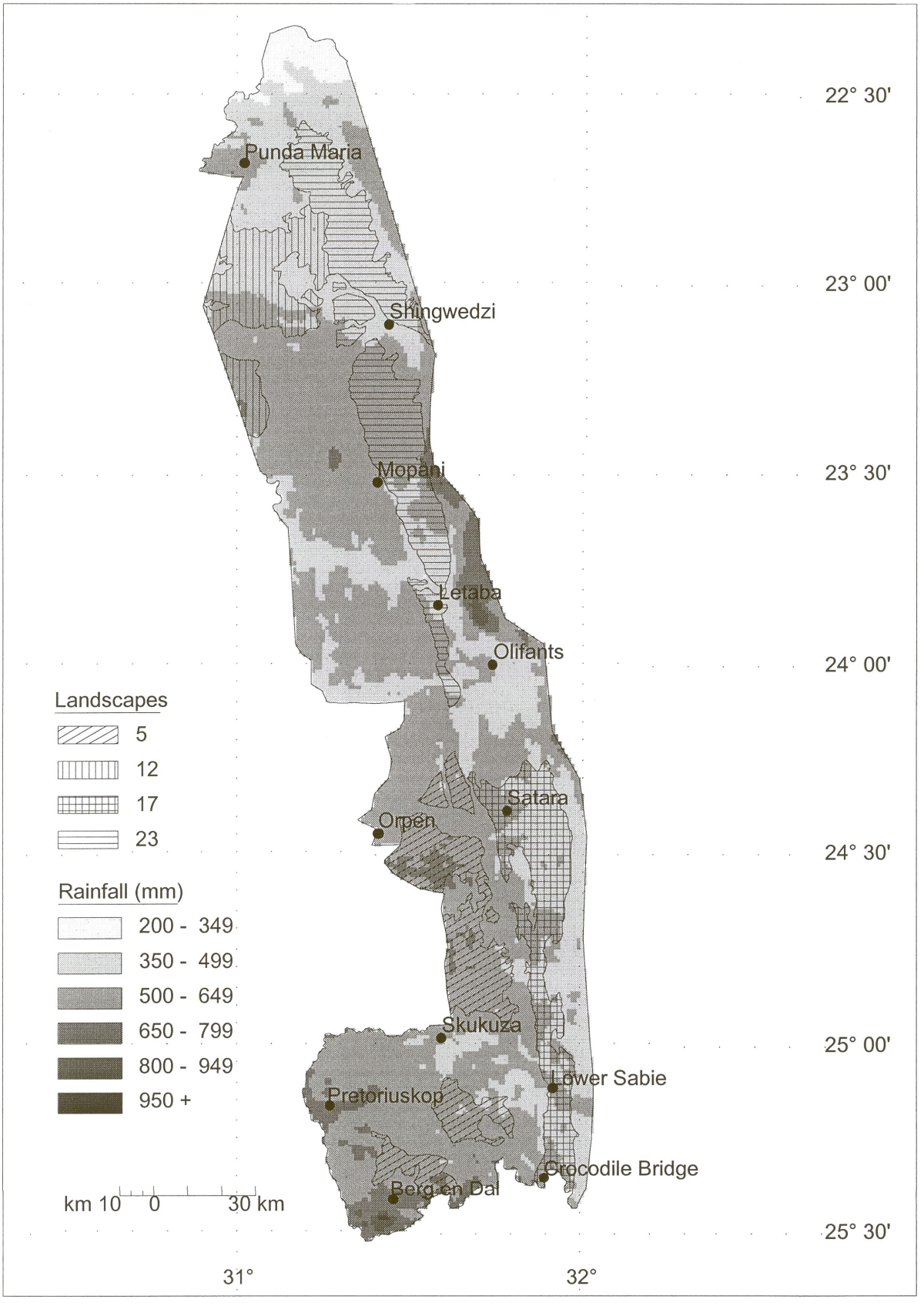
The Kruger National Park, which encompasses an area of 18 998 km^2 forms part of the Lowveld regions of Mpumalanga and the Northern Province, semi-arid regions of the southern temperate zone (Smuts 1975). The Kruger National Park occupies the area between 22°20' to 25°32' latitude south and 30°52' to 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.

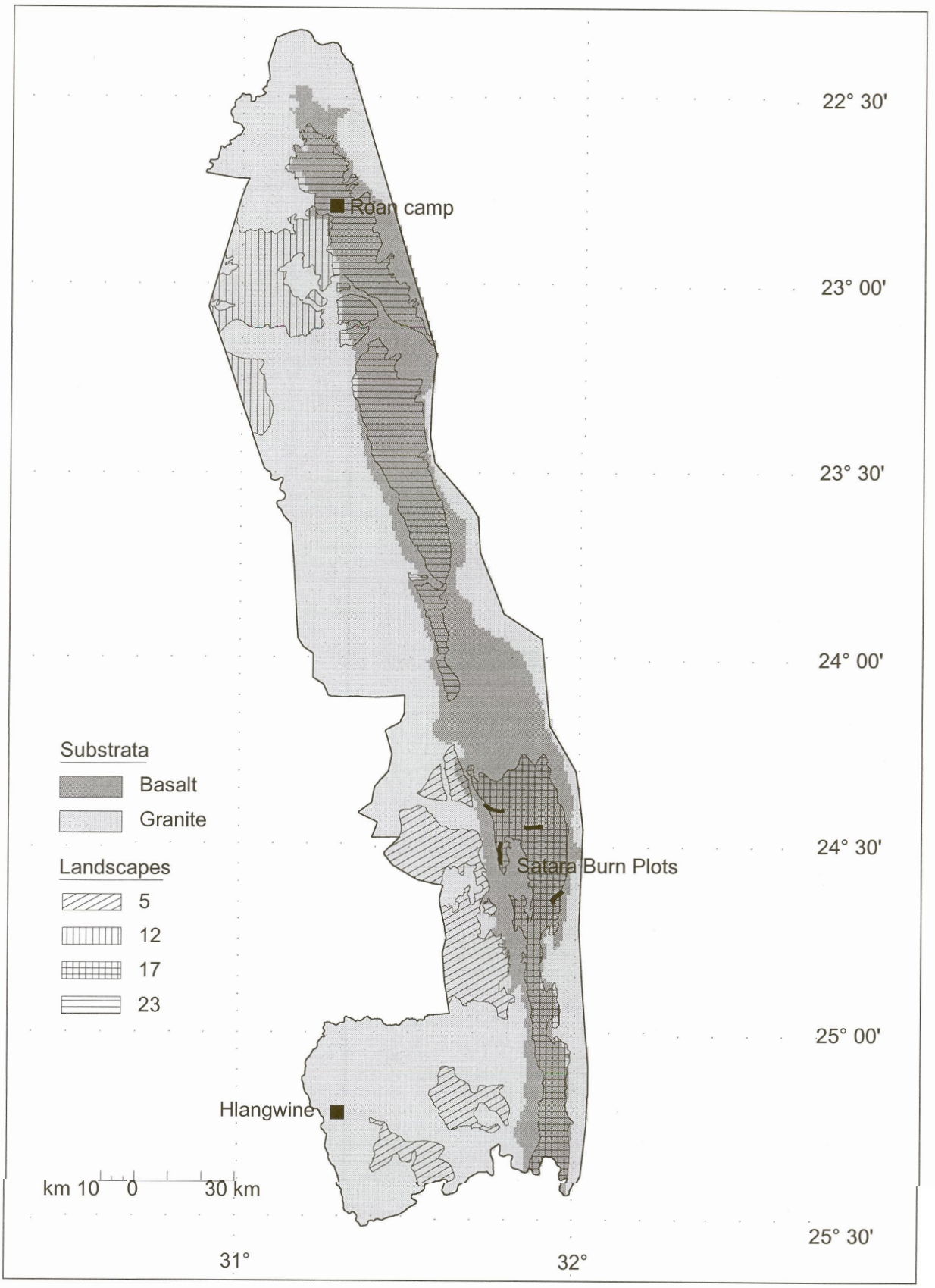
Gertenbach (1983) identified 35 landscapes within the Kruger National Park, each with specific geomorphology, climate, soil and vegetation pattern. These landscapes were described as functional management units, and Gertenbach (1983) suggested that management in the Kruger National Park should be based 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.



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:

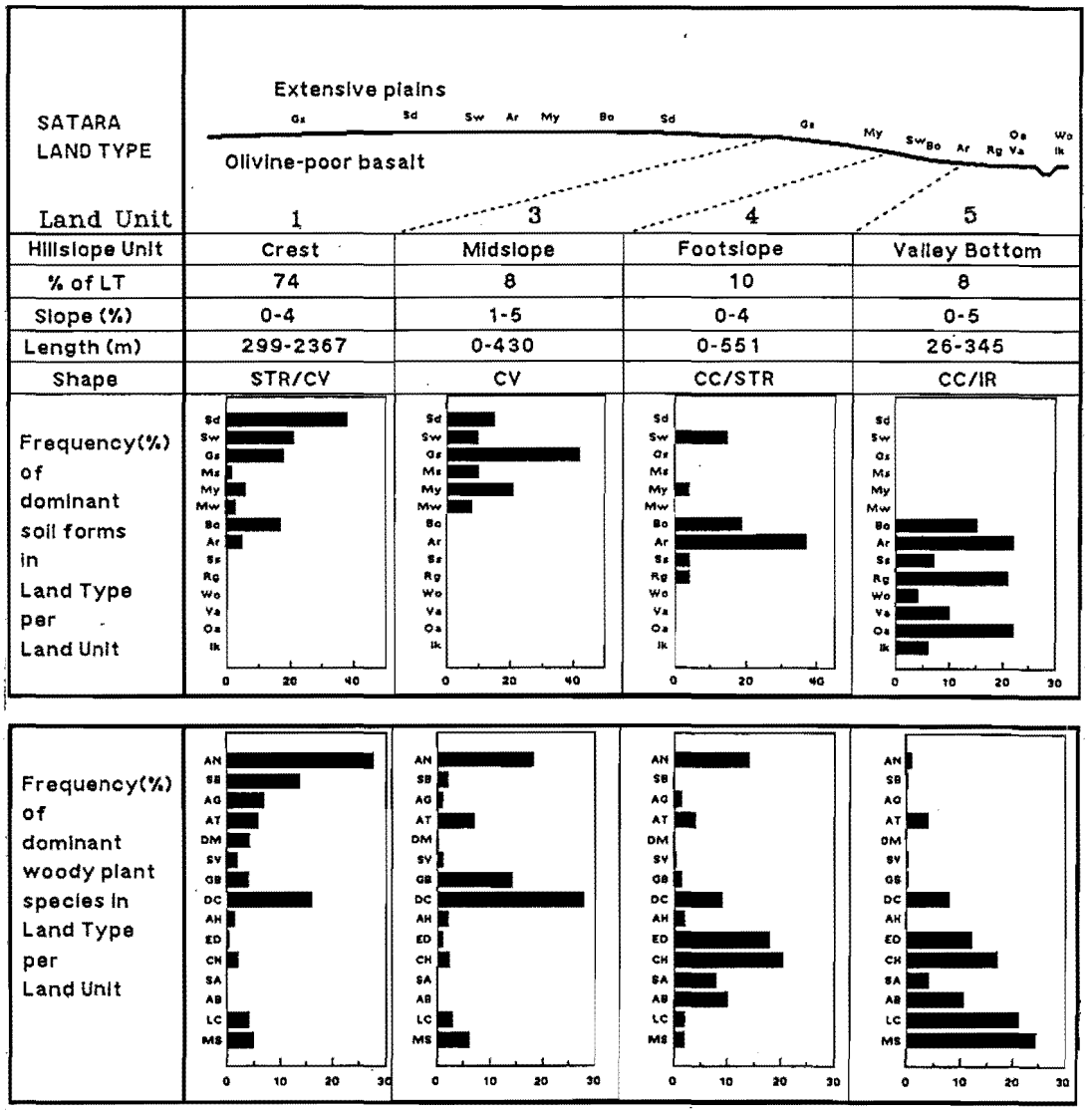
Of the 14 plant communities recognised by Coetzee (1983) and Gertenbach (1983), five closely-related tree veld plant communities are dominated by marula. These plant communities occur on relatively lightly grazed slopes and summits of undulating terrain. Their Central District distribution is from the 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*



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 km^2 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.

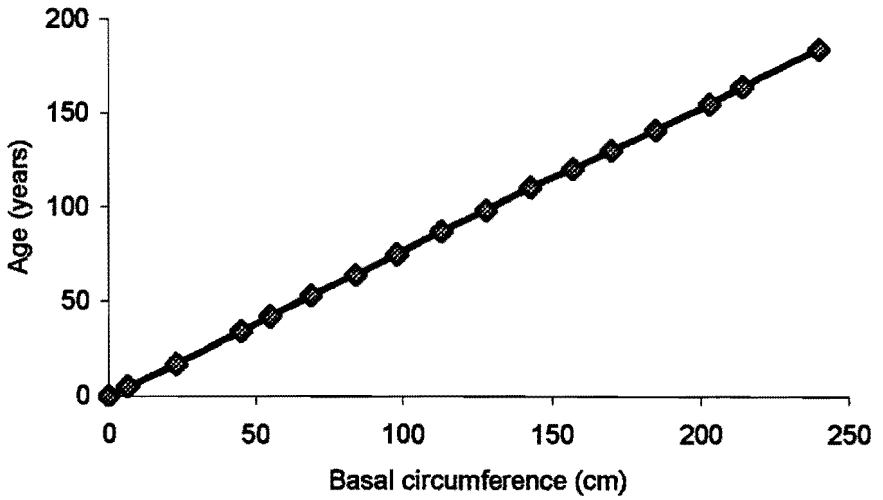


Figure 7. Graphical representation of age derived from basal circumference for *Sclerocarya birrea* trees (Source: Haig 1999).

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

References

COATES PALGRAVE, K. 1977. *Trees of Southern Africa*. C. Struik Publishers. Cape Town.

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

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

DENT, M.C., S.D LYNCH & SHULZE, R.E. 1989. Mapping mean annual and other rainfall statistics over southern Africa. WRC Report No. 109/1/89, ACRV Report No 27. Department of Agricultural Engineering. University of Natal, Pietermaritzburg.

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

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

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

GERTENBACH, W.P.D. 1987. 'n Ekologiese studie van die Suidelikste Mopanieveld in die Nasionale Kruger Wildtuin. Ph.D. thesis. Departement Plantkunde, Universiteit van Pretoria, Pretoria.

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

HOLTHAUSEN, L.C. 1996. Ennobling the wild African Marula (*Sclerocarya birrea* subsp. *caffra*). Internal Report, Kruger National Park, Skukuza.

JACANA & TWISISA. 1997. *Sappi Tree Spotting Lowveld, tree identification made easy*. Jacana Education, Johannesburg.

JOUBERT, S.C.J. 1970. A study of the social behaviour of the roan antelope *Hippotragus equinus equinus* (Desmarest, 1804) in the Kruger National Park. Master of Science, Faculty of Science, University of Pretoria, Pretoria.

LEWIS, D.M. 1987. Fruiting Patterns, Seed Germination, and Distribution of *Sclerocarya caffra* in an Elephant-Inhabited Woodland. *Biotropica*. 19(1): 50-565.

MCVICAR, A.T.P. BENNIE, J.M. DE VILLIERS, F. ELLIS, M.V. FEY, H.J. VON M. HARMSE, M. HENSLEY, J.J.N. LAMBRECHTS, R.W. BRUCE, T.E. DOHSE, J.F. ELOFF, D.C. GREY, M.O. HARTMANN, S.W.J. IDEMA, M.C. LOTTER, F.R. MERRYWEATHER, D. MICHAEL, B.H.A. SCHLOMS, A.P.G. SCHONAU, K. SNYMAN, B.J. VAN NIEKERK, E.VERSTER, R.F. LOTON, J.H. MEYER, D.G. PATERSON, J.L. SCHOEMAN, D.M. SCOTNEY, D.P. TURNER, T.H. VAN ROOYEN, YAGER, T.U. 1991. *Soil classification*. A Taxonomic System for South Africa. Department of Agricultural Development, Pretoria.

PALGRAVE, K.C. 1983. *Trees of southern Africa*. C. Struik Publishers, Cape Town.

POOLEY, E. 1993. *The complete field guide to trees of Natal, Zululand and Transkei. Natal* Flora Publication Trust, Durban.

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

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

TYSON, P.D. & DRYER, T.G.J. 1978. The predicted above-normal rainfall of the seventies and the likelihood of droughts in the eighties. *S. Afr. J. Sc.* 90: 322-329.

VAN WILGEN, B.W., H.C. BIGGS & POTGIETER, A.L.F. 1998a. Fire Management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe*. 41(1): 69-87.

VAN WILGEN, B.W., H.C. BIGGS, S.P.O. REGAN & MARE, N. 1998b. Fire regimes in savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. Internal Report, Skukuza.

VENTER, F. J. 1990. A classification of land for management planning in the Kruger National Park. Ph.D. thesis, University of South Africa.

VON TEICHMAN, I., J.G.C. SMALL & ROBBERTSE, P.J. 1986. A preliminary study on the germination of *Sclerocarya birrea* subsp. *caffra*. *S Afr. J.Bot*. 52: 145-148.

WALKER, B.H., L. STONE, L. HENDERSON & VERNEDE, M. 1986. Size structure analysis of the dominant trees in South African savanna. . *S Afr. J.Bot*. 52: 397-402.