THE VEGETATION AND FLORISTICS OF THE LETABA EXCLUSIONS, KRUGER NATIONAL PARK, SOUTH AFRICA

ABSTRACT

The construction of exclusions along two of the most important rivers in the Kruger National Park was done to investigate how patterns of spatial and temporal heterogeneity of the riparian zone are affected by fire, flood and herbivory. To assist this research programme, vegetation surveys were conducted within exclusions along the Letaba River to classify and map the vegetation of the area. The history and experimental design of the Letaba exclusions are similar to that of the Nkhuholu exclusions along the Sabie River, which is directly related to questions surrounding elephant management. The main difference between the Nkhuholu and Letaba exclusions is local heterogeneity, since the latter lies within the Mopaneveld, which is floristically and physiognomically much more homogenous than the vegetation of the southern Kruger National Park. Nevertheless, four plant communities, eight sub-communities and six variants were recognised and mapped for the Letaba exclusions. The vegetation description was done in relation to prevailing soil forms, differences in species richness, diversity and community structure, and therefore should serve as a basis for further detailed and broad-based botanical studies. Vegetation mapping was done to sub-community level and, where possible, to variant level. As expected in Mopaneveld vegetation, the plant communities could broadly be related to soil types, although smaller-scale variations correspond to soil moisture availability because the Mopaneveld is considered ‘event-driven’, especially in the herbaceous layer.

Conservation implications: Floristic surveying and vegetation mapping of a long-term monitoring site, such as the Letaba exclusions, is seen as a baseline inventory to assist natural resource management. Linking mapping units to biodiversity strengthens the understanding needed to maintain biodiversity in all its natural facets and fluxes.

INTRODUCTION

Situated on the banks of the Letaba River, in the northern half of the Kruger National Park (KNP), the Letaba exclusions were constructed in 2002. For the same reason and purpose as the Nkhuholu exclusions, namely to monitor spatial and temporal heterogeneity along the riparian zone and attempt to determine how these are affected by fire and herbivory (Siebert & Eckhardt 2008). Also, the history and experimental design of the Letaba exclusions are similar to those of the Nkhuholu exclusions (O’Keefe & Alard 2002), which is directly related to questions surrounding elephant management. The different treatment blocks at the Letaba exclusions vary in size, with 42 ha, 51 ha and 36 ha respectively, for the full exclusion, partial exclusion and unfenced area. The main difference between the Nkhuholu and Letaba exclusions is local heterogeneity, because the latter lies within the Mopane Bioregion (Mucina & Rutherford 2006), which is floristically and physiognomically much more homogenous than the southern savannas of the KNP. Animal concentrations are consequently relatively low, exacerbated by the fact that, approximately a decade ago, the Letaba River changed from a perennial river to a seasonal river (O’Keefe & Rogers 2003). The lower mean annual rainfall (approximately 400 mm), compared to the annual 560 mm at Nkhuholu, drives a different fire regime and mammal concentrations. These not only translate into less obvious differences between the different treatments at the Letaba exclusions, but also in a lower rate of changes overall.

In 2000, a flood caused the Letaba River to rise above its macro-channel banks, but did not cause as dramatic change to the riparian vegetation as was recorded for the Sabie River (Parsons, McLoughlin, Kotschy, Rogers & Rountree 2005). Nevertheless, the changes brought about by this large, infrequent disturbance provide an ideal opportunity and context to study and understand the dynamics of ecosystems subjected to different management options. Baseline vegetation surveys were conducted initially and repeated five years later, in 2007, to assess differences between the six treatments in terms of plant species composition and structure for both the woody and herbaceous component (O’Keefe & Alard 2002). The results from this survey will be published at a later stage. A detailed soil inventory was conducted by Paterson and Steenekamp (2003), the results of which were used to help delineate plant communities. Owing to their remoteness and other logistical reasons, the Letaba exclusions have not received the same degree of attention from researchers as the Nkhuholu exclusions. This has led to missed opportunities with regard to the flood legacy. The detailed vegetation classification and floristic description presented here will hopefully attract more interest from scientists, leading to research projects addressing key environmental questions.

STUDY AREA

The Letaba exclusions are situated approximately 5 km upstream of the Mingerhout Dam, along the northern bank of the Letaba River in the Kruger National Park. The exclusions consist of six treatments:

- a fully fenced area (42 ha) excluding all herbivores, divided into, (1) a burn block and (2) a no-burn block

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The total experimental area is 129 ha, excluding the area along the river, which forms a narrow strip inside the river bed (the so-called ‘sacrificial zone’) and the buffer zone adjacent to the three inland sides of the project area.

This summer rainfall region receives approximately 400 mm per annum, as measured at Letaba rest camp, while the mean daily temperature is 23.3 °C, ranging from 7.8 °C in winter, to a maximum of 34.1 °C in summer (Weather Bureau 1986). The most representative underlying geology is granite and Makhutswi gneiss, which contains Swaziland rock formations such as amphibolite and migmatite (Visser, Coertze & Walraven 1989).

According to Paterson and Steenekamp (2003), the Letaba exclosures have a relatively simple soil distribution, with Mispah being the most representative soil form along the mid-slopes and crests. Hutton soils form a strip of deeper apedal soils along the footslopes, whereas alluvial soils of the Oakleaf soil form characterises the banks of the Letaba River (Figure 1). The topography of the area is characterised by a gently undulating landscape without any prominent koppies.

The vegetation of the Letaba exclosures is classified as ‘Letaba River Rugged Veld’ (Landscape 10, Gertenbach 1983). The vegetation of the drier upper savanna areas contains elements of Landscape 22, the ‘Combretum spp. / Colophospermum mopane Rugged Veld’ (Gertenbach 1985) and is floristically linked to the ‘Colophospermum mopane – Combretum apiculatum – Digitaria eriantha Open Tree Savanna’, described by Van Rooyen, Theron and Grobbelaar (1981). The riparian zone of the Letaba site forms part of Subtropical Alluvial Vegetation (unit AAZa7 of the Inland azonal vegetation), whereas the zonal savanna area forms part of the Lowveld rugged mopaneveld (SVmp6) in the Mopane Bioregion (Mucina & Rutherford 2006). On a larger scale, the vegetation of the Letaba exclosures forms part of the Combretum apiculatum – Colophospermum mopane major plant community on granite and gneiss in the Cissus coriifolia – Colophospermum mopane vegetation type (Siebert, Breedenkamp & Siebert 2003). Mopaneveld on granitic substrates is typically in association with Combretum spp., where the latter dominates the sandy crests and Colophospermum mopane the more clayey substrates of the bottomlands (Du Plessis 2001). Of the four major plant communities identified and described by Breedenkamp and Van Rooyen (1993), three are represented at the Letaba site, of which some are typically found in the study area.

Species that characterise the riparian zone include woody species such as Croton megalobothrys, Nuxia oppositifolia, Gymnosporia senegalenesis, Philenoptera violacea, Diospyros mespiliformis, Combretum microphyllum and Trichilia emetica. Inland, the vegetation is typically dominated by Colophospermum mopane, with variation in species associations that co-exist in the woody layer. Woody species, other than Colophospermum mopane, that characterise the savanna zone of the Letaba site, include Combretum apiculatum, Terminalia prunioides, Dichrostachys cinerea, Maerua parvifolia, Cissus coriifolia, Commiphora mollis, C. africana, Grewia bicolor, Combretum imberbe, Acacia nigrescens, Acacia excelsum and Rhigozum zambeziacum. Grasses, such as Panicum coloratum, Schmitatia pappophoroides, Melinis repens, Bothriochloa radians, and forbs such as Crabbea celatina, Oecium americanum, Phyllanthus maderaspatiensis, Paciona burchellii, Hibiscus micranthus and Jasminum stenolobum, characterise the field layer.
METHOD

Classification and mapping

Vegetation sampling, classification and mapping was based on the approach followed in the study of the Nkhuhlu exclosures (Siebert & Eckhardt 2008). A total of 83 plots were identified through randomised stratification, of which 72 plots were sampled in detail using the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974). Total floristics were obtained for each 20 m × 20 m plot to allow for comparison of species diversity and richness between the different plant communities. Plant species names conform to those of Germishuizen and Meyer (2003).

Braun-Blanquet procedures were used to refine the classification results of the TWINSPAN (Hill 1979) application using the MEGATAB computer program (Hennekens 1996). The results are presented in a phytosociological table (see online Appendix). Results from the classification and subsequent refinement were used to construct a 1:5000 vegetation map for the Letaba exclosures (Figure 2). Mapping was done to the sub-community level in ArcMap™ of the ESRI ArcGIS 9.1® computer package. To improve the understanding of the map in terms of the topography, the distribution of the plant communities is presented in a profile drawing (Figure 3) that was constructed using Corel Draw Suite 9°.

Floristic analysis

Floristic data were analysed to allow floristic comparison across mapping units and were therefore presented on variant level where appropriate. The approach for floristic comparison followed the method used for the Nkhuhlu exclosures (Siebert & Eckhardt 2008), which entailed the use of Shannon-Wiener diversity indices to combine species richness and relative abundance among species (Barbour, Burk & Pitts 1987) for comparison across mapping units. The Braun-Blanquet scale was converted to percentage cover and the mean cover per species within the plant community was taken as its abundance value.

RESULTS

Classification and mapping

First order divisions, created by the hierarchical classification of the Letaba data set, separated riparian woodland from the dryland woodland communities, the latter of which are dominated by *Colophospermum mopane* and differentiated according to elevation and drainage. These two vegetation types represent four main communities, which include eight sub-communities and six variants after refinement:

1. **Hemizygia bracteosa – Acacia exuvialis crested savannah**
   1.1 *Xerophyta humilis* – *Oldenlandia herbaea* seepage
   1.2 *Sclerocarya birrea* – *Bothriochloa radicans* ridge bushveld
   2.1.1 *Lannea schweinfurthii* variant
   2.1.2 *Aristida canescens* variant
   2.2 *Maerua parvifolia* – *Agathisanthemum bojeri* Mopane bushveld
   2.1.1.1 *Eragrostis trichophora* – *Sporobolus stapfianus* mud pans
   2.1.2.1 *Barleria elegans* – *Acacia karroo* streambank woodland
   2.1.2.2 *Maerua parvifolia* variant
   2.2.1 *Nuxia oppositifolia* variant
   2.2.2.1 *Combretum imberbe* – *Enneapogon oenothriseus* Open Woodland

2. **Schmidtia pappophoroides – Colophospermum mopane lowland savanna**
   2.1 *Melhania rehmannii* – *Enneapogon scoparius* mixed bushveld
   2.1.1 *Lannea schweinfurthii* variant
   2.1.2 *Aristida canescens* variant
   2.2 *Maerua parvifolia* – *Agathisanthemum bojeri* Mopane bushveld

3. **Sporobolus fimbriatus – Grewia bicolor seasonally wet savanna**
   3.1 *Eragrostis trichophora* – *Sporobolus stapfianus* mud pans
   3.2 *Barleria elegans* – *Acacia karroo* streambank woodland

4. **Croton megalobotrys – Panicum deustum riverine woodland**
   4.1 *Phileopus violaceus* – *Jasminum fluminense* riverbank woodland
   4.1.1 *Hyphaene coriacea* variant
   4.1.2 *Nuxia oppositifolia* variant

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**Figure 2**
Vegetation map of the Letaba exclosures study site
Figure 3
Profile of the vegetation (corresponding to the mapping units of Figure 2) along a topographical gradient of the study area from the Letaba River riverbed to the crest of the landscape.
The vegetation and floristics of the Letaba exclosures

4.2 Combretum imberbe – Enneapogon cenchroides open woodland. The identified plant assemblies are distributed throughout the Letaba exclosures study area and are well-presented in all treatment blocks at plant community level (Figure 2). Some communities have a limited distribution range due to small-scale disturbances and patchiness, for example the Xerophyta humilis – Oldenlandia herbacea seepage (1.1) and the Eragrostis trichophora – Sporobolus stapfianus mud pans (3.1).

Sub-communities are easily identifiable in the field; some can even be distinguished at variant level, for instance the Lannea schweinfurthii – Aristida cuneo (2.1) and Aristida cuneo – Enneapogon scoparius mixed bushveld, as well as the Hyphaene coriacea (4.1.1) and Nuxia oppositifolia (4.1.2) variants of the Philenoptera violacea – Jasminum fluminense riverbank woodland. Vegetation mapping was therefore done up to variant level where possible, although sub-communities form the most representative units of the vegetation map (Figure 2).

A schematic presentation of plant community distributions – from the Letaba River to the crest of the landscape (Figure 3) – illustrates changes in the vegetation along the riparian calena. The riverbed and lower riverbank is characterised by plant species of the Nuxia oppositifolia variant (4.1.2). On the slightly elevated riverbank, the Hyphaene coriacea variant (4.1.1) can easily be recognised by the presence of prominent trees, such as Hyphaene coriacea, Philenoptera violacea, Croton megalobrys and Combretum hereroense. The Hyphaene coriacea variant is often interrupted by drier, open woodland, the Combretum imberbe – Enneapogon cenchroides open woodland (4.2), on the higher terraces of the Letaba River. Higher up into the savanna zone, the vegetation varies from a closed, almost homogenous mopane woodland (2.2), via a mixed bushveld (2.1) that is interrupted by narrow green ‘belts’ (2.1.1), to a crest bushveld (1), which includes the Sclerocarya birrea – Oldenlandia herbacea seepage (1.1) and the Eragrostis trichophora – Sporobolus stapfianus mud pans (3.1).

Description of plant communities

The Letaba exclosures experimental site lies in the geological and climatically uniform Landscape 10 of Gertenbach (1983), namely the ‘Letaba River Rugged Veld’. No major climatic variation occurs that could have an effect on the local differentiation of plant communities. Small-scale heterogeneity of environmental factors could contribute to variations in plant assemblages. Detailed descriptions of the plant communities are therefore important to explain and provide support for the delineation of each mapping unit in a heterogeneous landscape.

1. Hemizygia bracteosa – Acacia exuvialis crest savanna

This community forms one of four plant communities within the study area and comprises approximately 30% of the total sampling area (including the buffer zone). It is spread out across the exclosure fence lines, with little difference between the three exclosure types in terms of plant composition. It extends over the crests of the savanna landscape inland of the Letaba River and is associated with shallow, greyish-brown, gravelly loamy sand to sandy loam topsoil directly overlying hard rock of the Mispa soil form (Paterson & Steenekamp 2003) (Figure 1).

The Hemizygia bracteosa – Acacia exuvialis crest savanna varies from open to moderately open shrubveld. The field layer is dominated by forbs, whereas shrubs constitute the dominant growth form in the woody layer. It is floristically characterised by species group 4 (see online Appendix), which includes Acacia exuvialis in the woody layer, and Hemizygia bracteosa and Triclercas laceratum in the forb layer (species group 1). Dominant species include the trees Colophospermum mopane, Terminalia prunioides and Combretum apiculatum and the grass Panicum coloratum (species group 14). Species frequently present include the grasses Bothriochloa radyans, Tragus berteronianus (species group 3), Schmidia pappophoroides (species group 5) and Enneapogon scoparius (species group 10), whereas Euclea disionoides, Clerodendrum ternatum (species group 10), Lantana ragona, Ceratocladus triloba and Pavonia burchellii (species group 14) are commonly found in the forb layer. This community is floristically the poorest, with a total of 96 plant species recorded (Table 1), which contribute to only 41% of the species richness of the Letaba exclosures. Diversity and evenness scores are at a moderate level for the study area (Table 1). Taxa of the Fabaceae, Poaceae and Malvaceae (Table 2). The dominant growth forms in the study area are forbs, graminoids, trees and shrubs, although several climber species were recorded (Table 3). Succulents are less prominent, compared to the Nkhuulu exclosures.

FLORESCENT

At community level, the Schmidia pappophoroides – Colophospermum mopane lowland savanna (community 2) hosts the highest alpha diversity (species richness per unit area) at 32 species per plot and a total of 141 different plant species. However, the Shannon-Wiener Diversity Index, which combines both richness and equitability, revealed it has a low diversity and evenness (Table 1), attributable to the almost sole dominance of Colophospermum mopane (O’Connor 1992; Du Plessis 2001). The highest alpha diversity on sub-community level was recorded for the Philenoptera violacea – Jasminum fluminense riverbank woodland (4.1) and the Melhania rehmannii – Enneapogon scoparius mixed bushveld (2.1) (Figure 5). The highest floristic diversity on sub-community level was measured for the streambank woodland (3.2), with a value of 3.9 (Figure 5), which can be attributed to the variation in bordering savanna plant communities, from which individuals spread into this sub-community with moist soils.

FLORESCENT

Floristically, the study area is dominated by taxa from the Fabaceae, Poaceae and Malvaceae (Table 2). The dominant growth forms in the study area are forbs, graminoids, trees and shrubs, although several climber species were recorded (Table 3). Succulents are less prominent, compared to the Nkhuulu exclosures.

DISCUSSION

Species richness per area of the Nkhuulu and Letaba exclosures respectively as well as pooled (Letaba & Nkhuulu) in relation to the species richness of the entire Kruger National Park (KNP)

Species richness per area of the Nkhuulu and Letaba exclosures respectively as well as pooled (Letaba & Nkhuulu) in relation to the species richness of the entire Kruger National Park (Figure 4).

The vegetation and floristics of the Letaba exclosures

Species richness per area of the Nkhuulu and Letaba exclosures respectively as well as pooled (Letaba & Nkhuulu) in relation to the species richness of the entire Kruger National Park (KNP)
Figure 5

Analysis of species diversity, richness and cover of the eight sub-communities of the Letaba exclosures: (a) Shannon-Wiener Index of Diversity and Evenness, (b) total and mean species richness per unit area (i.e. per 20 m × 20 m plot) and (c) herbaceous versus woody layer cover percentages.
Acacia nigrescens. This savanna community is too distant to associate its plant assemblages with the riparian vegetation described by Bredenkamp and Van Rooyen (1993), although it does contain elements of the Colophospermum mopane – *Terminalia prunioides* Dry Riparian Woodland (community 1.1.2, Bredenkamp & Van Rooyen 1993).

Two sub-communities were identified for the Hemizygia bracteosa – *Acacia exsulalis* crest savanna:

1.1 Xerophyta humilis – Oldelandia herbacea seepage: This sub-community is not widely distributed in the Letaba exclosures site, nor in the adjacent Colophospermum mopane savanna surrounding the study area. It covers only a small patch (1% of the study area) on the crest of the landscape where underground water seeps through the surface, resulting in a seasonally wet area. Mispah is the dominant soil form, with a stony soil surface that is often underlain by rock plates where moisture accumulates. This somewhat unique plant community is found within the buffer zone of the full exclosure, extending into the full exclosure. It is an open savanna dominated by low Colophospermum mopane shrubs of approximately 3 m in height, which are interrupted by damp, open patches dominated by *Xerophyta humilis*. Woody cover percentage is the lowest in this sub-community. Cover in the herbaceous layer is approximately 25%.

The seepage, which is dominated by herbaceous species (Figure 5), is characterised by species group 2 (see online Appendix). Since this sub-community is not typically found in the study area it is undersampled, represented by only one relevé: sample plot 12. The most conspicuous woody species is Colophospermum mopane (species group 14) in its low shrub (± 3 m) form. Graminoids such as Melinis repens (species group 2), Schmidtiapappophoroides (species group 5) and Panicum coloratum (species group 14) occur, but with low percentage cover. Prominent forbs include, other than *Xerophyta humilis* and Oldelandia herbacea (species group 2), Konaunia virgata (species group 9), Evolvulus alsinoides (species group 10), Tephrosia purpurea and Ceratocletha triloba (species group 14).

This sub-community has a species richness value of 15, which is also the mean species number per sampling plot (Figure 5).

1.2 Sclerochrysa braera – Bothriochloa radicans ridge bushveld: This sub-community is widespread in the savanna uplands of the Letaba exclosures site, especially along the crests of the landscape which predominantly occurs within the 400 m buffer zone (Figure 2). Soils underlying this sub-community are mainly from the Mispah soil form. The vegetation is structurally characterised by an open to moderately open shrubveld. The herbaceous layer has a cover of 34% and the woody layer covers approximately 25% of the area (Figure 5).

This ridge bushveld is characterised by species group 3 (see online Appendix) and include Sclerochrysa braera in the woody layer and *Tragus berteronianus* and *Bothriochloa radicans* in the grass layer. The woody layer is dominated by Colophospermum mopane (species group 14). Prominent woody species comprise *Rigouzum zambesiacum* (species group 10), *Terminalia prunioides* and *Combretum apiculatum* (species group 14). Forbs include *Indigofera nebrowniana* (species group 7), *Evolvulus alsinoides*, *Dicoma tomentosa*, *Talinum caffrum*, *Clerodendrum ternatum* (species group 10), *Ceratotheca trioloba*, *Hibiscus micranthus*, *Lantana ragoa*, *Melhania forbesii* and *Schmidtiapappophoroides* (species group 14).

Species richness is 96, whereas mean species number per plot is 30 (Figure 5). The diversity for this sub-community is above average, common for plant communities found on ridges (Siebert et al. 2003). Evenness is average for the Letaba site (Figure 5).

Two variants were identified but do not represent different mapping units. These variants were:

1.2.1 Senna italica variant: This variant is structurally classified as a moderately open to open shrubveld on slightly elevated crests on shallow soils of the Mispah soil form. It is less stony than the Typical variant and occurs in the open control area, the partial exclosure and in the buffer zone outside the northeastern border of the partial exclosure. Characteristic species of this variant are listed in species group 4 and comprise Senna italica, Heteropterygium ovatifolium, *Boerhavia diffusa*, Cordichonia decumbens and *Pterodiscus speciosus*, all of which are in the herbaceous layer. Hemizygia bracteosa (species group 1) is less abundant here than the typical variant. Dominant species include Colophospermum mopane, *Terminalia prunioides* and *Panicum coloratum* (species group 14), whereas *Combretum apiculatum* (species group 14), *Bothriochloa radicans* (species group 3) and *Enneapogon scoparius* (species group 14) are locally prominent.

1.2.2 Typical variant: This variant occurs as interrupted patches of moderately open shrubveld and is in general associated with crests on shallow soils covered by granitic pebbles, associated with the Mispah soil form. It covers most of the upland savanna vegetation towards the north-eastern border of the partial exclosure, as well as outside the exclosure in the buffer zone. There are no species that typically characterise this variant, although the absence of species group 4 may serve as an indicator of this typical variant. The dominance of Hemizygia bracteosa (species group 1) is characteristic. Important species in the woody layer, other than Colophospermum mopane, include *Acacia exsulalis* (species group 1), *Sclerochrysa braera* (species group 5), *Rigouzum zambesiacum* (species group 10), *Terminalia prunioides*, *Combretum apiculatum*, *Acacia nigrescens* and Dichroastrachys cinerea (species group 14). Other species present in the herbaceous layer are grasses such as *Bothriochloa radicans* (species group 3), *Schmidtiapappophoroides* (species group 5), *Enneapogon scoparius* (species group 10), *Panicum maximum* (species group 21) and forbs such as *Indigofera nebrowniana* (species group 7), *Ocimum americanum*, *Ceratotheca triloba* (species group 14) and *Waltheria indicia* (species group 21).

2. Schmidtiapappophoroides – Colophospermum mopane lowland savanna

This lowland savanna typically belongs to the Lowveld Rugged Mopaneveld (SVmp6, Mucina & Rutherford 2006) and covers the largest portion of the Letaba exclosures site. It is a typical Mopaneveld plant community that is widespread in the KNP and adjacent savanna counterparts in plant communities, as have been described previously, is the Colophospermum mopane – *Combretum apiculatum* – *Digitaria eriantha* Open Tree Savanna (Van Rooyen et al. 1981), which occurs further north of the Letaba exclosures site, in the Punda Maria region. This typical mopaneveld community occurs on granitic soils of the Mispah soil form (Siebert et al. 2003).

Structurally, this savanna type varies from an open shrubveld to closed savanna woodland. The dominant growth form in the field layer is forbs, whereas shrubs dominate the woody layer. This community is floristically characterised by species group 5. The woody layer is dominated by Colophospermum mopane and *Terminalia prunioides* (species group 14). The grass layer is dominated by *Panicum coloratum* (species group 14) and *Schmidtiapappophoroides* (species group 5). The grasses *Enneapogon scoparius* (species group 10), *Eragrostis superba* and *Panicum maximum* (species group 21) are prominent. Forbs such as *Crabebe velutina*, *Hibiscus praeteritus*, *Ruellia cordata* (species group 5), *Evolvulus alsinoides*, *Linum frutetrum*, *Talinum caffrum*, *Clerodendrum ternatum* (species group 10), *Ocimum americanum*, *Phyllanthus maderaspatensis*, *Lantana ragoa*, *Hibiscus micranthus* (species group 14), *Waltheria indica*, *Kyllinga alba* and *Melhania forbesii* (species group 21) are present in this community.

Total species count for this community is 141, which is the
highest for the Letaba study area (Table 1). This community scored the lowest on the diversity index and its low evenness (Table 1) can be attributed to the almost complete dominance by Colophospermum mopane in both the tree and the shrub layer. Despite its low diversity, this community contains the highest richness of forbs, graminoids and annuals for the study area (Table 3). Half of its species are members of the Fabaceae and Poaceae, although the highest number of species in the Malvaceae has been recorded in this community (Table 2).

The lowland savanna consists of two sub-communities that are easily recognisable in the field. Even the variants are distinguishable and are represented by different mapping units (Figure 2).

### 2.1 Melanaria rehmannii – Enneasporum scoparius mixed bushveld

Mixed bushveld of the Letaba exclosures study site is typically associated with middiscs and footslopes, extending over all exclosure fence lines into the buffer zone. It covers the largest area of the study site. The dominant soil form underlying this sub-community is Mispah (Paterson & Steenekamp 2003). Structurally, it varies from open shrubveld to closed high shrubveld, and is dominated alternately by Colophospermum mopane and Combretum apiculatum. As in most other plant communities of the Letaba exclosures site, the highest vegetation cover is in the herbaceous layer (Figure 5; Table 3).

Species from group 6 (see online Appendix) characterise the floristic composition of this sub-community and include Melanaria rehmannii, Aiptosium lineare, Asparagus setaceus, Abutilon angulatum, Becium filamentosum, Dumasia villoa and Cocinia abyssins, all of which are representative of the forb layer. Conspicuous woody species include Cassia cornifolia (species group 5), Colophospermum mopane, Combretum apiculatum, Dichrostachys cinerea (species group 14), Cassia abbreviata (species group 20) and Combretum hereroense (species group 21). Forb species such as Crabbea velutina (species group 5), Eucalytus alpinus, Combemelia africana, Talinum caffrum and Clerodendrum ternatum (species group 10) are also present.

### 2.1.1 Lannea schweinfurthii variant

This mosaic of moderately closed to closed savanna occurs throughout the study area on slightly deeper soils of the Mispah soil form. The Lannea schweinfurthii variant is very apparent from an aerial view and appears as green ‘tongues’ dissecting the savanna Mopaneveld (Figure 2). It is conspicuously present in the study area and structurally it becomes more dense towards the Letaba River, in particular the area surrounding the mud pans (community 3.1) (Figure 2).

Species group 7 (see online Appendix) characterises this variant and include tree species such as Lannea schweinfurthii and Combemilia africana. The herbaceous layer is characterised by the climbers Vigna luteola and the forbs Lannea schweinfurthii, L cryptantha and Ocimum gratissimum. The vegetation is dominated by the tree Colophospermum mopane (species group 14) and the grasses Enneasporum scoparius (species group 10) and Schmidtia pappophoroides (species group 5). Prominent species include the trees Terminalia prunioides and Combretum apiculatum, the grasses, Panicum coloratum (species group 14) and Panicum americanum (species group 21) and the forbs, Kyalima alba and Walltheria indica (species group 21). Other woody species present, include Maerua parvofolia (species group 9), Philenoptera violaceas (species group 16), Cassia abbreviata (species group 20) and Combretum hereroense (species group 21). Forb species such as Crabbea velutina (species group 5), Eucalytus alpinus, Combemelia africana, Talinum caffrum and Clerodendrum ternatum (species group 10) are also present.

### 2.1.2 Aristida canescens variant

The Aristida canescens variant makes up the open to moderately open part of this mixed bushveld, overlying shallow soils of the Mispah soil forms (Paterson & Steenekamp 2003). It is found throughout the study area, stretching over all exclosure types and along the buffer zone in the north and the west (Figure 2).

Species group 8 (see online Appendix) floristically characterises the variant, which includes no woody species, but only the grass Aristida canescens and the forbs Rhynchosia toota, Cleome monophylla and Mariscus sumatrensis. Trees such as Colophospermum mopane, Terminalia prunioides and Combretum apiculatum (species group 14) dominate the woody layer, with prominent species in the forb layer being Crabbea velutina (species group 5), Ocimum americanum, Phyllanthus madakensis, Ceratotheca triobla and Phyllanthus incurvus (species group 21). Schmidtia pappophoroides (species group 5), Enneasporum scoparius (species group 10), Panicum coloratum (species group 14), Eragrostis superba, Urochloa mosambicensis and Panicum americanum (species group 21) are the most conspicuous grasses.

### 2.2 Maerua parvofolia – Agathisanthemum bojeri mopane bushveld

This mopane bushveld occurs along the bottomlands of the landscape, on the elevated terraces above the riparian zone of the Letaba River. It forms a continuous band of moderately closed, tall Colophospermum mopane shrubland, except in the full exclosure, where it extends higher up into the middiscs where the structure is significantly more open shrubveld. Structurally, it resembles the Lannea schweinfurthii variant (2.1.1), although the mopane bushveld is weaker in terms of species richness. This sub-community is associated with moderately deep to deep, brown to reddish-brown, unstructured sandy loam topsoil of the Hutton soil form (Paterson & Steenekamp 2003).

This moderately closed shrubland is characterised by species group 9 (see online Appendix), of which the shrub Maerua parvofolia and the forbs Acalypha indica and Heliotropium stracheni are the most prevalent. It has floristic affinities to the Lannea schweinfurthii variant, of which Maerua parvofolia, Agathisanthemum bojeri and Eragrostis rigidior provide evidence (species groups 8 and 9). Colophospermum mopane (species group 14) dominates the tree and shrub layer, although other species, such as Maerua parvofolia (species group 9), Rhigozum zambeiscusam (species group 10), Terminalia prunioides and Dichrostachys cinerea (species group 14) occur, but in low abundance values. Other conspicuous species include those in the forb and grass layer, for example, Schmidtia pappophoroides, Crabbea velutina, Hibiscus

### Table 1: Richness, Shannon-Wiener diversity and evenness at plant community level of the Letaba exclosures study site

<table>
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<th>Plant communities</th>
<th>1</th>
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<td>3.609</td>
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<td>0.66</td>
<td>0.75</td>
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</table>
Sporobolus stapfianus, character species of this community are listed in species loam of the Hutton soil form. Underlying this sub-community, include deep, gravelly sandy (community 2.1.1), develop into mopane woodland. Soils exclosure on the bottomlands towards the Letaba River (Figure 3.1 families in this community (Table 2). The mopane bushveld has the highest richness and percentage cover of annuals in the study area and the second highest richness of forbs (Table 3). The overall species richness is 95 and the number of species recorded per sampling plot is 32, which is an average cover for the study area. Diversity and evenness is slightly below average for the Letaba study area (Figure 5), as expected in a community dominated by a single species, Colophospermum mopane (see online Appendix).

3. Sporobolus fimbriatu – Grevia bicolor seasonally wet savanna

The seasonally wet savanna of the Letaba exclosures study site refers to the seasonal streams and mud pans that are habitat for the azonal savanna vegetation, excluding the riparian zones. Plant species that differentiate this community are floristically closer to the savanna communities (communities 1 and 2), because they receive water for limited periods of the year only. Soil forms underlying this community vary from moderately deep Hutton along the mud pans, to sandy Mispah along the seasonal stream.

Structurally, this community is classified as a moderately open to moderately closed woodland, typically found along the edges of the watercourses, including the pans. Forbs dominate the field layer, whereas shrubs dominate the woody layer. Species groups 11, 12, and 14 (species groups 11, 12, and 14) are prominent diagnostic species, whereas climbers, Eragrostis trichophora (species group 21), and the woody shrub Fluegga virosa (species group 21).

This community has an average species richness (calculated at 119), although the average number of species per sampling plot is above average (27) (Table 1) for the Letaba site. It has the second highest diversity and the highest evenness of all communities (Table 1). It hosts the highest richness of climber species (Table 3). Poaceae and Fabaceae are the dominant plant families in this community (Table 2).

3.1 Eragrostis trichophora – Sporobolus stapfianus mud pans

This sub-community comprises the vegetation associated with the zoonogenic mud pans that are scattered in the Letaba exclosure site. The four most prominent mud pans are located in the full enclosure on the bottomslands towards the Letaba River (Figure 2). These muddy patches, created by large herbivores seeking surface water to create a mud bath, are surrounded by tall mopane trees that, other than the surrounding high shrubland (community 2.1.1), develop into mopane woodland. Soils underlying this sub-community, include deep, gravelly sandy loam of the Hutton soil form.

Character species of this community are listed in species group 12, of which Eragrostis trichophora is dominant. Other character species include an Oxalis species, Cyperus esculentus, Sporobolus stapfianus, Heniziaja bracteosa, Sporobolus africanus, Urochloa panicoides, Sesbania hispina and Polygala splenopetra. Along the edges of the open mud pans are trees and shrubs, for example Terminalia prunioides, Combretum apiculatum, Jasminum stenolobum (species group 14) and Fluegga virosa (species group 21), although they occur in low abundances. Dominant grass species include Eragrostis trichophora (species group 12), and Panicum maximum (species group 21).

This sub-community consists of a unique composition of graminoids and geophytes, which contribute to the high cover percentage of herbaceous species in the study area (Figure 5). It has a below average diversity and evenness (Figure 5), due to the significantly high cover abundance and dominance of Eragrostis trichophora.

3.2 Barleria elegans – Acacia karroo streambank woodland

Streambank vegetation in the Letaba exclosures site is associated with the two seasonal streams that dissect the study area from north to south. The larger flows through the partial exclosure, where the vegetation is also more typical of this community. The streambank vegetation is not well developed along the smaller tributary that flows through the full exclosure that contains many elements of the surrounding savanna areas. Structurally, it is classified as moderately closed woodland. The woodland becomes more and more integrated with the surrounding savanna area as the distance away from the stream increases. Soils are not the typically shallow Mispah, as is the case in the adjacent savanna areas, but over lain by gravelly sandy sediments of variable depths that are washed down from higher lying areas.

Diagnostic species for the streambank woodland include trees and shrubs such as Manilkara mochisia, Gymnosporia baccifera, Acacia karroo, Tricalysia lanceolata and Eucla distorum. Barleria elegans is a prominent diagnostic species, whereas climbers, such as Vigna frutescens and Cardiospermum corindum are also present. Colophospermum mopane, Terminalia prunioides, Combretum apiculatum, Dichrostachys cinerea, Acacia nigrescens, Jasminum stenolobum (species group 14) and Combretum hereroense (species group 21) are some of the conspicuous species in the woody layer. Other important species in the field layer include Sporobolus fimbriatu (species group 11), Lantana ragosa, Pavonia burchellii (species group 14), Eragrostis superba and Panicum maximum (species group 21). This woodland contains species that are common in the riparian woodland, such as Gymnosporia senegalensis (species group 15), Philenoptera violacea, Diospyros melporphinis (species group 16), Phyllanthus reticulatus, Combretum microphyllum, Cassia abreviata, Cocculus hirsutus and Monordica fortila (species group 20).

This moderately closed woodland is rich in tree and liana species. It is the only community in which the woody cover percentage is highest (Figure 5). All other growth forms are well represented in this community, although of lower percentage cover (see online Appendix). A total of 78 species have been recorded in

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**TABLE 2**

<table>
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<tr>
<th>Family</th>
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<th>Letaba exclosures site</th>
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</tr>
<tr>
<td>Poaceae</td>
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<td>Lamiaceae</td>
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<tr>
<td>Rubiaceae</td>
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<td>Acanthaceae</td>
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<td>Asteraceae</td>
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<td>Compositae</td>
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<tr>
<td>Cyperaceae</td>
<td>3 4 5 4 7</td>
<td></td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>4 2 4 6 7</td>
<td></td>
</tr>
</tbody>
</table>

Number of species: 55 59 71 76 134

Percentage of total (233 spp): 23 34 30 33 57
this woodland type, with an average of 30 species per 400 m² (Figure 5). Species diversity and evenness is the highest of all communities that occur at the Letaba enclosures site (Figure 5) and can be ascribed to the less clear-cut boundary between the streambank vegetation and the surrounding savanna vegetation.

4. Croton megalobotrys – Panicum deustum riverine woodland

This riverine woodland comprises the communities that are separated from the zonal communities at the first hierarchical level of classification. It contains elements of several major communities identified by Bredenkamp and Van Rooyen (1993), for example the 'Lonchocarpus capensis (= Philenoptera violacea) – Croton megalobotrys – Colophospermum mopane Dry Riparian Woodland', the 'Croton megalobotrys – Maytenus senegalensis (= Gymnosporia senegalensis) Riparian Forest' and the 'Phragmites mauritianus – Cycnodon dactylon Reed Communities'. According to the description of the Subtropical Alluvial Vegetation (AZa7), given by Macuna and Rutherford (2006), the Croton megalobotrys – Panicum deustum riverine woodland described here partially forms part of this inland azonal vegetation type with common species in the woody layer being Phoenix reclinata, Ziziphus mucronata, Acacia nigrescens, Colophospermum mopane, Combretum hereroense, Philenoptera violacea, Euclea divinorum and Gymnosporia senegalensis and, in the reedbeds, Phragmites mauritianus and Cycnodon dactylon.

This community covers approximately 10% of the total Letaba site (including the 400 m buffer zone). It stretches along the Letaba River bank from west to east, crossing exclosure fence lines. The largest part of this community is associated with deep, greyish-brown, sandy loam topsoil on brown, sandy-loam subsoil of the Oakleaf soil form (Paterson & Steenkamp 2003).

The vegetation structure of the Croton megalobotrys – Panicum deustum riverine woodland varies between an open grassy shrubveld to moderately closed woodland. True to its structural characteristic species in the field layer. The tree 

\[ \text{Croton megalobotrys} \]

The total species count for this community is 131, the second highest at the Letaba enclosures site. It has average evenness, but scored the highest diversity (Table 1), suggesting that there is a lack of dominance of a single or few species and that all species are evenly distributed within the community. Shrubs and trees are the dominant growth forms, and this community hosts the highest richness in tree species (Table 3). It is dominated by taxa of the Fabaceae and Poaceae, and is characterised by many taxa of the Rubiaceae, Asteraceae and Euphorbiaceae (Table 2).

The riverine forest is subdivided into sub-communities that represent small-scale differences in habitat and floristic composition. These sub-communities comprise:

4.1 Philenoptera violacea – Jasminum fluminense riverbank woodland:

The riverbank woodland delineates the riparian zone of the Letaba River, as it includes the riverbank, lower riverbank and riverbed. This sub-community is present in all the excursion types, as well as in the buffer zone. The dominant soil form underlying this sub-community is Oakleaf (Paterson & Steenkamp 2003). It is structurally classified as moderately closed woodland, where the trees and shrubs reach their maximum heights at the Letaba enclosures site, albeit areas closer to the riverbed being classified as moderately open woodland and open riverbank vegetation. Typical of riverbank vegetation, this sub-community has a high percentage cover by trees and shrubs, although percentage grass cover remains the highest.

The riverine woodland community is similar to the ‘Croton megalobotrys – Maytenus senegalensis (= Gymnosporia senegalensis) Riparian Forest’ community described by Bredenkamp and Van Rooyen (1993). Tree species common to both communities include Croton megalobotrys, Tripiliha emetica, Philenoptera violacea, Nuxia oppositifolia and Diosyros mespiliformis.

Species from species group 16 (see online Appendix) characterise the floristic composition of this sub-community and include Philenoptera violacea, Diosyros mespiliformis, Combretum microphyllum, Jasminum fluminense, Trichilia emetica and Lippia javanica. Other species that occur, but in lower abundance values, include the succulent shrub Gardenia volkensii (species group 17), the grass Cycnodon dactylon and the tree Nuxia oppositifolia, which is conspicuously present on the lower riverbank. Taxa of species group 20 are all present in this community, of which some are more conspicuous than others. They include Phyllanthus reticulatus, Combretum mosambicense and Cassia abbreviata in the woody layer and lianas such as Cacculus hisratus and Momordica balsamina. Prominent tree and shrub species, other than the character species, include Croton megalobotrys, Gymnosporia senegalensis (species group 15), Combretum hereroense and Flueggea virosa (species group 21). Important grasses are Eragrostis superba and Panicum maximum (species group 21) whereas Melanisia forbesii and Waltheria indica (species group 21) are among the more conspicuous forbs in the field layer.

This sub-community has the highest species richness (116) of all sub-communities and its diversity is second highest in the study area (Figure 5). Tree and shrub species richness are also the highest in this sub-community (Table 3).

4.1.1 Hyphaene coriacea variant: This variant is similar to the ‘Croton megalobotrys – Hyphaene coriacea Riparian and Floodplain Woodland’ described by Bredenkamp and Van Rooyen (1995). It is a relatively moist woodland that covers the typical evergreen moderately closed riparian woodland zone along the Letaba River on deep Oakleaf soils. It is well represented in the full and partial exclosures, but discontinuous and fading in the open area and buffer zone. Several tall (up to 12 m) riparian forest trees characterise this variant in the Letaba enclosures site with its relatively high vegetation cover of trees and shrubs. Philenoptera violacea is the most prominent ‘big tree’ species in this variant, whereas several individuals of Diosyros mespiliformis is a diagnostic feature.

Diagnostic species for this variant are listed under species group 17 (see online Appendix), of which the succulent shrub or tree Gardenia volkensii, the lala-palm Hyphaene coriacea and the tree or high shrub Euclia natansis, are the major contributors to the woody cover. In the forb layer Thunbergia neglecta and Tragia glabula are most prominent, with no grass species being diagnostic for this variant. Panicum deustum (species group 15) and P. maximum (species group 21) are dominant in the field layer. Other prominent trees and shrubs are Croton megalobotrys (species group 15), Cassia abbreviata (species group 20) and Combretum hereroense (species group 21). Forb species are rare in this community, whereas the climber Jasminum fluminense (species group 16) are conspicuously present.

4.1.2 Nuxia oppositifolia variant: This variant falls into the ‘Croton megalobotrys – Nuxia oppositifolia Riparian Terrace Bush’ (Bredenkamp & Van Rooyen 1993). According to Bredenkamp and Van Rooyen (1993), this riverine bush represents typical Croton megalobotrys dominated vegetation, the most conspicuous and conspicuous vegetation type on the riverbanks and terraces and widespread along most parts of the Letaba River. Soils underlying this community are mainly of the Oakleaf soil form that is associated with deep sandy-loam topsoil on sandy loam subsoil (Paterson & Steenkamp 2003). This is well represented in all zones, including the sacrificial zone. It is better developed in the full enclosure than in the other zones. This variant varies
from an open riverbank in the control site, to moderately open woodland in the full and partial exclosures. It is typically more open nearer to the Letaba River, where it is associated with Phragmites mauritianus clumps.

Diagnostic species for this sub-community are listed in species group 18 (see online Appendix), of which the grass Cynodon dactylon and the tree Nuxia oppositifolia being the most conspicuous. Other differential species include woody species, such as Phyllanthus reticulatus (species group 20), Peltophorum africanum and Flueggea virosa (species group 21). Panicum maximum (species group 21) and Cynodon dactylon dominate the grass layer.

This variant is in some areas covered by a dense grass sward, especially by Cynodon dactylon (species group 18). Similar to the ‘Lippia javanica – Gymnosporia senegalensis Riverbank Scrub’ of the NKnhulu exclosures site (Siebert & Eckhardt 2008), scattered clusters of woody species are found within this variant. These clusters serve as a microhabitat for colonisation by riparian woodland species. Many precursors of riparian woodlands were recorded from this variant and include Combretum hereroense, Peltophorum africanum and Cassia abbreviata.

4.2 Combretum imberbe – Enneapogon cenchroides open woodland: This open woodland sub-community occurs discontinuous within the riverbank woodland. It is best developed in the full exclosure along the lower terraces of the Letaba River and is easily recognised in the field as an opening in the riverbank woodland, characterised by a dense grass sward and several scattered trees and shrubs. It is similar to the ‘Colophospermum mopane – Combretum imberbe Dry Riparian Woodland’ (Bredenkamp & Van Rooyen 1993). The dominant soil form and series underlying this sub-community is Oakleaf (Paterson & Steenekamp 2003).

Diagnostic species of importance are listed in species group 19 (see online Appendix) and include the dominant grass Enneapogon cenchroides, the tree Combretum imberbe, the shrub Pechuel-Loesheia leubnitzi and two geophytes, Albuca setosa and Ledebouria revoluta. Croton megalobrotys (species group 15) and Combretum hereroense (species group 21) are important contributors to the woody layer, whereas Urochloa mosambicensis (species group 21) is an abundant annual grass species. Forb species are not abundant, although Kyllinga alba (species group 21) is the most prominent.

Grass cover is high in this sub-community, which contributes to the overall cover by the herbaceous layer of 45%, with only 16% in the woody layer (Figure 5). Species richness is low and the diversity below average (Figure 5).

CONCLUSION

An investigation into the natural vegetation of the study area revealed different plant communities, some of which are unique in its plant assemblage, such as the Xerophyta humilis – Oldenlandia herbacea (community 1.1), and others that contain little variance within and between. Mapping of the vegetation could be done down to sub-community level and, in some cases, even variant level. As expected in mopaneveld vegetation, plant communities of the exclosures are broadly associated with soil types. Although not tested here, it is known that smaller scale variations in Mopaneveld vegetation corresponds to soil moisture availability, because the mopaneveld is considered ‘event-driven’, especially in the field layer (Du Plessis 2001).

The description of the distinguished plant communities, as well as ecological and floristic interpretations thereof, contribute significantly to the knowledge required for the future management of the vegetation. As ecologically sound plant communities were distinguished during this survey, the description of the vegetation should serve as a basis for further detailed and broad-based botanical studies at this long-term monitoring site to inform KNP’s adaptive management approach.

ACKNOWLEDGEMENTS

The authors would like to thank South African National Parks (SANParks) for funding the project. Our sincere thanks to Jacques Venter, SANParks for logistic support during field surveying. Izak Smit, SANParks is thanked for providing spatial images. The Post-flood Programme is thanked for making available digital aerial maps of the study area. GIS assistance was received from Ms. Marie du Toit (North-West University). All field rangers are thanked for keeping a watchful eye over the field surveying team.

### Table 3

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The central column of figures for each of the communities indicates the species richness of that community. [a], annual grasses; [s], succulent plants.
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