NORTH-WEST UNIVERSITY
YUNIBESITI YA BOKONE-BOPHIRIMA
NOORDWES-UNIVERSITEIT
POTCHEFSTROOM CAMPUS

A phytosociological synthesis of Mopaneveld vegetation at different spatial scales using various classification methods

F Siebert
21074968

Thesis submitted for fulfillment of the degree *Philosophiae Doctor* in Botany at the North-West University, Potchefstroom campus

Promotor: Prof. S.S. Cilliers

August 2012

ACKNOWLEDGEMENTS

First and foremost I would like to thank my Almighty Father for providing me with this opportunity and for being my guide through all my ventures.

I would like to thank the following people for their valuable contributions:

- My promotor, Prof. Sarel Cilliers, for his time, guidance and valuable input.
- Prof. Leon van Rensburg for his support and for providing me with opportunities to develop my research career.
- My husband, Stefan Siebert, for his scientific advice and moral support throughout the assemblage of this thesis.
- My parents for their support throughout the development of my academic career.
- School of Biological Sciences, and in particular the subject group Botany, for granting me the time and freedom to complete this thesis.
- University of Pretoria for access to the vegetation database and to all contributors of Mopaneveld vegetation data.
- Proff. Noel van Rooyen and George Bredenkamp, Mr Albie Götze and Mrs Andrea Straub for access to their riparian vegetation data.
- Marié du Toit for her assistance with maps.
- North-West University, specifically the Institutional Research Office and the Research Unit: Environmental Sciences and Management, for financial support.

ABSTRACT

Classification of relevé data aims to present the best possible explanation of the vegetation within a specific study area. The variety of multivariate techniques available to classify vegetation into ecological communities has developed in recent years, which contributes to uncertainty among vegetation scientists as to which methods and computer software to select for optimum classification results. The wide application of the classical TWINSPAN algorithm along with the Braun-Blanquet approach of plant community descriptions and diagnostic species identification in southern Africa prompted a comparison of classification results between these classical approaches and a modern approach. The modern approach, as being referred to in this study, entails the recent improvement on the classical TWINSPAN algorithm, namely the Modified TWINSPAN algorithm in combination with statistical measures of species fidelity. Comparisons between classification end-results were undertaken at various spatial scales to test whether discrepancies between results obtained from the different approaches are similar when applied to a broad-scale synthesis, an intermediate synthesis and a local-scale classification within a similar vegetation type, the Mopaneveld. Such a comparative study is envisaged to present insight on the credibility of the use of classical approaches in phytosociology at various spatial scales.

A modern approach was tested upon three previous vegetation classification studies which followed the classical approach. These vegetation classification studies were all undertaken at different spatial scales and are being referred to as the reference classifications. The data that were subjected to the modern approach were analogous to those used in the reference classifications. The computer package JUICE 7.0 was used in which the Modified TWINSPAN algorithm was applied in combination with statistical measures of species fidelity, which was obtained as a function directly in the JUICE program. Classification hierarchies were constructed for both the classical and modern approach results to compare and describe similarities and discrepancies between the different hierarchical dendrograms. Fidelity syntables were constructed to assist in the grouping of diagnostic species according to highest fidelity values. Such diagnostic species groups were compared with the lists of diagnostic species in the reference classifications.

At the broadest spatial scale, comparisons revealed discrepancies between classification results from the classical and the modern approach. The modern approach presented a more robust synthesis of the Mopaneveld in southern Africa since the vegetation units and their associated diagnostic species are ecologically better expressed. The intermediate-scale synthesis comparison revealed similar discrepancies, which again question the credibility of the classical approach at broader spatial scales. The application of the modern approach to the local scale classification, however, revealed little difference with the results obtained through the classical approach. Although more alternative classification techniques need to be applied to report on the most robust technique for vegetation classifications across spatial scales, it could be reported that the classical TWINSPAN algorithm is not favorable for vegetation classifications and syntheses beyond the local scale.

The ecological reliability of the modern approach at the intermediate scale prompted its application in a synthesis of the riparian vegetation within the Mopane Bioregion of South Africa, which was not achieved in any previous study. Riparian vegetation plays an important role in maintaining good water quality and also provides habitat for many species. Riparian vegetation therefore needs to be classified and described. The synthesis of the riparian vegetation in the Mopane Bioregion of South Africa revealed six distinct plant communities which are described and discussed in terms of diagnostic, constant and dominant species along with variance in plant species diversity.

Keywords: TWINSPAN, Modified TWINSPAN, fidelity, Mopane Bioregion, *Colophospermum mopane*, riparian vegetation, species diversity

OPSOMMING

Die doel van relevé data klassifisering is grootliks om die beste moontlike verduideliking te bied van die plantegroei binne ‘n spesifieke studiegebied. Die verskeidenheid van beskikbare meerveranderlike tegnieke om plantegroei te klassifiseer in ekologiese gemeenskappe, het ontwikkel oor die afgelope tyd. Hierdie verskeidenheid lei tot onsekerheid by plantegroeiwetenskaplikes oor die keuse van metodes en rekenaarsagteware vir optimale klassifikasieresultate. Die wye toepassing van die klassieke TWINSPAN algoritme tesame met die Braun-Blanquet benadering vir die beskrywing van plantgemeenskappe en die identifisering van diagnostiese spesies in suider Afrika, het gelei tot die behoefte aan ‘n vergelykende studie tussen resultate wat verkry is deur die toepassing van die klassieke benadering teenoor dié wat verkry is deur die toepassing van die moderne benadering. Die moderne benadering, soos verwys word in hierdie studie, omvat die onlangse verbetering van die klassieke TWINSPAN algoritme, naamlik die gewysigde (Modified) TWINSPAN algoritme, gekombineer met statistiese metings van spesie-getrouheid. Vergelykings tussen eindresultate is toegepas op verkillende ruimtelike skale ten einde te toets vir soortgelyke teenstrydighede tussen resultate wanneer verskillende benaderings toegepas word op ‘n breë skaal, intermediêre skaal en ook op ‘n plaaslike skaal. Hierdie toepassings is deurgaans op dieselfde plantegroeitipe, naamlik die Mopanieveld, gedoen. Dit is moontlik dat so ‘n vergelykende studie insig sal bied op die geloofwaardigheid van die gebruik van klassieke benaderings in fitososiologie op verskeie ruimtelike skale.

Drie plantegroeiklassifikasiestudies wat onderneem is op verskillende ruimtelike skale en wat verkry is deur die toepassing van die klassieke benadering, is gebruik om die moderne benadering teen te toets. Hierdie plantegroeiklassifikasies en daaropvolgende beskrywings word in die teks na verwys as die verwysingsklassifikasies. Die data wat gebruik is in die toepassing van die moderne benadering is analoog tot dit wat gebruik is in die verwysingsklassififikasies. Die rekenaarpakket JUICE 7.0 is gebruik waarin die gewysigde (Modified) TWINSPAN algoritme in kombinasie met statistiese metings van spesie-getrouheid as ‘n direkte funksie uitgevoer kon word in die JUICE program. Klassifikasiehierargieë is gevorm vir beide die klassieke- en die moderne benadering om gelyksoortigheid en teenstrydighede tussen the hierargiese dendrogramme te vergelyk en te beskryf. Getrouheid-sintabelle is gevorm om die groepering van diagnostiese spesies ten opsigte van die hoogste getrouheidswaardes te vergemaklik. Diagnostiese spesiegroepe is dan vergelyk met lyste van diagnostiese spesies soos verskyn in die verwysingsklassifikasies.

Die breedste skaal vergelykings het teenstrydighede openbaar tussen klassifikasieresultate van die klassieke en die moderne benadering. Die moderne benadering het ‘n meer geloofwaardige sintese van die Mopaneveld in suider Afrika gebied weens die verbeterde ekologiese uitdrukking van plantegroei-eenhede en hul gepaardgaande diagnostiese spesies. Die vergelyking van die intermediêre-skaal sintese het soortgelyke teenstrydighede openbaar wat weereens die betroubaarheid van die klassieke benadering bevraagteken op breër skale. Die toepassing van die moderne benadering op die klassifikasie op plaaslike skaal het egter geringe verskille openbaar met resultate soos verkry is uit die klassieke benadering. Alhoewel die toepassing van verdere alternatiewe klassifikasietegnieke benodig word om te kan rapporteer oor die mees betroubare tegniek vir plantegroeiklassifikasies oor ruimtelike skale, kan dit egter berig word dat die klassieke TWINSPAN algoritme nie wenslik is vir plantegroeiklassifisering en sinteses buite ‘n plaaslike skaal nie.

Die ekologiese betroubaarheid van die moderne benadering op ‘n intermediêre skaal, het die toepassing daarvan in ‘n sintese van die rivieroewerplantegroei binne die Mopanie Biostreek van Suid-Afrika moontlik gemaak. Rivieroewerplantegroei speel ‘n belangrike rol in the handhawing van goeie waterkwaliteit en dit skep habitat vir verskeie ander spesies. Die klassifisering en beskrywing van rivieroewerplantegroei word dus belangrik geag. Die rivieroewerplantegroeisintese wat hier aangebied word, het ses duidelik-verskillende plantgemeenskappe geopenbaar wat beskryf en bespreek word ten opsigte van diagnostiese, konstante en dominante spesies tesame met variansie in plantspesiediversiteit.

Sleutelwoorde: TWINSPAN, Modified TWINSPAN, getrouheid, Mopanie Biostreek, *Colophospermum mopane*, rivieroewerplantegroei, spesiediversiteit

TABLE OF CONTENTS

CHAPTER 5 EVALUATION OF THE BROAD-SCALE VEGETATION SYNTHESIS 63

CHAPTER 6 EVALUATION OF THE INTERMEDIATE-SCALE VEGETATION SYNTHESIS: A RE-ASSESSMENT OF THE LOWVELD MOPANEVELD IN SOUTH AFRICA 85

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER 1

INTRODUCTION

1.1 Background

Research on savanna plant ecology has extended the understanding of species composition and functioning, although it has also revealed its complexity and dynamic nature (Furley, 2010). The heterogeneity of southern African savannas is expressed in diverse ecosystems, each comprising a complex combination of specific organisms, objects, structures and processes (Pickett *et al.*, 2003). Maintenance of this notable biological wealth depends on the understanding of the ecosystems that underlie this rich biodiversity. Since vegetation largely reflects ecological processes, it deserves to be described and classified (Mucina, 1997), although the sensitivity of scale should be recognized (Wiens, 1989; Pickett *et al.*, 2003). The term ‗*scale*‘ is widely regarded as a fundamental concept in ecology (Wiens, 1989; Wu & Li, 2006; Farina, 2007) and is considered indispensable for describing and understanding landscape pattern (Wu, 2007). The scale at which ecological patterns are being investigated may have considerable effects on the patterns that are being revealed (Wiens, 1989), a phenomenon commonly referred to as the scale effect (Wu & Li, 2006). Studying vegetation heterogeneity, distribution patterns and dynamics at various spatial scales is therefore considered essential for identifying and understanding ecological processes and hence, providing subsequent insight for managing ecological systems and the highly valued renewable resources (Pickett *et al.*, 2003; Gillson, 2004).

The word *scale* has multiple meanings and therefore the definition of scale should be appropriate to the ecological study at hand (Schneider, 2001). For its application in this study, scale refers to the spatial or temporal dimension of a phenomenon (Wu & Li, 2006) and is characterized by components, of which grain, extent and coverage are most applicable to this study. Grain is the finest level of spatial or temporal resolution of a data set (Wu, 2007) within which homogeneity is assumed (Wu & Li, 2006). Extent is the spatial (or temporal) span of a phenomenon or study, i.e. the study area (Wiens, 1989). Extent and grain therefore define the upper and lower limits of the study resolution (Wiens, 1989). Coverage is explained as the proportion of the study area, i.e. the sampling density or intensity (Wu, 2007), hence the number of samples. When vegetation classification and description is considered at various spatial scales, the extent, grain and coverage vary inevitably. For example, in broad-scale (i.e. coarse-scale) classifications, the extent would typically present a large, heterogenous landscape across environmental extremes, oppose to a smaller area (e.g. within a nature reserve) with rather similar environmental conditions when the extent is reduced to the local-scale (i.e. fine-scale). The coverage (i.e. the number of samples) within the broad-scale (coarse-scale) should therefore also be much higher than in a local-scale (fine-scale) study. An intermediate-scale study would therefore fall between these two concepts. Considering the variability in grain (i.e. homogenous units), extent (i.e. size of study area) and coverage (i.e. number of relevés) when vegetation is classified across various spatial scales, the credibility of classical, scale-independent classification approaches becomes uncertain.

Numerical-analytical approaches along with computer software and computing equipment have improved considerably during the last two decades (e.g. Belbin, 1991; Belbin & McDonald, 1993; Podani, 2006; Tichý *et al.*, 2009; Kindt & Coe, 2005; McCune & Mefford, 2006; Schmidtlein *et al.*, 2010). The increased number of multivariate methods available for the detailed analysis of vegetation is a reflection of an overall shift in emphasis, from the provision of classifications, to the provision of techniques which are designed to serve particular ecological purposes (Van der Maarel, 2005). Since species serve the function of ecological indicators (Noy-Meir & Van der Maarel, 1987), the communities in which they are assembled should be known and typified to contribute to the conservation of biodiversity. The selection of the most reliable classification algorithm in combination with objective measures to efficiently discriminate each community from one another according to faithful or diagnostic species, has therefore become increasingly important.

Despite the development of numerical classification techniques, little progress has been made in terms of comparisons between classical and novel numerical approaches (De Cáceres *et al.* 2009), especially at different spatial scales. According to Loehle (2011), the classification method or degree of resolution needs to become an object of study. De Cáceres *et al.* (2009) furthermore suggested that, since vegetation classifications are mostly regionally restricted, solutions for biogeographical issues would be another interesting research topic. However, studying vegetation at various spatial scales requires variable-size data sets for the adequate representation of vegetation (Roleček *et al.*, 2009).

Savannas are ideal ecosystems for studying vegetation heterogeneity at a range of spatial and temporal scales (Gillson, 2004). Access to Mopaneveld vegetation data sets, ranging from local-scale (fine-scale) classifications to a broad-scale (coarse-scale) phytosociological synthesis, which were all based on traditional classification approaches, has therefore prompted the critical evaluation of classical approaches in vegetation science at various spatial scales.

1.2 Rationale

Two-way-indicator-species-analysis (TWINSPAN, Hill, 1979) along with classical, subjective measures to identify diagnostic species, are the most popular and best known methods applied in southern African vegetation classifications (e.g. Van Rooyen *et al.*, 1981a; Van Rooyen *et al.*, 1981b; Van Rooyen *et al.*, 1981c; Coetzee, 1983; Bredenkamp & Theron, 1990; Bredenkamp & Theron 1991; Bredenkamp *et al.*, 1993; Brown *et al.*, 1995a; Brown *et al.*, 1995b; Brown *et al.*, 1996; Dekker & Van Rooyen, 1995; Bezuidenhout, 1996; Visser *et al.*, 1996; Straub, 2002; Mostert *et al.*, 2008; Götze *et al.*, 2008; Mostert *et al.*, 2009; Daemane *et al.*, 2012). Based on this approach, referred to in this thesis as *the classical approach* (see Figure 1-1 for background), a broad-scale (coarse-scale) analysis of the Mopaneveld vegetation was presented by Du Plessis (2001) and later published (Siebert *et al.*, 2010). This synthesis was based on the classification of over 2 000 relevés (i.e. high coverage) over environmental extremes, which spans across several different countries (i.e. large extent) hosting the same vegetation type, the Mopaneveld. At an intermediate scale, Du Plessis (2001) presented a synthesis of the Mopaneveld in the Lowveld Savanna of South Africa. Similar classical approaches have been used to classify and describe the vegetation of this region. At a local-scale (fine-scale), Siebert *et al.* (2010) classified, described and mapped the vegetation of a small section of Mopaneveld at long-term monitoring herbivory and fire exclosures along the Letaba River in the Kruger National Park. A summary on the context of these studies within this thesis, including their specific scales in terms of extent and coverage is presented in Tables 4-1 and 4-2.

European vegetation syntheses across broad spatial scales are mostly based on the traditional two-step approach proposed by Van der Maarel *et al.* (1987). This bottom-up approach involves scale-dependent stratification of homogenous units (i.e. grain). These stratified units are commonly referred to as synrelevés. Each synrelevé is assembled by several relevés (from a single data set) that constitute a described and published plant community. Clustering of stratified units (i.e. synrelevés) proceeds upwards, which ultimately implies an increase of the grain. Due to limited published descriptions of plant communities in Mopaneveld vegetation from which the bottom-up approach should be performed, Du Plessis (2001) proposed a top-down approach in a vegetation synthesis of the Mopaneveld vegetation in which the extent and coverage decreases, but grain remains unchanged as clustering proceeds downwards.

The classical techniques that were used by Du Plessis (2001) in the top-down approach to classify and describe Mopaneveld vegetation have, however been critically evaluated and recently been reviewed. In a recent review of TWINSPAN, Roleček *et al.* (2009) proposed a modification to the classical TWINSPAN algorithm, in which the hierarchy respects cluster heterogeneity. Due to the popularity of the application of the classical TWINSPAN algorithm (Hill, 1979) in southern Africa, this improved algorithm, i.e. the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) was selected for application to all the above studies to compare classification results against.

The importance of diagnostic species in plant community descriptions has been recognized along with criticism on subjective diagnostic species identifications (e.g. Bruelheide, 2000). Objective, statistical measures of species fidelity were proposed by Chytrý *et al*. (2002) shortly thereafter. The application of these objective measures to select diagnostic species groups have therefore been considered for the comparison of classification results.

The collective term for the use of TWINSPAN (Hill, 1979) in combination with subjective measures of diagnostic species identification, is referred to in this thesis as the ‗Classical approach‘, whereas the application of the Modified TWINSPAN classification algorithm (Roleček *et al*., 2009) in combination with statistical measures of species fidelity (Chytrý *et al*., 2002) is referred to in this thesis as a ‗Modern approach‘ (Figure 1-1). It is important to note that the term ‗modern approach‘ is to be used within the context of this thesis only and should not be applied in the broader context of vegetation science. Modern numerical-analytical techniques for vegetation classification are far beyond what is exclusively selected to present a true modern approach.

Although it is beyond the scope of this thesis to report on the effect of scale on patterns and processes within Mopaneveld, scale is recognized as an important phenomenon in vegetation heterogeneity and surely classification methods should be designed to depict the variation across various spatial scales.

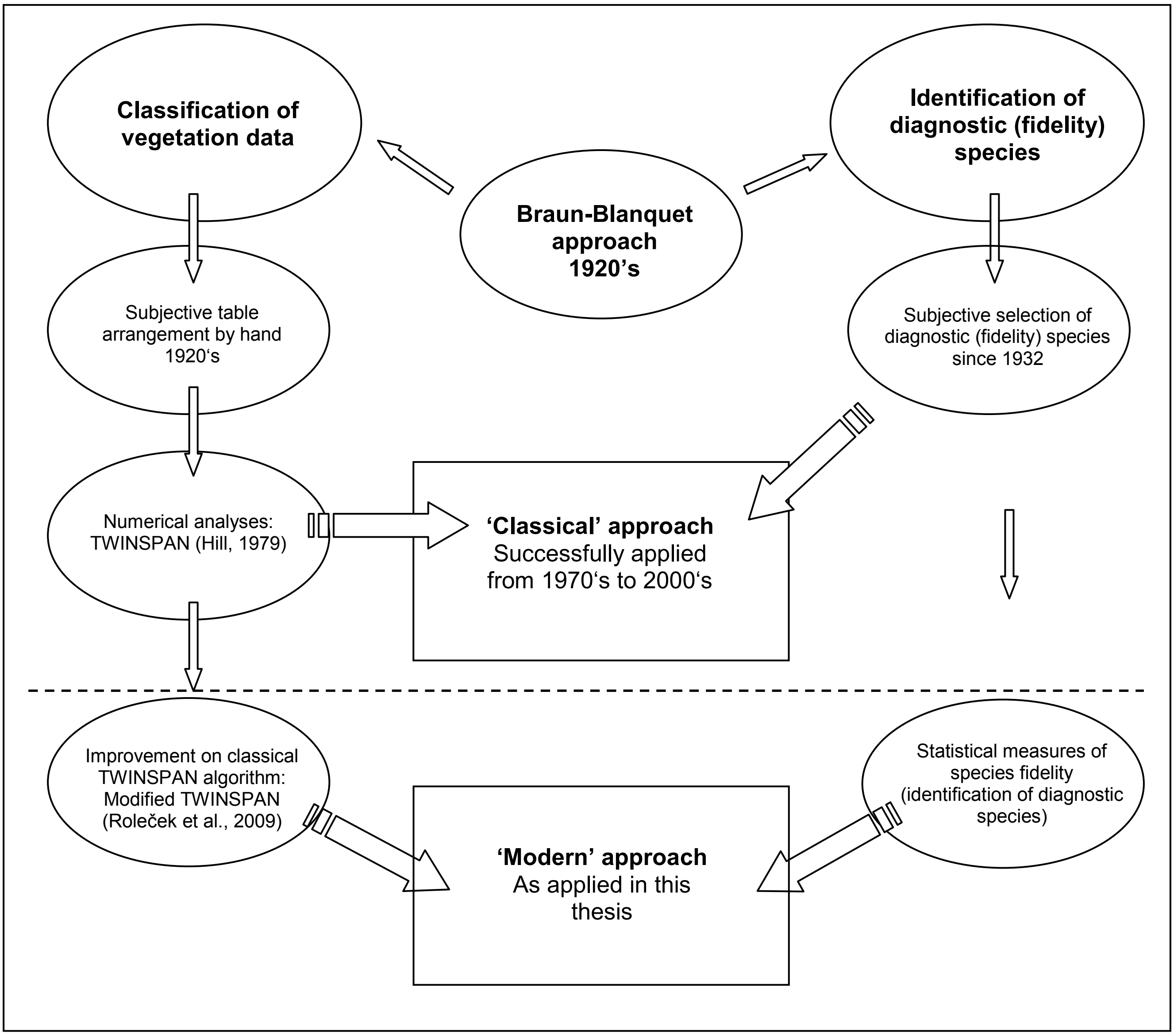


Figure 1-1. The development of the classical approach of vegetation classification into the modern approach as will be referred to in this thesis.

1.3 Objectives

1.3.1 Key objective

The key objective of the research contained in this thesis is to compare results obtained through the application of the traditionally-used classical approach with those obtained through the application of a modern approach at all the pre-identified spatial scales within the Mopaneveld study area in southern Africa.

It is envisaged that such a comparison will evidently reveal answers to the credibility of the use of the classical approach in vegetation science.

1.3.2 Secondary objective

As a secondary outcome of the results obtained through the comparative study and due to access to vegetation data sampled along the major rivers and tributaries draining Mopaneveld in South Africa, the first phytosociological synthesis of riparian vegetation in the Mopane Bioregion of South Africa (Mucina & Rutherford, 2006) will be presented in this thesis.

1.4 Hypotheses

1. The classical approach in vegetation classification reveals different results from the modern approach at various spatial scales within the Mopaneveld study area of southern Africa.

2. The modern approach reveals distinctly different plant communities at an intermediate-scale synthesis of the riparian vegetation of the Mopane Bioregion in South Africa.

1.5 Thesis layout

This thesis complies with the guidelines set for a standard research thesis at the North-West University. It encompasses nine chapters, of which the scientific results and discussions are presented in four chapters. Since each of these four chapters involves different variations on the study area, methodology and literature (i.e. presented in detail in Chapters 2-4), these chapters (i.e. Chapters 5-8) were formulated to present a complete view of the research undertaken respectively, similarly to a format in which manuscripts are being prepared for submission to scientific journals. Chapter 9 is aimed at drawing all the outcomes of the research together in a general discussion and conclusions. References cited in the text are included in the list of references at the end of each chapter of the thesis. In this respect, a certain amount of duplication was inevitable.

The content of each chapter is abbreviated below:

Chapter 2

A detailed overview of all the literature that is relevant to the research title is presented in this chapter. It covers literature on classification approaches, including criticism and the development of alternative methods for vegetation classification. It furthermore provides background on Mopaneveld vegetation in southern Africa, the study area in which the research has been conducted.

Chapter 3

This chapter presents the study area by defining its location and extent as well as its biophysical environment.

Chapter 4

Background of the development in classification approaches is presented against which the selection of a modern approach to compare the classical approach with should be viewed. Background on the reference classifications is also presented here after which the general methodological approach applied to in this thesis is presented. This general presentation of methods is however refined within each chapter that presents the research findings (i.e. Chapters 5–8).

Chapter 5

This chapter presents the results obtained through a comparative study between the classical and a modern classification approach at the broadest scale, which is referred to in this thesis as the ‗broad-scale vegetation synthesis‘. In comparison with results obtained by Siebert *et al.* (2003), the credibility of the classical approach in broad-scale vegetation syntheses is critically evaluated and discussed.

Chapter 6

Similar to the procedures followed in Chapter 5, an intermediate-scale synthesis of Mopaneveld vegetation is compared in terms of the different classification approaches. In comparison with the results obtained from Du Plessis (2001), the credibility of the classical approach in intermediate-scale vegetation syntheses is critically evaluated and discussed.

Chapter 7

Chapter 7 presents the local-scale classification comparison between the classical and modern approach. In comparison with results obtained from Siebert *et al*. (2010), the credibility of traditional approaches in local-scale vegetation classifications is critically evaluated and discussed.

Chapter 8

In this chapter, the modern approach in combination with further refinement of species selections in community descriptions have been applied to present a detailed synthesis accompanied by a description of the riparian vegetation within the Mopane Bioregion (Mucina & Rutherford, 2006) of South Africa.

Chapter 9

Since the research findings are discussed respectively within Chapters 5 – 8, this chapter integrates these discussions in a general discussion and concludes the relevance of the research.

1.6 References

BELBIN, L. 1991. PATN Technical Reference Manual. Division of Wildlife and Ecology, CSIRO, Canberra.

BELBIN, L. & McDONALD, C. 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science,* 4:341–348.

BEZUIDENHOUT, H. 1996. The major vegetation communities of the Augrabies Falls National Park, Northern Cape. 1. The southern section. *Koedoe,* 39(2):7–24.

BRAUN-BLANQUET, J. 1932. Plant Sociology. The Study of Plant Communities. Authorized English translation of 'Pflanzensoziologie' (Fuller, G.D. & Conard, H.S. *eds*. New York: McGraw-Hill).

BREDENKAMP, G.J. & THERON, G.K. 1990. The vegetation of the fersiallitic soils of the Manyeleti Game Reserve. *Coenoses*, 5(3):167–175.

BREDENKAMP, G.J. & THERON, G.K. 1991. The *Euceo divinori – Acacietum nigricentis*, a new association from the calcareous bottomland clays of the Manyeleti Game Reserve, Eastern Transvaal Lowveld, Gazankulu, South Africa. *Vegetatio,* 93:119–130.

BREDENKAMP, G.J., DEUTSCHLÄNDER, M.S. & THERON, G.K. 1993. A phytosociological analysis of the *Albizio harveyi – Eucleetum divinori* from sodic bottomland clay soils of the Manyeleti Game Reserve, Gazankulu, South Africa. *South African Journal of Botany*, 59(1):57–64.

BROWN, L.R., BREDENKAMP, G.J. & VAN ROOYEN, N. 1995a. The phytosociology of the southern section of Borakalalo Nature Reserve. *Koedoe,* 37(2):59–72.

BROWN, L.R., BREDENKAMP, G.J. & VAN ROOYEN, N. 1995b. The phytosociology of the western section of Borakalalo Nature Reserve. *Koedoe,* 38(2):49–64.

BROWN, L.R., BREDENKAMP, G.J. & VAN ROOYEN, N. 1996. The phytosociology of the northern section of Borakalalo Nature Reserve. *Koedoe,* 39(1):9–24.

BRUELHEIDE, H. 2000. A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science*, 11:167–178.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA–DUKÁT, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13:79–90.

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

DAEMANE, M.E., CILLIERS, S.S & BEZUIDENHOUT, H. 2012. Classification and description of the vegetation in the Spitskop area in the proposed Highveld National Park, North West Province, South Africa. *Koedoe*, 54(1): Art. #1020, 7 pages. http://dx.doi.org/10.4102/koedoe. Date of access: February 2012.

DE CÁCERES, M., FONT, X., VICENTE, P. & OLIVA, F. 2009. Numerical reproduction of traditional classifications and automatic vegetation identification. *Journal of Vegetation Science,* 20:620–628.

DEKKER, B. & VAN ROOYEN, N. 1995. The physical environment and plant communities of the Messina Experimental Farm. *South African Journal of Bot*any, 61(3):158–167.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

FARINA, A. 2007. Principles and Methods in landscape ecology. Springer, Dordrect.

FURLEY, F. 2010. Tropical savannas: Biomass, plant ecology, and the role of fire and soil on vegetation. *Progress in Physical Geography*, 34(4):563–585.

GILLSON, L. 2004. Evidence of Hierarchical Patch Dynamics in an East African Savanna? *Landscape Ecology,* 19:883–894.

GÖTZE, A.R., CILLIERS, S.S., BEZUIDENHOUT, H. & KELLNER, K. 2008. Analysis of the vegetation of the sandstone ridges (Ib land type) of the north-eastern parts of the Mapungubwe National Park, Limpopo Province, South Africa. *Koedoe,* 50(1):72–81.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

KINDT, R. & COE, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (CRAF): Nairobi, Kenya.

LOEHLE, C. 2011. Complexity and the problem of ill-posed questions in ecology. *Ecological complexity*, 8:60–67.

McCUNE, B. & MEFFORD, M.J. 2006. PC-ORD v.5.2. Multivariate analysis of ecological data. MJM Software: Gleneden Beach, OR.

MOSTERT, T.H.C., BREDENKAMP, G.J., KLOPPER, H.L., VERWEY, C., MOSTERT, R.E. & HAHN, N. 2008. Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *Koedoe,* 50(1):32–48.

MOSTERT, T.H.C., BREDENKAMP, G.J. & MOSTERT, R.E. 2009. Plant communities of the Soutpansberg Arid Northern Bushveld. *Koedoe*, 51(1), Art. #687,11 pages. DOI: 10.4102.

MUCINA, L. 1997. Classification of vegetation: Past, present and future. *Journal of Vegetation Science*, 8:751–760.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

NOY-MEIR, I. & VAN DER MAAREL., E. 1987. Relations between community theory and community analysis in vegetation science: some historical perspectives. *Vegetatio*, 69:5–15.

PICKETT, S.T.A., CADENASSO, M.L. & MENNING, T.L. 2003. Biotic and Abiotic Variability as Key Determinants of Savanna Heterogeneity at Multiples Spatiotemporal Scales. (*In* Du Toit, J.T., Rogers, K.H. & Biggs, H.C., *eds*. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Washington: Island Press. p. 447–468).

PODANI, J. 2006. Braun-Blanquet‘s legacy and data analysis in vegetation science. *Journal of Vegetation Science,* 17:113–117.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

SCHMIDTLEIN, S., TICHÝ, L., FEILHAUER, H. & FAUDE, U. 2010. A brute-force approach to vegetation classification. *Journal of Vegetation Science,* 21:1162–1171.

SCHNEIDER, D.C. 2001. The rise of the concept of scale in ecology. BioScience 51(7):545–553.

SIEBERT, F. ECKHARDT, H.C. & SIEBERT, S.J. 2010. The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa. *Koedoe*, 52(1): Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777. Date of access: November 2010.

STRAUB, A. 2002. The vegetation of Breslau Game Farm, Northern Province, Souh Africa. Pretoria: UP (Dissertation, MSc) 150p.

TICHÝ, L., CHYTRÝ, M., HÁJEK, M., TALBOT, S. & BOTTA-DUKÁT, Z. 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science,* 21:287–299.

VAN DER MAAREL, E. 2005. Vegetation ecology – an overview. Blackwell: Oxford, UK.

VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. 1981a. A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 1. The Higrophilous communities. *Journal of South African Botany,* 47(2):213–246.

VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. 1981b. A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 2. The Sandveld communities. *Journal of South African Botany,* 47(3):405–449.

VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. 1981c. A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 3. The *Colophospermum mopane* communities. *Journal of South African Botany,* 47(4):585–626.

VISSER, N., VAN HOVEN, W. & THERON, G.K. 1996. The vegetation and identification of management units of the Honnet Nature Reserve, Northern Province, South Africa. *Koedoe,* 39(1):25–42.

WIENS, J.A. 1989. Spatial Scaling in ecology. *Functional Ecology*, 3:385–397.

WU, J. 2007. Scale and scaling: a cross-disciplinary perspective. (*In*: Wu, J. & Hobbs, R.J., *eds*. Key topics in Landscape Ecology, Ecosystem Function in Heterogeneous Landscapes. Cambridge University Press, Cambridge, pp. 92–114).

WU, J. & LI, H. 2006. Concepts of scale and scaling. (*In*: Wu, J., Jones, K.B., Li, H., Loucks, O.L. *eds*., Scaling and Uncertainty Analysis in ecology: Methods and applications. Springer, pp. 3–15).

CHAPTER 2

LITERATURE REVIEW

2.1 Classification of vegetation data

2.1.1 Introduction

Ecosystems are open systems in which energy, matter and information can flow freely. These continually changing environmental conditions make them complex entities which should not only be considered separately, but also be examined holistically, disregarding the size of the ecosystem (Cole, 1986). Systems ecology, i.e. the science of ecosystems, as well as Landscape ecology, i.e. the study of patterns and processes at multiple scales, developed rapidly during the last few decades to address holism in ecology opposed to reductionism. Jørgensen *et al.* (1992) stated that, if we sacrifice important properties of the whole by separating systems into parts, we cannot understand systems. In their book on ecosystem theories, Jørgensen and Müller (2000) present various philosophies on the complexity of ecosystems, after which they concluded that ‗*we need to see the forest, not the trees*.‘ To bring this into context with the work presented here, it could be adapted to ‗*we also need to see Mopaneveld, and not only mopane trees*‘.

A synthesis could be viewed as a holistic approach of analysis. It is commonly referred to the combination of two or more entities that together form something new (Oxford dictionary, 1999). A phytosociological synthesis can be described as a study of which the major objective is to compile a synthesis of vegetation information based on phytosociological data (Pignatti, 1995). The data are usually collected by various researchers at various times, but within a particular study area to ultimately reveal a refreshed look on the vegetation at a larger scale. Phytosociological syntheses usually deal with large data sets due to the accumulation of information in the form of vegetation relevés (Van der Maarel *et al.*, 1987).

Broad-scale vegetation classifications, i.e. classifications of large vegetation data sets of which the data were accumulated across spatially distributed areas, are more common in European phytosociology. Despite the wealth of phytosociological data accumulated in Europe, accompanied by detailed vegetation classifications at a regional scale (Van der Maarel, 2005), the practical feasibility of meta-analyses of historical data remains a challenge. Observer bias, inconsistent sampling, limitations in common standards for vegetation sampling prior to Mucina *et al.* (2000), subjectivity in diagnostic species identification and classification algorithm selection resulted in considerable differences in national classifications of corresponding vegetation types, even between neighbouring countries (Bruelheide & Chytrý, 2000). These challenges are incessantly being addressed and alternatives proposed in vegetation science related literature (e.g. Barkman, 1989; Dufrêne & Legendre, 1997; Belbin & McDonald, 1993; Botta-Dukát & Borhidi, 1999; Bruelheide & Chytrý, 2000; Chytrý, 2001; Chytrý *et al.*, 2002a; Chytrý *et al.*, 2002b; Grabherr *et al.*, 2003; Wallace & Dale, 2005; Cesa-Bianchi *et al.*, 2006; Podani, 2006; Chiarucci, 2007; Diekmann *et al.*, 2007; Hedl, 2007; Roleček *et al.*, 2007; De Cáceres *et al.*, 2009; Roleček *et al.*, 2009; Zhang *et al.*, 2010).

Phytosociological syntheses and the treatment of large vegetation data sets, which are mostly amalgamated from heterogeneous landscapes, are however limited in southern African vegetation studies.

2.1.2 Criticism on the phytosociological approach

‗Vegetation, the central object of study in vegetation ecology, can be loosely defined as a system of largely spontaneously growing plants‘ (Van der Maarel, 2005). This definition seems uncomplicated to a non-vegetation scientist, although many years of research and criticism have lead to more uncertainties and debates on the credibility of vegetation classifications globally.

Europe stands father to the development of phytosociology as a science in community ecology, which was lead by J. Braun-Blanquet, after which the approach to classify and describe vegetation was named. Within the Braun-Blanquet approach, a certain set of assumptions and techniques were developed to compare floristic composition among communities (Braun-Blanquet, 1932). Ever since its development and generous application in Europe, there has been a substantial growth in the field of community ecology and theory-testing, which lead to criticism on the techniques, assumptions and definitions of the Braun-Blanquet approach.

Criticism on the phytosociological approach will be discussed very broadly to provide background to the development of a remarkable variety of sampling and classification techniques from which the modern vegetation scientist must select from.

2.1.2.1 Sampling

Non-random versus random sampling

Lájer (2007) heavily criticized phytosociological sampling since the data, which are commonly used in statistical measures are collected using subjective selection of sampling points. He claims that this leads to unreliable results since the non-random approach violates the properties of randomness, known probability and independence of statistical sampling upon which statistical tests are built. According to Chiarucci (2007) these problems are linked to the inaccurate definition of the ‗plant community‘.

In response to criticism on site selection, Roleček *et al.* (2007) claimed that, although random vegetation sampling would achieve statistical independence, it would not guarantee ecological representativeness. He suggested stratified random sampling as an alternative, which is considered the best midway approach to obtain reasonable statistical inference. This approach of site selection is commonly applied in South African vegetation studies.

Grabherr *et al.* (2003) tested the objectivity of the Braun-Blanquet approach by resampling a forest type that was classified according to the classical approach and syntaxonomical descriptions. Instead of pre-selecting sampling sites within homogeneous vegetation units, Grabherr *et al.* (2003) made use of various stratifications available in GIS to select sampling sites. His results however, appeared to be very similar to the classification revealed by classical approaches and therefore suggested that the Braun-Blanquet approach should be appreciated and supported.

Non-random sampling data are commonly applied to test species abundance, richness and diversity patterns. Diekmann *et al.* (2007) and Hedl (2007) independently tested and compared diversity results obtained through randomly and non-randomly sampled units. Both studies confirmed that non-random sampling results in biased species richness and abundance. They concluded that non-randomly sampled data should not be used in the examination of patterns of species abundance and biodiversity. Hedl (2007) furthermore stated that more random sampled data will be needed to maximize diversity calculation precision.

Plot size

Chytrý (2001) reported discrepancies in plot size in European phytosociological data due to the subjective, preferential method of field sampling used in phytosociology. He claimed that the consequences of unequal plot size results in unreliable species richness data accumulated through phytosociological data.

Cover abundance estimates

In addition to criticism on plot selection, estimating abundances of species according to the Braun-Blanquet cover abundance scale has been criticized widely. Apart from estimation error by field observers, which ultimately leads to inconsistent estimates (Haveman & Janssen, 2008), the scale is ordinal and cannot be directly applied to conventional statistical analysis (Hahn & Scheuring, 2003). Differences in estimations by different observers at various categories revealed that estimating cover in 10 categories is the most precise method, provided that the categories are of identical width (Hahn & Scheuring, 2003).

2.1.2.2 Hierarchy and scale

Hierarchy theory emphasizes the importance of considering scale (Kotlier & Wiens, 1990). The scale at which vegetation classifications is applied should therefore be considered when classification hierarchy is applied in phytosociology.

A hierarchy is mostly designed to link entities either directly or indirectly, and either vertically or horizontally. Hierarchical classifications are used to express the structure of a dataset in a way that corresponds to the traditional view of hierarchical relationships among communities (Rolečeck *et al.*, 2009). Hierarchical classifications are therefore very useful in community ecology, especially in vegetation science where the hierarchical relationships are distinct, ecologically interpretable entities. There are two major approaches in data clustering, namely agglomerative techniques in which hierarchical classification is constructed bottom-up, and divisive techniques in which hierarchy is constructed from top to bottom (Gauch & Whittaker, 1981). Two-way-Indicator-Species-Analysis (TWINSPAN) (Hill, 1979), the most popular classification algorithm in vegetation science, is a polythetic divisive technique, meaning that clusters are partitioned using all possible species in the data set, clustering from top to bottom. The TWINSPAN algorithm has been criticized widely due to various reasons of which the most common failure is to present a reliable hierarchy due to its dependence on a predominant primary ordination gradient (see section 2.1.2.3).

The inconsistent treatment of scale in vegetation classifications cause illogical placement of plant associations in a certain hierarchy. Phytosociological studies are therefore viewed as subjective descriptions obtained through subjective hierarchies. According to Ewald (2003), the answer to the scaling phenomena in phytosociology is a hierarchy of discrete scales for classification, hence distinct clusters of unique combinations of vegetation plots. Heterogeneity in the phytosociological context is therefore considered and treated as a mosaic of homogeneous units that are distinct, describable units, hence rejecting the continuum concept of plant communities (Danserou, 1968; Goodall, 2002).

A concise overview of scale in the context of vegetation classification is presented under section **2.3** in this chapter.

2.1.2.3 Classification techniques

TWINSPAN

Up to 1981 TWINSPAN (Hill, 1979) was reported by Gauch & Whittaker (1981) as the algorithm that performed the best in terms of clustering of community data. After criticism on the TWINSPAN algorithm (Van Groenewoud, 1992; Belbin & McDonald, 1993; Dufrêne & Legendre, 1997) and the development of alternative numerical methods (e.g. Belbin, 1987; Dufrêne & Legendre, 1997; Cesa-Bianchi *et al.*, 2006; De Cáceres *et al.*, 2009, Roleček *et al.*, 2009; Tichý *et al.*, 2009), vegetation scientists tested various techniques of clustering and classification algorithms. Belbin and McDonald (1993) compared three types of clustering algorithms that are commonly used in community ecology. These results revealed that both flexible UPGMA and ALOC (Belbin, 1987) performed significantly better than the classical TWINSPAN algorithm for clustering. The reason for the poor performance of the classical TWINSPAN algorithm could be ascribed to its dependence on a predominant primary gradient and due to its dichotomising character at an inappropriate point of this axis (Van Groenewoud, 1992), which leads to poor performance, especially after the first division. This was also confirmed by Bruelheide and Chytrý (2000), which stimulated the development of an improved TWINSPAN algorithm. Due to its common and successful application in vegetation classifications, Roleček *et al.* (2009) used the basis of the TWINSPAN algorithm, although most of the subjectivity and hierarchical ‗flaws‘ were corrected, to put forward the Modified TWINSPAN algorithm.

Zhang *et al.* (2010) tested the outcomes of self-organizing feature map clustering (SOFM) and compared the results with Possibilistic C-Means and TWINSPAN algorithms. His results, however, indicated that all three algorithms were effective in the analysis of ecological data.

Criticism on the use of TWINSPAN circled out to the users of the algorithm in South Africa. The subjectivity of the Braun-Blanquet method, i.e. observer bias in both sampling and classification, encouraged the development of an alternative classification and analysis of relevé data, named PHYTOTAB-PC (Westfall *et al.*, 1997).

Despite the criticism received by various ecologists for the application of TWINSPAN in community ecology, the algorithm is still successfully applied to relevé data for community clustering, not only in southern Africa (e.g. Manhas *et al.*, 2009).

Combination with gradient analyses

Another major condemnation of most phytosociological studies is the combination of classical TWINSPAN results with conventional multivariate analysis (e.g. PCA, CA and CCA ordinations) to support species-environmental relationships. According to Podani (2006), the application of cover-abundance values to such statistical measures is inappropriate and fails to present reliable clustering. Podani (2006) proposed the use of Non-Metric Multidimensional Scaling (NMDS) instead. The use of gradient analyses to support vegetation descriptions, however, has been applied successfully in southern African vegetation studies (e.g. *Götze et al*., 2003; Stalmans *et al*., 2004; Mostert *et al*., 2009; Stalmans & Peel, 2010).

2.1.2.4 Diagnostic species identifications

Fidelity can broadly be defined as the degree to which a species is concentrated within a specific vegetation unit. Fidelity is expressed through diagnostic species since it contains character and differential species (Bruelheide, 2000; Chytrý *et al.*, 2002a). Diagnostic species could be considered ecological ‗labels‘ since they reflect certain aspects of a plant community or vegetation unit. They also assist in field surveys when researchers need to identify communities in existing classification systems (Chytrý *et al.*, 2002a). However, since the description of vegetation, the concept of fidelity has been critically evaluated (e.g. Poore, 1955; Barkman, 1989; Ewald, 2003). According to Barkman (1989) it is unusual for a syntaxon and its faithful taxon to have the same distribution. He suggested that not only is the taxon characteristic of a syntaxon, but the growth-form and micro-habitat should also be considered.

Bruelheide (2000) suggested a new, less subjective measure of fidelity on which Chytrý *et al.* (2002a) built forth and developed statistical measures of fidelity to identify diagnostic species. Chytrý *et al.* (2002a) concluded that lists of diagnostic species published in a phytosociological table are dependent on the context, which are useful for the identification of vegetation units at a local scale. Care should therefore be taken before vegetation scientists use these lists out of its context (Chytrý *et al.*, 2002b).

After testing various statistical measures of fidelity, Chytrý *et al.* (2002a) concluded that the Phi-coefficient produces the best objective measure, but failing to measure statistical significance, it performs best in combination with the Fischer‘s exact test, especially in large, heterogeneous vegetation data sets of unequal size.

2.1.2.5 Nomenclature

As a parallel to the taxonomy of plants, a syntaxonomical nomenclature was formalized by Weber *et al.* (2000). The success of applying syntaxonomical nomenclature to vegetation classifications is unclear, mainly due to problems with fidelity and hierarchy (Van der Maarel, 2005). The review on phytosociology presented by Pignatti (1995) stated that nomenclature should not be treated as the ultimate goal of phytosociology, but should serve as a tool only. According to his view, formal nomenclature can be circumvented if considered unnecessary or unreliable due to insufficient source of regional (local-scale) classifications.

2.1.3 The context of phytosociology and vegetation syntheses in South Africa

The Braun-Blanquet approach was initiated and successfully applied to especially the Grassland and Savanna biomes of South Africa since the 1970‘s. Vegetation surveys were undertaken as part of national initiatives to map the vegetation riches on South Africa (Mucina & Rutherford, 2006). The one major technical constraint to vegetation scientists was their dependence on main-frame software to classify relevé data according to the TWINSPAN algorithm. Bezuidenhout *et al.* (1996) therefore proposed a method to analyse Braun-Blanquet phytosociological data sets on a personal computer, which could be used outside academic institutions.

The introduction of software packages to treat and classify vegetation relevés (e.g. TURBOVEG (Hennekens & Schaminée, 2001) and MEGATAB (Hennekens, 1996) facilitated relevé data management and analyses to a large extent. Although the National Vegetation Database of South Africa is almost 50 000 vegetation plots strong (Rutherford *et al.*, 2012), a substantial proportion of South Africa has not been sampled, nor described in published format. The main reason for the decreasing vegetation surveying projects in South Africa, but also globally, is limited research funding, limited experienced field observers and wide criticism and negative opinions on phytosociology, also by scientific journals. In the modern scientific world, collated by modern, highly computerized equipment, phytosociology is often considered a science that is preoccupied with the description of vegetation that lacks the foundation for ecological theory testing. Still, vegetation surveys and meta-analyses of existing vegetation data remain relevant in South Africa due to its highly diverse vegetation (Rutherford *et al.*, 2012). Despite a geographic imbalance in relevé data available for meta-analyses for the entire country, regional syntheses could contribute substantially to the understanding of vegetation patterns. The value of vegetation syntheses for large conservation areas was identified by Solomon *et al.* (1999), who encouraged a meta-analysis of the vegetation of the Kruger National Park since the application of the existing classification hierarchies to management was scale-dependant. South African vegetation scientists are reluctant to present vegetation syntheses due to the pressure, mainly by European phytosociologists and European-based scientific journals to use formal nomenclature in vegetation descriptions. The lack of adequate local-scale, published vegetation classifications for the entire country limits the accurate application of international codes for syntaxonomical nomenclature and inevitably results in invalid names of plant associations.

2.1.3.1 Treatment of large vegetation data sets

One of the first attempts to analyse large phytosociological data sets in South Africa, was the three-step method proposed by Bredenkamp and Bezuidenhout (1995). Winterbach (1998) also performed this method in a synthesis of *Acacia*-dominated vegetation of the Central Bushveld of South Africa. The three-step method for a phytosociological synthesis of grasslands in South Africa (Bredenkamp & Bezuidenhout 1995) was based on the two-step procedure proposed by Van der Maarel *et al.* (1987).

The attempts of Van der Maarel *et al.* (1987) and Bredenkamp and Bezuidenhout (1995) provide valuable holistic insights on the descriptions of plant communities. However, multivariate analyses applied to vegetation data of limited geographical scale, e.g. vegetation classifications applied in management plans for a game farm or small nature reserve, always include relevés that do not convincingly fit into a specific plant community. These ‗marginal‘ relevés, which form part of a higher level syntaxon, are usually artificially placed within another plant community. This rather subjective placement of relevés contributes to the weakening of transition zones or ecotone vegetation identification (Ewald, 2003). Van der Maarel (1990) later emphasized the great ecological importance of ecotones and stressed that it deserves more attention in research. Ecotonal plant communities (i.e. communities with variation in plant species prevalence) are considered as ecological boundaries in the physical environment (e.g. Cadenasso *et al*., 2003) and form important research objects in Landscape ecology (Strayer *et al*., 2003). Ecotonal plant communities need to be classified since they may require a different management approach.

Considering the rather ‗conservative‘ computer era during which these studies were performed, the manual consolidation of vegetation clusters from previously described plant communities was considered adequate to express variation within larger types. New computer tools have however been developed in the meantime, e.g. JUICE (Tichý, 2002) to treat large vegetation data sets.

2.1.4 New trends in phytosociology and the syntheses of large vegetation data sets

2.1.4.1 Beyond vegetation descriptions

Applications of phytosociological data to ecological theory testing have been criticised widely (see section 2.1.2). Despite this, a refreshed function of phytosociological data has been identified and applied. Some vegetation scientists make use of historical plant community distributions, which is based on phytosociological studies, to comment on vegetation changes commonly ascribed to global environmental change. These conservation projects, which focuses on potential concern and early warning systems, are accomplished through the monitoring of plant community distributions over time, (e.g. Biondi *et al.*, 2004; Van der Maarel, 2005; Feoli *et al.* 2006; Guisan *et al.*, 2006; Haveman & Janssen, 2008; Török & Szitár, 2010) and the monitoring of herbivory pressures (e.g. Cooper & McCann, 2010). Another application of phytosociological data is the mapping of potentially natural vegetation such as the study by Capelo *et al.* (2007).

2.1.4.2 Modern clustering techniques and software for vegetation classification

Vegetation scientists are commonly challenged by the selection of suitable classification methodologies, mainly due to the wide variety of numerical-analytical tools available to disentangle complex ecosystems (e.g. Hill, 1979; Campbell, 1978; Gauch & Whittaker, 1981; Jongman *et al.* 1995; Legendre & Legendre, 1998; Hennekens & Schaminée, 2001; Tichý, 2002; McCune & Mefford, 2006; Rolečeck *et al.*, 2009; Tichý *et al.*, 2009; Kent, 2012). Some of the most commonly used techniques will be discussed briefly.

JUICE (Tichý, 2002) is the most recent computer programme that was developed to challenge the international problem of dealing with the classification and analysis of large vegetation data sets. JUICE is an expert system, which comprises analytical methods such as COCKTAIL (Bruelheide, 1995, Bruelheide, 2000) and TWINSPAN (Hill 1979). After the analytical phase, synoptic tables can be created in the program using user-defined fidelity measures. The classification results can be exported to WORD, EXCEL, DMAP and IDRISI (Tichý, 2002).

Phytosociological classification algorithms have also received some attention in the last decade. The Modified TWINSPAN algorithm (Roleček *et al.*, 2009) is aimed at producing divisive classifications that better respect the structure of the data. The success of this algorithm is that unsubstantiated divisions of homogeneous clusters are prevented, and classifications with any number of terminal clusters can be created. Modified TWINSPAN combines the classical TWINSPAN algorithm with analysis of heterogeneity of the clusters prior to each division. Whittaker‘s beta, total inertia, average Sørensen dissimilarity and average Jaccard dissimilarity are used to measure heterogeneity within the data set.

Classical synoptic tables have been widely used in phytosociological literature in which diagnostic value is subjectively given to species according to frequency values. Chytrý *et al.* (2002a) therefore proposed a revised method for (1) structuring synoptic tables from large phytosociological data sets and (2) defining diagnostic species using statistical measures of fidelity.

COCKTAIL (Bruelheide, 1995, Bruelheide, 2000) is designed to produce groups of species, rather than random species distribution in the relevé data set. The user of the programme preselects a starting point (species) or a small starting species group. This pre-selection determines to some extent, the final composition of the resulting species groups.

OptimClass (Tichý *et al*., 2010) is one of the latest contributors to advanced techniques to classify vegetation data sets. OptimClass is designed to identify the optimal partition of vegetation data based on species with the highest fidelity, called faithful species. Faithful species are determined on the *P*-value of the Fischer‘s exact test as a measure of fidelity. OptimClass is suitable for especially vegetation classifications that rely on the use of diagnostic species for plant community identification and descriptions (Tichý *et al*., 2010).

2.1.4.3 The concept of fidelity in objective approaches to measure diagnostic species

Diagnostic species include species that are confined to a vegetation unit (character species) or to a few vegetation units (differential species) and are traditionally subjectively identified during plant community descriptions (Braun-Blanquet, 1932). In their approach to determine diagnostic species with statistical fidelity measures, Chytrý *et al.*, (2002) demonstrated that classical table analysis fails to determine diagnostic species of general validity in different habitats and large areas. In the determination of diagnostic species in a large data set, Chytrý *et al.* (2002) showed that the approach of using statistical measures of fidelity yield diagnostics which are ecologically more specialized.

2.1.4.4 The probability of applying modern techniques to a heterogeneous savanna vegetation type, such as Mopaneveld

Mopaneveld occurs along a unique environmental gradient ranging from arid regions (Damaraland in Namibia; Angola), crossing semi-arid areas (Owamboland in Namibia; Caprivi in Namibia; Botswana; southern and western Zimbabwe; southwestern Zambia;

north of the Soutpansberg in South Africa) to semi-moist areas (South African Lowveld; northern and eastern Zimbabwe; eastern Zambia; Malawi; Mozambique) (Mapaure, 1994). Because of its distribution across environmental extremes, high α-ánd β-diversity is expected. The major constraint in studying Mopaneveld vegetation is the limitations in vegetation studies with adequate phytosociological data over its entire distribution range (see Chapter 5). Inadequate published local-scale vegetation descriptions in southern African Mopaneveld make the application of both the two-step (Van der Maarel *et al*., 1987) and three-step methods (Bredenkamp & Bezuidenhout, 1995) unfeasible. The development of advanced computer software to treat large relevé databases made it possible for Du Plessis (2001) to apply the full complement of the raw data to the classical TWINSPAN algorithm (Hill, 1979) in MEGATAB (Hennekens, 1996).

Since the presentation of a synthesis of Mopaneveld vegetation in 2001 (see Appendix 5-1 for the published version, Siebert *et al.*, 2003), not only did computer hardware and software improve for comfortable analyses, but alternatives to classical classification approaches have also been introduced, such as the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) and statistical measures of diagnostic species identification (Chytrý *et al*., 2002a). These developments opened opportunities to re-evaluate classification results, especially at a broader scale (De Cáceres *et al.*, 2009).

2.2 The concept of scale in vegetation classifications

In his overview on ecological complexity and common ill-posed questions in ecology, Loehle (2011) stated amongst others, that inconsistent classifications are problematic and that classifications at different scales should be context-based. Most vegetation syntheses are based on earlier European approaches in which a bottom-up re-assembly of previously described plant associations (i.e. upscaling) reveals clusters containing similar plant associations. This method has been criticized widely, in particular by Ewald (2003) due to the misplacement of ‗transition' type vegetation that are subjectively clustered within a plant association at a local scale and hence, being neglected in the regional or national-scale syntheses. Knollová *et al.* (2006) compared such classical local-scale classifications with numerical syntheses, which revealed the misplacement of certain plant associations through local-scale studies, which are biased towards scale and geographic boundaries.

The growth in capturing detailed vegetation relevés in both regional and national databases worldwide (e.g. Rodwell *et al*., 1995; Dengler *et al*., 2011; Rutherford *et al*., 2012) in combination with the development of revised clustering methods and classification algorithms along with modern computer software (see section 2.1 of this chapter) however, make meta-analyses of vegetation data possible at various spatial scales. It is however, commonly expected that classification outputs are dependent on the scale at which it is performed (e.g. Chýtry & Otýpkóva, 2003; De Cáceres *et al.*, 2009) since vegetation is explained by various environmental factors that are drivers of heterogeneity at different spatial scales (Decocq, 2002; Ekblom & Gillson, 2010).

The classification of Mopaneveld vegetation in southern Africa has either occurred at a local site-based scale for only a few parts of the entire southern African study area (i.e. those mentioned under section 2.2.4 of this chapter), or at a much broader national scale (e.g. Rattray, 1962; Barbosa, 1970; Weare & Yalala, 1971; Guy, 1975; White, 1983; Acocks, 1988; Giess, 1998; Low & Rebelo, 1998; Rutherford *et al.*, 2006). These broad-scale classifications are mostly based on structural vegetation patterns along broad climatic and geological boundaries. Only after these broad units have been delineated, they are linked to dominant plant species. Prior to the synthesis of Mopaneveld by Du Plessis (2001), which was based on the culmination of a large vegetation relevé data set, no regional studies on a single, large vegetation type have been presented in southern Africa. A synthesis of the Central Bushveld in the savanna biome of South Africa was presented by Winterbach (1998), although it contained several different vegetation classes within one region.

If the meta-database from which vegetation syntheses are being conducted is presented by detailed floristic sampling plots, should different techniques be applied at different spatial scale analyses? According to Loehle (2011), ‗the classification method or degree of resolution needs to become an object of study'. This thesis will partially address this concern by presenting the application of similar methods across different spatial scales and compare the outcomes of classical versus modern algorithms on the same clustering approach.

2.3 Mopaneveld in southern Africa

2.3.1 Definition of Mopaneveld

After applying the three-step method (Bredenkamp & Bezuidenhout, 1995) to the Central Savanna of South Africa, Winterbach (1998) identified the vegetation unit in which *Colophospermum mopane* (J. Kirk ex Benth.) J.Kirk ex J. Léonard is the most conspicuous character species, as the Commiphoro mollis – Colophospermetea mopani. This prompted further research on the vegetation in which *Colophospermum mopane* dominates. The name *Mopaneveld* is the suggested common name for this vegetation class, a name derived from

Mopani Veld (Acocks 1953). Acocks (1953) delineated veld types according to farming potential in South Africa. Since Mopaneveld, as will be referred to in this thesis, extends across South African borders, the name ―Mopani Veld” is not considered. Even the name ‗Mopane Bushveld‘ proposed by Low and Rebelo (1998) for the vegetation type in which *Colophospermum mopane* dominates is not considered. Contrary to the definition of ‗vegetation type‘, which Low and Rebelo (1998) described as a vegetation unit representing a coherent array of communities which shares common species (or abundance of species), possesses a similar vegetation structure (vertical profile) and shares the same set of ecological processes, vegetation structure and ecological processes along the distribution range of *C. mopane* vary considerably (Timberlake, 1999). Mucina and Rutherford proposed the concept of ‗Bioregion‘, of which vegetation dominated by *Colophospermum mopane*, is referred to as the ‗Mopane Bioregion‘, although the bioregion is more focused on floristic composition than on climatic and geological variability. Although the term ‗bioregion‘ suits Mopaneveld best, the Mopaneveld across its entire distribution range in southern Africa does not fall under the Mopane Bioregion due to the its association with South Africa only. Therefore, neither Veld Type nor Vegetation Type or Bioregion truly reflects *C. mopane* vegetation in southern Africa. Mopaneveld could therefore be defined as ‗a vegetation unit in which *Colophospermum mopane* generally dominates or co-dominates the woody component‘. Despite the nature of *C. mopane* to form the major contributor to woody biomass in savannas where it occurs, it was reported by Du Plessis (2001) that Mopaneveld not necessarily need to be dominated by *Colophospermum mopane*. Mopaneveld is often interrupted by other vegetation types or smaller associations in which *Colophospermum mopane* becomes the sub-dominant, or even considered as a non-conspicuous woody species. **The definition of Mopaneveld proposed for the purpose of this study is ‘a broad vegetation unit in which *Colophospermum mopane* forms at least a conspicuous species in the woody vegetation at a scale larger than the basic plant community (association)’**.

2.3.2 The species *Colophospermum mopane* (J. Kirk ex Benth.) J. Kirk ex J. Léonard

Colophospermum mopane, often referred to as "mopane", has extensively been reviewed in terms of its biology and ecology (eg. Thompson, 1960; Jarman & Thomas, 1969; Henning & White, 1974; Van Voorthuizen, 1976; Scholes, 1990; Madams, 1990; Choinski & Tuohy, 1991; Mapaure, 1994; Smit *et al.*, 1994; Timberlake, 1995; Timberlake, 1996; Timberlake, 1999; Smit & Rethman, 1998a; Smit & Rethman, 1998b; Jordaan, *et al.*, 2000; Smallie & O‘Connor, 2000; Smit & Rethman, 2000; MacGregor & O‘Connor, 2002; Ferreira *et al.*, 2003; Kennedy & Potgieter, 2003; Smit, 2003; Ekosse *et al.*, 2005; Mlambo *et al.*, 2005; Hempson *et al.*, 2007; Gandiwa & Kativu, 2009; Khavhagali & Ligavha-Mbelengwa, 2009;

Makhado *et al.*, 2009). Since this study focuses mainly on the vegetation of Mopaneveld and not on the species itself, discussions on the species will not be presented here, although a review on the species can be found in Timberlake (1999) and Du Plessis (2001).

2.3.3 Mopaneveld vegetation structure

The key determinants of savanna vegetation structure are rainfall, soil nutrients, fire and herbivory (Walker, 1985). Landscape heterogeneity in southern African savannas in combination with a diversity of land use and rainfall variability, constitutes structural diversity in southern African savannas. In some savanna types, gradual floristic and physiognomic changes mark the transition from one type of savanna to another, whilst in others changes are abrupt presenting sharp boundaries (Cole, 1986). The variety of factors influencing the distribution of Mopaneveld vegetation constitutes variance in physiognomic structure over its distribution in southern Africa. Apart from anthropogenic influences, Mopaneveld physiognomy is mainly driven by soil properties. In many parts of Mopaneveld, the physiognomical structure has been modified by fire, herbivory or harvesting, most often leaving dense stands of multi-stemmed shrubs (Mapaure & Ndeinoma, 2011).

Although the majority of Mopaneveld vegetation is associated with woodland or savanna vegetation structure, *Colophospermum mopane* has four growth forms: (i) a tall tree form growing up to 20 m high; (ii) a small to medium sized tree usually from 5–12 m tall; (iii) a shrubby form up to 6 m tall, differing from (i) and (ii) in that the main stem is not well developed, and (iv) a bushy scrub form usually less than 3 m tall (Madams, 1990; Timberlake, 1995; Timberlake, 1996). The closed mopane woodlands (type i), also referred to as ‗cathedral mopane' (Timberlake, 1995) occur in the semi-moist northern parts of its distribution range with trees up to 25 m in height (Werger & Coetzee, 1978). Cathedral mopane is associated with deeper, less compacted soil, such as alluvium, and higher mean annual rainfall (Werger & Coetzee, 1978; White, 1983; Timberlake 1995; Rutherford *et al.*, 2006). The dominant physiognomic representation of *C. mopane*, namely medium-sized trees and shrubs, i.e. types (ii) and (iii), is predominantly found on shallow, sodic, heavier textured solonetzes (Werger & Coetzee 1978; Timberlake 1995). The shrubby, multi-stemmed type (type iv) is associated with heavy clays, often of vertic character (Werger & Coetzee 1978; Cole 1986; Rutherford *et al.*, 2006). Hempson *et al.* (2007) tested whether the structural variance in *Colophospermum mopane* is driven by fine-scale environmental variability in available water, but concluded that structure could not be correlated to variance in available water.

2.3.4 Mopaneveld distribution in southern Africa

The southern African Mopaneveld is estimated to cover an area of approximately 555 000 km^2 (Mapaure, 1994) across eight different countries in southern Africa on fine-textured soil of dry valley bottoms in a water-limited ecosystem (Timberlake, 1999). The well-known economically- and ecologically important tree species, *Colophospermum mopane* forms the dominant woody species across its range, especially on insufficiently drained soil (Werger & Coetzee, 1978). It is however reported that the species ranges further than the distribution of the vegetation type (Timberlake, 1999).

Colophospermum mopane is certainly one of the most extensive plant species in Africa due to its character to dominate the woody layer of a plant community if conditions are favourable (Du Plessis, 2001). Considering the extensive areas occupied by Mopaneveld in the savannas of southern Africa (Figure 3-1), factors influencing its distribution are not easily detectable. Distribution limits of *Colophospermum mopane*, hence Mopaneveld, is presumably determined by different ecological factors over different parts of its range. The distribution of *Colophospermum mopane* is principally influenced by moisture availability expressed through altitude, rainfall and soil texture (Cole, 1986; Mapaure, 1994). *Colophospermum mopane* generally occupies areas where moisture accumulates at shallow soil depths. It is therefore often found on solid bedrock (e.g. granite) overlain by shallow soil or on an impervious layer of transported clay (e.g. riverine silt). Where there is a combination of low rainfall and severe heat as a result of clay being dispersed by exchangeable sodium, *C. mopane* also occurs (Cole, 1986). The shallow rooting system of *Colophospermum mopane* places it in a competitive advantage in areas where conditions lead to the development of a zone of maximum water retention near the surface. Such zones are commonly found in semi-arid savannas due to low rainfall and great heat, which consequently lead to moisture retention near the soil surface (Mlambo *et al.*, 2005).

The distribution of Mopaneveld is generally associated with fine-textured soil in the wide, flat valley bottoms of river valleys such as the Limpopo (Botswana, South Africa, Zimbabwe & Mozambique), Zambezi (Botswana, Zimbabwe, Zambia & Mozambique), Chobe (Botswana), Okavango (Botswana), Cunene (Namibia & Angola), Shire (Malawi) and Luangwa (Zambia & Malawi) (Werger & Coetzee, 1978; Cole, 1986; Mapaure, 1994). *Colophospermum mopane* is profoundly found in the 400 m and 700 m altitudinal range. Following seasonal summer rainfall patterns, it receives between 200 mm and 800 mm annually, which generally corresponds with high temperatures (Mapaure, 1994), hence high rates of mean annual potential evaporation (Rutherford *et al.*, 2006). Low winter temperature, in particular the 5°C isotherm, is considered an important distribution limiting factor towards its southernmost distribution (Henning & White, 1974; Cole 1986).

Colophospermum mopane is one of several species of the Zambezian Region (White, 1983) which penetrates far into the western desert along watercourses. It is however found not to dominate the woody layer in areas receiving less than 300 mm rainfall annually (Timberlake, 1995), but rather occurring in the form of bushy trees. *Colophospermum mopane* can tolerate extreme environmental conditions, e.g. surviving on as little as 125 mm rainfall per year in the Kaokoland of Namibia, whilst tolerating high annual rainfall (i.e. up to 1 000 mm) in the Luangwa Valley, Zambia and central Malawi. The majority of plant communities dominated by *Colophospermum mopane* are distributed between the *Brachystegia* – *Isoberlinia* – *Julbernardia* savanna woodlands (miombo) and the *Acacia*-dominated low tree and shrub savanna (Kalahari vegetation). According to Cole (1986) this alternation of different savanna types provides important evidence on the interacting influences of factors and processes affecting the distribution of savannas and of the plant communities within them.

The distribution of Mopaneveld as well as the vegetation associations and plant communities within are related not only to the prevailing climatic and edaphic conditions but also to the geomorphological evolution of the landscape, bedrock geology and to geological events and changes of climate (White, 1983).

The distribution of *C. mopane*-dominated vegetation types have been reviewed by Mapaure (1994) according to vegetation maps from the different hosting countries (e.g. Acocks (1988) for South Africa, Weare & Yalala (1971) for Botswana, Rattray (1962) for Zimbabwe, Barbosa (1970) for Angola, Giess (1998) for Namibia and Wild & Barbosa (1967) for the Flora Zambesiaca area).

2.3.5 Summary of Mopaneveld vegetation in each hosting country

2.3.5.1 Angola

Angola hosts the largest portion of Mopaneveld in southern Africa (112 500 km^2) (Mapaure, 1994). It is restricted to the south-western part of the country between Lobito in the north and the Cunene River, bordering Namibia in the south. Angolian Mopaneveld occurs on a variety of soil types mainly derived from granite. Rainfall seems to be the major determinant in its distribution in Angola (Mapaure, 1994). The Angolian Mopaneveld continues into the north-western Mopaneveld of Namibia.

Mopaneveld stretches from the semi-arid savannas, receiving 300 mm mean annual precipitation where *Colophospermm mopane*- dominated vegetation is interrupted by *Baikiaea* woodlands, which are predominantly located on the Kalahari sands, whereas

Mopaneveld inhabits the more clayey substrates (Huntley, 1974). Further westwards to the Kaokoland (Namibia) and Chela (Angola) escarpments, at an altitude of approximately 250 m, low shrubs of *Colophospermum mopane* along with *Balanites welwitschii* occur predominantly in dry riverbeds at mean annual rainfall of less than 100 mm annually (Werger & Coetzee, 1978).

2.3.5.2 Botswana

Mopaneveld in Botswana covers approximately 85 000 km^2 from the Limpopo River in the east to the Makgadikgadi pans in the north, including the areas surrounding the Okavango swamps (Mapaure, 1994). Rainfall is considered the main distribution factor, which varies from 400 mm to 600 mm annually (Mapaure, 1994). Soil with a sandy silt, clay loam and clayey texture support mixed tree and bushland savanna whilst mopane woodlands are associated with fersiallitic soil on uplands and siallitic colluvial soil with impeded drainage in the valleys (Mapaure, 1994). Mopaneveld of Botswana can be subdivided into dry deciduous forest, riparian forest, woodland, thicket, tree or shrub savanna or open shrubland (Weare & Yalala, 1971), therefore hosting most of the physiognomic forms of Mopaneveld.

2.3.5.3 Malawi

Malawi hosts the smallest portion (i.e. 10 000km^2) of the Mopaneveld across its total distribution in southern Africa. It occurs on altitudes between 450 m and 500 m receiving 800 mm or less rainfall annually (Mapaure, 1994). In the mid-Shire Valley, deep soil produces *C. mopane* woodland where individuals reach 30–31 m, considerably higher than recorded elsewhere (Dudley, 1994). In the lower Shire Valley and along the southern shores of Lake Malawi, Mopaneveld is found on compact, alkaline, dark grey soil of texture sandy clay with free calcium carbonate (Wild & Barbosa, 1967; Werger & Coetzee, 1978) supporting a tree savanna dominated by *Colophospermum mopane* (Mapaure, 1994).

2.3.5.4 Mozambique

Mozambican Mopaneveld is principally dominated by woodlands and savanna, considered to be distributed according to annual rainfall patterns (Mapaure, 1994). Approximately 98 000 km^2 area is covered by Mopaneveld vegetation in Mozambique (Mapaure, 1994). The Save and Limpopo valleys contain calcareous alluvium on which mopane savanna predominates, whilst both mopane woodland and savanna is found in the Zambezi valley, mainly composed of relatively deep, compact, clayey and calcareous soil derived from Karoo formations (Mapaure, 1994).

2.3.5.5 Namibia

The vegetation of Namibia is divided into three major types, namely the Namib Desert, savannas, and woodlands (Erkkilä & Siiskonen, 1992). Covering approximately 77 000 km^2, of the savannas and woodlands, the Namibian Mopaneveld stretches from the Cunene River in the north towards the Ugab in the south and north-eastwards towards Namutoni. It is also sparsely distributed in patches in the Caprivi (Mapaure, 1994). Erratic, variable rainfall patterns in combination with local variance in soil texture are considered the main factors driving the distribution of Mopaneveld in Namibia (Mapaure, 1994). In Namibia, *Colophospermum mopane* is often associated with spaced woodland with a shrubby understorey, rather than the more typical mopane savanna or woodland found in other parts of its distribution range.

Receiving an annual rainfall of 50–100 mm at 250 m altitude, the western limits of Namibian Mopaneveld along the Kaokoland escarpment toward the Namib Desert is characterised by a low shrub savanna type. Although still dominating the woody layer, *Colophospermum mopane* is confined to depressions and small riverbeds (Werger & Coetzee, 1978; Giess, 1998). Mopaneveld in the Etosha National Park is mostly associated with shallow lithosols on a calcrete substrate (Le Roux *et al.*, 1988), although mopane shrubveld occurs in small depressions on loamy soil with high clay content (Le Roux *et al.*, 1988). In Owamboland of the Cuvelai Delta, Mopaneveld is associated with an open tree savanna dominated by *Colophospermum mopane*. Owamboland, a broad plain at approximately 1 100 m altitude, is located in the northern parts of Namibia on aeolian Kalahari sands of varying depth with scattered patches of calcareous concretes. This area receives between 350 mm rainfall per year in the southwest, while the northeastern parts receive 550 mm annually (Erkkilä & Siiskonen, 1992).

A study on the leaf habits to correlate the distribution of Namibian savannas to physiographic and annual rainfall patterns revealed that the evergreen notophyll savanna is exclusively linked to the distribution of mopane savanna in Namibia (Okitsu, 2005). It is further hypothesized that mopane savanna distribution in Namibia is not driven by annual precipitation nor by physiographic properties, but rather by a unique combination of these. Mopaneveld distribution in Namibia, and probably in southern Africa, is rather driven by the unique ecology of *Colophospermum mopane* itself (Okitsu, 2005).

2.3.5.6 South Africa

Covering a total area of 23 000 km^2, the South African Mopaneveld is distributed along the semi-arid Limpopo River Valley in the north where it extends towards its affinities in the neighbouring Zimbabwe and Botswana. Mopaneveld extends from the northern border of the Kruger National Park along the eastern end of the Soutpansberg in Venda, to its most southern distribution limit just south of the Olifants River in the Kruger National Park where the annual rainfall is slightly higher, i.e. approximately 400 mm (Gertenbach, 1987). The most recent account on the vegetation of South Africa, classified Mopaneveld into its own Bioregion (Mucina & Rutherford, 2006). Mopaneveld in South Africa ranges from cathedral mopane woodlands, in which *C. mopane* dominate the 12 m high tree layer, to a short, multi-shrub vegetation type on vertic clays (Rutherford *et al.*, 2006). The mopane shrubveld is however not restricted to the heavy clays derived form basalt and gabbro, but also occurs in the Limpopo River Valley on calcareous soil of an intersected to undulating landscape (Gertenbach 1983; Mapaure 1994). This unique landscape (Gertenbach, 1983) is underlain by the Malvernia Formation, which decomposes to give rise to soil with many lime concretions (Gertenbach, 1983). A less common Mopaneveld type is the Olifants River Rugged Veld on metamorphic rock (Gertenbach, 1983). The vegetation shows xerophytic characteristics supporting a sparse field layer. Similar to this vegetation type, is the Limpopo Ridge Bushveld, which is typically associated with dry ridges and hills with interspersed *Adansonia digitata* and *Kirkia acuminata* individuals (Rutherford *et al.*, 2006).

2.3.5.7 Zambia

Mopaneveld in Zambia is generally associated with extended, often single-storey (i.e. single-stratum) woodlands, found in the valleys of the Luangwa, Luano, Kafue as far north as Mofu in the Kafue National Park, Zambezi west to Katima and the Mashi to just north of the Sesheke-Senanga border (Fanshawe, 1969). It covers an area of approximately 43 500 km^2, which is limited in distribution according to underlying soil. *Colophospermum mopane* forms the dominant woody species throughout its distribution in Zambia. The Luangwa Valley receives approximately 900 mm rainfall annually and lies in a wide, flat-bottomed depression bounded by steep, dissected escarpments that rise to 700 m and 800 m above its floor (Werger & Coetzee, 1978). Extensive stands of *Colophospermum mopane* trees from 10 m to 17 m in height inhabit the alkaline soil of the valley alluvium (Fanshawe, 1969; Werger & Coetzee, 1978). These poor fluvisols and vertisols, impregnated with nodular concretions, are normally flooded during the wet season and almost completely dried out during the dry season, which coincides with high temperatures (Fanshawe, 1969; Cole, 1986; Mapaure, 1994). Mopaneveld in the Luangwa Valley is however also frequently interrupted by patches of *Acacia* savanna and *Combretum-Terminalia sericea* woodland where conditions tend towards lower extremes (Werger & Coetzee, 1978). On soil texture where a sandy sheet overlays a hard and compact, alkaline sandy loam with a columnar structure, mopane woodlands with trees reaching heights of 25 m is found. Mopaneveld in the Zambezi River

Valley of the Lake Kariba region differs from the Luangwa and associated valleys. The former is a bit drier, although still receiving more or less 700 mm rainfall per annum (Werger & Coetzee, 1978).

2.3.5.8 Zimbabwe

Zimbabwean Mopaneveld covers 101 500 km^2 (Mapaure, 1994) represented in approximately twelve major types. These types can be distinguished according to general physiognomical appearance and species composition, which follow the variance of a combination of factors, of which substrate type, soil depth, altitude and annual rainfall are probably the most important determinants for their distribution (Guy, 1975; Timberlake *et al.,* 1993; Mapaure, 1994). Mopaneveld in Zimbabwe is associated with the Zambezi, Limpopo, Sabi and Shangani valleys with medium size *Colophospermum mopane* trees to tall mopane woodlands (Werger & Coetzee, 1978; Mapaure, 1994). In the higher rainfall areas, e.g. in the northern Zambezi Valley in Zimbabwe, Mopaneveld varies between woodland and woodland savanna whereas in the drier south, woodland savanna, tree savanna and tree/bush savanna prevails. Pure *C. mopane* woodlands, often forming ‗cathedral mopane' occur on the valley floors of large rivers dissecting Zimbabwe. In the Zambezi Valley this deciduous woodland occurs as the most extensive vegetation type of the valley floor (Guy, 1975). Although not very common and occurring in small patches, a *Colophospermum mopane* woodland type exists on a gently undulating expanse of sandy soil along the border of Mozambique in the Zambezi Valley (Du Toit, 1993). *Colophospermum mopane* often occurs in a woodland type of alternating dominance of *Kirkia acuminata* and *Acacia nigrescens* on shallower lithosols or skeletal soil, mainly derived from basalt (Rattray, 1962; Du Toit, 1993; Timberlake *et al.*, 1993).

2.3.6 Mopaneveld vegetation classifications

Du Plessis (2001) presented a detailed account on all the plant communities at various hierarchical levels that have been described in published articles as well as in unpublished reports. A few areas within the Mopaneveld have been classified and described since the overview by Du Plessis (2001) and will be presented only curtly as background knowledge for this thesis.

2.3.6.1 Mopaneveld in South Africa

The vegetation of South Africa, Lesotho and Swaziland (Mucina & Rutherford, 2006) presented the Mopaneveld as a Bioregion within the Savanna Biome (Rutherford *et al.*, 2006). The Mopane Bioregion is subdivided into eight different Mopaneveld types across its distribution in South Africa. They include: (i) Musina Mopane Bushveld, (ii) Limpopo Ridge

Bushveld, (iii) Cathedral Mopane Bushveld, (iv) Mopane Basalt Shrubland, (v) Tsende Mopaneveld, (vi) Lowveld Rugged Mopaneveld, (vii) Phalaborwa-Timbavati Mopaneveld, and (viii) Mopane Gabbro Shrubland.

Local-scale vegetation classification studies in the Mopaneveld of the Limpopo Valley in South Africa received considerable interest since the overview by Du Plessis (2001). A phytosociological study on the vegetation of Mapungubwe National Park (MNP) is presented in a Master‘s dissertation (Götze, 2002) and subsequent publications, e.g. Götze *et al.* (2003), which present the riparian plant communities, and Götze *et al.* (2008), which present the vegetation on the sandstone ridges. The general vegetation of the MNP is characterized by a fairly dense growth of *Colophospermum mopane* along with *Combretum apiculatum*, *Acacia nigrescens*, *A. tortilis*, *Adansonia digitata*, *Commiphora* spp., *Boscia albitrunca*, *Terminalia prunioides*, *Kirkia acuminata* and *Sclerocarya birrea* in the woody layer (Götze, 2002). *Colophospermum mopane* communities in MNP are distributed along a variety of soil forms, which ranges from shallow Glenrosa to deep red sandy soil. Collectively, these communities are classified under the *Colophospermum mopane* – *Brachiaria deflexa* group (Götze, 2002).

Another vegetation study along the Limpopo River was presented in the form of a Master‘s dissertation by Straub (2002). In her study, Straub (2002) classified the study area into two distinct vegetation units, the *Colophospermum mopane* – *Hibiscus micranthus* major communities, and the *Salvadora australis* – *Acacia tortilis* major woodland communities. The first, which is characteristically considered Mopaneveld is typically found as open shrubland on soil derived from basalt. The herbaceous layer is sparse and dominated by annual grasses with scattered perennials, such as *Schmidtia pappophoroides* and *Cenchrus ciliaris* (Straub, 2002). The woody layer is dominated by *Colophospermum mopane* and *Grewia bicolor*, but *C. mopane* becomes a sub-dominant on stony soil and sloping landscapes with conspicuous species in the tree and shrub layer being *Terminalia prunioides*, *Adansonia digitata*, *Kirkia acuminata* and *Sclerocarya birrea* (Straub, 2002).

A first phytosociological account of the Soutpansberg Conservancy was presented by Mostert (2006) in a PhD thesis and subsequent publications. Major vegetation types were described and discussed of which some areas of the *Adansonia digitata–Acacia nigrescens* Soutpansberg Arid Northern Bushveld fall within Mopaneveld, although *Colophospermum mopane* almost never forms the dominant species in the tree layer (Mostert *et al.*, 2009).

Local-scale detailed vegetation descriptions were done for the Letaba River long-term monitoring herbivory and fire exclosures in the Kruger National Park (Siebert *et al.*, 2010). Four plant communities containing eight sub-communities and six variants were identified and described after TWINSPAN classifications. Details on species richness and diversity across the different plant communities were also presented. The *Schmidtia pappophoroides* – *Colophospermum mopane* lowland savanna contains most of the typical assemblages within Mopaneveld vegetation, although *C. mopane* occurs in lower densities in most of the other units, even along the riparian fringes (Siebert *et al.*, 2010).

2.3.6.2 Mopaneveld in other southern African countries

Published vegetation classifications outside the South African borders are limited. In south-western Zimbabwe, Timberlake and Mapaure (2007) described and discussed the vegetation of the Bubiana Conservancy as a basis for long-term monitoring programmes on the vegetation of the area. Mopane Woodland on depositional soil, mostly sandy loams to sandy clay loams, formed one of the major vegetation units identified through phytosociological classification. This *Colophospermum mopane* woodland is characterized by trees between 8 m and 12 m in which *C. mopane* dominates, but in co-dominance with other trees, such as *Acacia nigrescens*, *Acacia nilotica*, *Albizia harveyi*, *Combretum apiculatum*, *Commiphora glandulosa* and *Ziziphus mucronata*. *Spirostachys africana* occurs mostly on deeper and moister soil. The shrub layer is diverse and dominated by *Dichrostachys cinerea*, *Grewia flavescens* and *Grewia monticola*, and co-dominated by *Euclea divinorum*, *Flueggea virosa*, *Ehretia obtusifolia*, *Dalbergia melanoxylon*, *Ormocarpum trichocarpum*, *Ximenia americana* and *X. caffra*. The grass layer consists of *Heteropogon contortus*, *Eragrostis* species, *Panicum maximum* and *Urochloa mosambicensis* (Timberlake & Mapaure, 2007).

In the mid-Zambezi Valley of Zimbabwe, Poilecot and Gaidet (2010) classified and described an area typically classified as Mopaneveld vegetation. They described a Mopane woodland, *Combretum* shrubland, Mixed shrubland, and *Acacia* shrubland. The Mopane woodland is dominated by high trees of *Colophospermum mopane* and corresponds to previous descriptions of ‗cathedral mopane‘. Other common woody species in this woodland include *Diospyros quiloensis*, *Combretum apiculatum*, *Kirkia acuminata* and *Sterculia africana*. The poorly developed shrublayer is dominated by *Grewia bicolor*, *Combretum mossambicensis* and *Ximenia americana* (Poilecot & Gaidet, 2010). Consistent with the findings by Siebert *et al.* (2003), their study revealed that Mopaneveld vegetation is not constantly dominated by *Colophospermum mopane*. Although herbaceous layer assemblages are more consistent throughout Mopaneveld, the tree layer is mostly co-dominated by *Terminalia* spp., *Grewia* spp. and *Combretum* spp. (Poilecot & Gaidet, 2010).

Botswana vegetation classifications are limited, although Ringrose *et al.* (2003) presented some broad classifications, although they are presented towards vegetation cover trends. Typical of Mopaneveld vegetation, their results showed dominance of *Colophospermum mopane* in the Maun district, where this species forms monotypic stands along with *Grewia flava* and *Terminalia* species (Ringrose *et al.*, 2003).

Mopaneveld type vegetation in Mozambique has been more extensively surveyed and described as baseline vegetation descriptions for the proclaimed Limpopo National Park (Parque Nacional do Limpopo, Moçambique). Based on detailed Braun-Blanquet sampling and after TWINSPAN analyses, Stalmans *et al.* (2004) revealed the identification of several vegetation units at various scales. *Colophospermum mopane* is the dominant woody species in two of the identified plant communities, namely the *Colophospermum mopane* – *Panicum maximum* short woodland (Community 6) and the *Colophospermum mopane* – *Combretum imberbe* tall shrubland (Community 7), although it falls within the distribution of Mopaneveld (Stalmans *et al.*, 2004) as the broad vegetation type. Subjective comparison of the results obtained through the classification, revealed the relationship between the identified units and those identified by Gertenbach (1983) for the Kruger National Park. The authors identified ten Landscapes of Gertenbach (1983) that is considerably similar to the identified vegetation units of the Limpopo National Park, of which five are *Colophospermum mopane* associated Landscapes.

Similar to the study for the Limpopo National Park, the Banhine National Park (Stalmans & Wishart, 2005) and the Zinave National Park (Parque Nacional de Zinave, Mozambique) (Stalmans & Peel, 2010) were surveyed and the vegetation described. The Zinave National Park lies on the interface between Mopaneveld and Miombo vegetation. TWINSPAN analyses revealed the identification of the *Colophospermum mopane* – *Urochloa mosambicensis* woodland in which *C. mopane* dominates, although it is conspicuously present in the areas outside Miombo, which also falls within Mopaneveld, and is also termed the Mopane Landscape (Stalmans & Peel, 2010). In the Banhine National Park, typical Mopaneveld vegetation units, the *Colophospermum mopane* – *Urochloa mosambicensis* woodlands community on clayey soil and the *Colophospermum mopane* – *Eragrostis pallens* woodlands community on sandier substrates were described by Stalmans and Wishart (2005). Although not dominant in the *Acacia borlea* shrublands and in the wooded grasslands, *Colophospermum mopane* occurs as an important woody shrub.

A complete revised map of the vegetation and descriptions of Namibian vegetation is underway (Strohbach, 2001). Kangombe and Strohbach (2008) summarized the major vegetation types identified at the Ogongo Agricultural Farm and surrounds, of which *Colophospermum mopane* dominates three of the identified units.

2.3.7 Mopaneveld floristics

Since the overview of Mopaneveld and *Colophospermum mopane* by Du Plessis (2001) and Timberlake (1999), very little studies have been conducted on diversity patterns in Mopaneveld vegetation. The standing hypothesis is that Mopaneveld is characterized by low β-diversity (O‘Connor, 1985; O‘Connor, 1992) and γ-diversity (Timberlake, 1995). Even in the broad description of the diversity patterns in the savanna biome (Rutherford *et al.*, 2006), Mopaneveld vegetation diversity is not mentioned, probably due to a lack of quantitative studies on diversity patterns within this Bioregion. On a very small scale, Siebert *et al.* (2010) reported on the diversity of the various plant communities identified at the Letaba exclosures in the Kruger National Park. Khavhagali and Ligavha-Mbelengwa (2009) compared plant species richness of monotypic stands of *Androstachys johnsonii* and *Colophospermum mopane* at the Makuya Nature Reserve in the north-eastern part of the Limpopo Province, South Africa. Results indicated lowest species richness in the *A. johnsonii* stands on both loamy and sandy substrates. The study, however, failed to present species diversity index values and statistical measures due to pseudoreplication.

Poilecot and Gaidet (2010) reported high floristic heterogeneity in Mopaneveld savanna of the mid-Zambezi valley, although lowest species richness was recorded in stands of *Colophospermum mopane* dominance, whereas species richness was higher in the mixed woodland communities, which are broadly classified under the ‗Mopane belt‘.

Mopaneveld lies in an area subjected to profound direct and indirect utilization by humans. Rutherford *et al.* (2012b) studied the effects of heavy grazing on diversity patterns in communal lands in the Mopane Bioregion of South Africa. They concluded that the implications of heavy grazing appear to be less severe for plant speces diversity than for changes in composition and structure. This study is, however not finalized and the data not available in published format, although these preliminary findings are promising for the better understanding of diversity patterns in Mopaneveld.

2.3.8 Mopaneveld ecology and management

The most extensive research topic in Mopaneveld vegetation remains its management. Despite its wide distribution and dense cover, the high demand for wood by humans, deforestation by elephants and the treatment of fire cause concern to the sustainability of Mopaneveld vegetation in southern Africa (e.g. Eckhardt *et al.*, 2000; Kennedy & Potgieter, 2003; De Beer *et al.*, 2006; Gandiwa & Kativu, 2009; Makhodo *et al.*, 2009; O'Connor, 2010). The impact of sustained drought in combination with human impact is also reasonably covered during the last decade (e.g. Smit & Rethman, 2000; MacGregor & O'Connor, 2002; Mlambo *et al.*, 2005; O'Connor, 2010). Mopaneveld pasture management is also a topic that is frequently addressed in Mopaneveld vegetation (e.g. Smit, 2003; Mlambo *et al.*, 2005).

Species cannot necessarily only live in the area to which it is confined presently. It may not have completed its natural migrations and may still be in the process of extending its range (Rattray, 1962). Therefore, great concerns on increasing densities of *Colophospermum mopane* and the resulted decreasing of grass cover encouraged further research. The South African Environmental Observation Network (SAEON) is currently conducting research on the potential expansion of Mopaneveld outside its natural distribution range as a result of global climate change (Stevens & Swemmer, 2010).

2.4 Conclusions

The extent of information available on phytosociology and on Mopaneveld across its distribution range in southern Africa encouraged a meta-analysis to integrate the information on its complexity. Since the Mopaneveld is extensive in its distribution range, this unique savanna vegetation type serves an ideal experimental subject to study the relevance of methodologies at different spatial scales, i.e. from the broadest scale across geographical and political boundaries through landscape level, up to the smallest local-scale vegetation unit. The development of analytical methods along with modern software packages and more powerful computers therefore prompted a re-assessment of the Mopaneveld vegetation synthesis by Du Plessis (2001) with the application of more recent analytical techniques, but on the same data sets.

2.5 References

ACOCKS, J.P.H. 1953. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa,* 28:1–192.

ACOCKS, J.P.H. 1988. Veld Types of South Africa. 3rd ed. *Memoirs of the Botanical Survey of South Africa,* 57:1–146.

BARBOSA, L.A.G. 1970. Carta fitogeográfica de Angola. Luanda, Angola. Instituto de Investigaçâo Científica de Angola.

BARKMAN, J.J. 1989. Fidelity and character-species, a critical evaluation. *Vegetatio,* 85:105–116.

BELBIN, L. 1987. The use of non-hierarchical allocation methods for clustering large sets of data. *Australian Computer Journal*, 19:32–41.

BELBIN, L. & McDONALD, C. 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science,* 4:341–348.

BEZUIDENHOUT, H. 1996. The major vegetation communities of the Augrabies Falls National Park, Northern Cape. 1. The southern section. *Koedoe,* 39(2):7–24.

BEZUIDENHOUT, H., BIGGS, H.C. & BREDENKAMP, G.J. 1996. A process supported by the utility BBPC for analysing Braun-Blanquet data on a personal computer. *Koedoe,* 39(1):107–112.

BIONDI, E., FEOLI, E. & ZUCCARELLO, V. 2004. Modelling environmental responses of plant associations: a review of some critical concepts in vegetation study. *Critical reviews in Plant Sciences,* 23(2):149–156.

BOTTA-DUKÁT, Z. & BORHIDI, A. 1999. New objective method for calculating fidelity. Example: the Illyrian beechwoods. *Annali di Botanica*, 57:73–91.

BRAUN-BLANQUET, J. 1932. Plant Sociology. The Study of Plant Communities. Authorized English translation of 'Pflanzensoziologie' (Fuller, G.D. & Conard, H.S. *eds*. New York: McGraw-Hill).

BREDENKAMP, G.J. & BEZUIDENHOUT, H. 1995. A proposed procedure for the analysis of large phytosociological data sets in the classification of South African grasslands. *Koedoe,* 38(1):33–39.

BRUELHEIDE, H. 1995. Die Grünlandgesellschaften des Harzes und ihre Standortsbedingungen. Mit einem Beitrag zum Gliederungsprinzip auf der Basis von statistisch ermittelten Artengruppen. *Dissertationes Botanicae,* 244:1–338.

BRUELHEIDE, H. 2000. A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science,* 11:167–178.

BRUELHEIDE, H. & CHYTRÝ, M. 2000. Towards unification of national vegetation classifications: A comparison of two methods for analysis of large data sets. *Journal of Vegetation Science,* 11:295–306.

CADENASSO, M.L., PICKETT, S.T.A., WEATHERS, K.C. & JONES, C.G. 2003. A framework for a theory of ecological boundaries. *BioScience*, 53(8):750–758.

CAMPBELL, B.M. 1978. Similarity coefficients for classifying relevés. *Vegetatio,* 37:101–109.

CAPELO, J., MESQUITA, S. COSTA, J.C., RIBEIRO, S. ARSÉNIO, P., NETO, C., MONTEIRO-HENRIQUES,T., AGUIAR, C., HONRADO, J., ESPÍRITO-SANTO, D. & LOUSÃ, M. 2007. A methodological approach to potential vegetation modelling using GIS techniques and phytosociological expert-knowledge: application to mainland Portugal. *Phytocoenologia,* 37(4):399–415.

CESA-BIANCHI, N., GENTILE, C. & ZANIBONI, L. 2006. Incremental algorithms for hierarchical classification. *Journal of Machine Learning Research,* 7:31–54.

CHIARUCCI, A. 2007. To sample or not to sample? That is the question...for the vegetation scientist. *Folia Geobotanica,* 42:209–216.

CHOINSKI, J.S. & TUOHY, J.M. 1991. Effect of water potential and temperature on the germination of four species of African savanna trees. *Annals of Botany*, 68:227–233.

CHYTRÝ, M. 2001. Phytosociological data give biased estimates of species richness. *Journal of Vegetation Science,* 12:439–444.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. 2002a. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science,* 13:79–90.

CHYTRÝ, M., EXNER, A., HRIVNÁK, R., UJHÁZY, K., VALACHOVIČ, M. & WILLNER, W. 2002b. Context- dependence of diagnostic species: A case study of the central European spruce forests. *Folia Geobotanica,* 37:403–417.

CHYTRÝ M. & OTÝPKOVÁ, Z. 2003. Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science,* 14:563–570.

COLE, M.M. 1986. The Savannas: biogeography and geobotany. Academic Press: London. 438 p.

COOPER, A. & McCANN, T. 2010. Cattle exclosure and vegetation dynamics in an ancient, Irish wet oakwood. *Plant Ecology* DOI 10.1007/s11258-010-9805-y. Date of access: February 2011.

DANSEROU, P. 1968. The continuum concept of vegetation: responses. *The Botanical Review,* 34(3):253–332.

DE BEER, Y., KILIAN, W. VERSFELD, W. & VAN AARDE, R.J. 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments,* 64:412–421.

DE CÁCERES, M., FONT, X., VICENTE, P. & OLIVA, F. 2009. Numerical reproduction of traditional classifications and automatic vegetation identification. *Journal of Vegetation Science,* 20:620–628.

DECOCQ, G. 2002. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. *Journal of Vegetation Science,* 13:91–106.

DENGLER, J., JANSEN, F., GLÖCKLER, F., PEET, R.K., DE CÁCERES, M., CHYTRÝ, M., EWALD, J., OLDELAND, J., LOPEZ-GONZALEZ, G., FINCKH, M., MUCINA, L., RODWELL, J.S., SCHAMINÉE, J.H.J. & SPENCER, N. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science,* 22:582–597.

DIEKMANN, M., KÜHNE, A. & ISERMAN, M. 2007. Random vs non-random sampling: effects on patterns of species abundance, species richness and vegetation-environment relationships. *Folia Geobotanica,* 42:179–190.

DUDLEY, C.O. 1994. The flora of Liwonde National Park, Malawi. *Proc. XIIIth Plenary Meeting AETFAT, Malawi*, 2:1485–1509.

DUFRÊNE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67(3):345–366.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

DU TOIT, R. 1993. Reconnaissance vegetation survey of the Chewore – Angwa – Kanyemba area of the Zambezi Valley, Zimbabwe. *Kirkia,* 14(1):61–77.

ECKHARDT, H.C., VAN WILGEN, B.W. & BIGGS, H.C. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology,* 38:108–115.

EKBLOM, A. & GILLSON, L. 2010. Hierarchy and scale: testing the long term role of water, grazing and nitrogen in the savanna landscape of Limpopo National Park (Mozambique). *Landscape Ecology,* 25:1529–1546.

EKOSSE, G.E., NGILA, J.C. & FORCHEH, N. 2005. Multivariate analyses of heavy metals in soils and *Colophospermum mopane* leaves around the Selebi Phikwe nickel-copper mine and smelter/concentrator plant area, Botswana. *Journal of Applied Science and Environmental Management,* 9(1):177–185.

ERKKILÄ, A. & SIISKONEN, H. 1992. Forestry in Namibia. Silve Carelica 20. University of Joensuu, Faculty of Forestry.

EWALD, J. 2003. A critique for phytosociology. *Journal of Vegetation Science,* 14:291–296.

FANSHAWE, D.B. 1969. The vegetation of Zambia. *Forest Research Bulletin*, 7:1–67. Division of Forest Research, Kitwe, Zambia.

FEOLI, E., FERRO, G. & GANIS, P. 2006. Validation of phytosociological classifications based on a fuzzy set approach. *Community Ecology,* 7(1):99–108.

FERREIRA, D., MARAIS, J.P.J. & SLADE, D. 2003. Phytochemistry of the mopane, *Colophospermum mopane*. *Phytochemistry,* 64:31–51.

GANDIWA, E. & KATIVU, S. 2009. Influence of fire frequency on *Colophospermum mopane* and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. *Koedoe,* 51(1):1–13.

GAUCH, H.G. & WHITTAKER, R.H. 1981. Hierarchical classification of community data. *Journal of Ecology,* 69:537–557.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe,* 26:9–121.

GERTENBACH, W.P.D. 1987. ‗n Ekologiese studie van die suidelikste Mopanieveld in die Nasionale Krugerwildtuin. Pretoria: UP (Thesis, DSc) 321p.

GIESS, W. 1998. A preliminary vegetation map of Namibia. *Dinteria,* 4:1–112.

GOODALL, D.W. 2002. Probabilistic classification and its application to vegetation science. *Community Ecology,* 3(2):147–157.

GÖTZE, A.R. 2002. The classification of plant communities and the evaluation of restoration technologies in different land-use areas in the Vhembe-Dongola National Park, Northern Province, South Africa. Potchefstroom: NWU (Potchefstroom Univ. Of C.H.E) (Dissertation, MSc) 167p.

GÖTZE, A.R., CILLIERS, S.S., BEZUIDENHOUT, H. & KELLNER, K. 2003. Analysis of the riparian vegetation (Ia land type) of the proposed Vhembe-Dongola National Park, Limpopo Province, South Africa. *Koedoe*, 46(2):45–64.

GÖTZE, A.R., CILLIERS, S.S., BEZUIDENHOUT, H. & KELLNER, K. 2008. Analysis of the vegetation of the sandstone ridges (Ib land type) of the north-eastern parts of the Mapungubwe National Park, Limpopo Province, South Africa. *Koedoe,* 50(1):72–81.

GRABHERR, G., REITER, K. & WILLNER, W. 2003. Towards objectivity in vegetation classification: the example of the Austrian forests. *Plant Ecology,* 169:21–34.

GUISAN, A., LEHMANN, A., FERRIER, S., AUSTIN, M., OVERTON, J.M.C., ASPINALL, R. & HASTIE, T. 2006. Making better biogeographical predictions of species‘ distributions. *Journal of Applied Ecology,* 43:386–392.

GUY, P.R. 1975. Notes on the vegetation types of the Zambezi Valley, Rhodesia, between the Kariba and Mpata gorges. *Kirkia,* 10:543–557.

HAHN, I. & SCHEURING, I. 2003. The effect of measurement scales on estimating vegetation cover: a computer-assisted experiment. *Community Ecology,* 4(1):29–33.

HAVEMAN, R. & JANSSEN, J. 2008. The analysis of long-term changes in plant communities using large databases: the effect of stratified resampling. *Journal of Vegetation Science,* 19:355–362.

HEDL, R. 2007. Is sampling subjectivity a distorting factor in surveys for vegetation diversity? *Folia Geobotanica,* 42:191–198.

HEMPSON, G. P., FEBRUARY, E. C. & VERBOOM, G.A. 2007. Determinants of savanna vegetation structure: Insights from *Colophospermum mopane*. *Austral Ecology,* 32:429–435.

HENNEKENS, S.M. 1996. MEGATAB: A visual editor for phytosociological tables. User's guide version October 1996. IBN-DLO: Wageningen, Lancaster University, Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HENNING, A.C. & WHITE, R.E. 1974. A study of the distribution of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard: the interactions of nitrogen, phosphorous and soil moisture stress. *Proceedings of the Grassland Society South Africa,* 9:53–60.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

HUNTLEY, B.J. 1974. Outlines of wildlife conservation in Angola. *Journal of the southern African Wildlife Management Association,* 4(3):157–166.

JARMAN, P.J. & THOMAS, P.I. 1969. Observations on the distribution and survival of mopane (*Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard) seeds. *Kirkia,* 7:103–107.

JONGMAN, R.H.G., TER BRAAK, C.J.F. & VAN TONGEREN, O.F.R. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge.

JORDAAN, A., DU PLESSIS, H.J. & WESSELS, D.C.J. 2000. Roots of *Colophospermum mopane*. Are they infected by rhizobia? *South African Journal of Botany,* 66(2):128–130.

JØRGENSEN, S.E., PATTEN, B.C. & STRAŠKRABA, M. 1992. Ecosystems emerging: towards an ecology of complex systems in a complex future. *Ecological Modelling,* 62(1–3):1–27.

JØRGENSEN, S.E. & MÜLLER, F. *eds*. 2000. Handbook of Ecosystem Theories and Management. Lewis Publishers: Boca Raton.

KANGOMBE, F.N. & STROHBACH, B.J. 2008. Vegetation mapping and description of Ogongo Agricultural Farm and surrounds. SAAB Annual Meeting Abstracts. *South African Journal of Botany*, DOI: 10.1016/j.sajb.2008.01.146. Date of access: March 2008.

KENNEDY, A.D. & POTGIETER, A.L.F. 2003. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology,* 167:179–192.

KENT, M. 2012. Phytosociology and the Zurich-Montpellier (Braun-Blanquet) school of subjective classification. (*In* Kent, M., *ed*. Vegetation description and analysis: a practical approach, 2nd edn, John Wiley & Sons: England. p 245–275).

KHAVHAGALI, V.P. & LIGAVHA-MBELENGWA, M.H. 2009. Assessment of plant species richness within and outside *Androstachys johnsonii* and *Colophospermum mopane* woodlands of Makuya Nature Reserve, Limpopo Province. Grassroots*: Newsletter of the Grassland Society of Southern Africa,* 9(1):26–30.

KNOLLOVÁ, I., CHYTRÝ, M., TICHÝ, L. & HÁJEK, O. 2006. Local ranges of phytosociological associations: are they reflected in numerical classification? *Biologia, Bratislava*, 61(1):71—77.

KOTLIER, N.B. & WIENS, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59:253–260.

LÁJER, K. 2007. Statistical tests as inappropriate tools for data analysis performed on non-random samples of plant communities. *Folia Geobotanica,* 42:115–122.

LEGENDRE, P., & LEGENDRE, L. *eds*. 1998. Numerical Ecology. Elsevier: Amsterdam. 853 p.

LE ROUX, C.J.G., GRUNOW, J.O., MORRIS, J.W., BREDENKAMP, G.J. & SCHEEPERS, J.C. 1988. A classification of the vegetation of the Etosha National Park. *South African Journal of Botany,* 54(1):1–10.

LOEHLE, C. 2011. Complexity and the problem of ill-posed questions in ecology. *Ecological complexity*, 8:60–67.

LOW, A.B. & REBELO, A.G. 1998. Vegetation of South Africa, Lesotho and Swaziland: A companion to the Vegetation Map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs & Tourism: Pretoria.

MacGREGOR, S.D. & O'CONNOR, T.G. 2002. Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid African savanna. *Austral Ecology,* 27:385–395.

MADAMS, R.W. 1990. The biogeography of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard at its distribution limit in eastern Botswana. London: University of London (Thesis, PhD).

MAKHADO, R.A., POTGIETER, M.J. & WESSELS, D.C.J. 2009. *Colophospermum mopane* wood utilisation in the northeast of the Limpopo Province, South Africa. *Ethnobotanical Leaflets,* 13:921–945.

MANHAS, R.K., GAUTAM, M.K. & KUMARI, D. 2009. Two Way Indicator Species Analysis (TWINSPAN) of the herbaceous vegetation in an inland wetland ecosystem of the Doon Valley Himalaya, India. *Journal of Wetlands Ecology,* 3:23–31.

MAPAURE, I. 1994. The distribution of *Colophospermum mopane* (Leguminosae – Caesalpinioideae) in Africa. *Kirkia,* 15(1):1–5.

MAPAURE, I. & NDEINOMA, A. 2011. Impacts of local-level utilization pressure on the structure of mopane woodlands in Omusati region, Northern Namibia. *African Journal of Plant Science,* 5 (5):305–313.

McCUNE, B. & MEFFORD, M.J. 2006. PC-ORD v.5.2. Multivariate analysis of ecological data. MJM Software: Gleneden Beach, OR.

MLAMBO, D., NYATHI, P. & MAPAURE, I. 2005. Influence of *Colophospermum mopane* on surface soil properties and understorey vegetation in a southern African savanna. *Forest Ecology and Management,* 212:394–404.

MOSTERT, T.H.C. 2006. Vegetation ecology of the Soutpansberg and Blouberg area in the Limpopo Provice. Pretoria: UP (Thesis, PhD) 319p.

MOSTERT, T.H.C., BREDENKAMP, G.J. & MOSTERT, R.E. 2009. Plant communities of the Soutpansberg Arid Northern Bushveld. *Koedoe*, 51(1), Art. #687,11 pages. DOI: 10.4102.

MUCINA, M., SCHAMINÉE, J.H.J. & RODWELL, J.S. 2000. Common data standards for recording relevés in field survey for vegetation classification. *Journal of Vegetation Science,* 11:769–772.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

O'CONNOR, T.G. 1985. A synthesis of long term experiments concerning the grass layer of southern African savannas. *National Scientific Programmes Unit: CSIR, SANSP Report*, 114:1–126.

O'CONNOR, T.G. 1992. Woody vegetation–environment relations in a semi-arid savanna in the northern Transvaal. *South African Journal of Botany,* 58(4):268–274.

O'CONNOR, T.G. 2010. Transformation of riparian forest to woodland in Mapungubwe National Park, South Africa, between 1990 and 2007. *Austral Ecology,* 35:778–786.

OKITSU, S. 2005. Factors controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs (supplementary issue)*, 30:135–151.

OXFORD DICTIONARY, 1999. Oxford Dictionary, Tenth edition. Oxford University Press, New York.

PIGNATTI, S. 1995. A new spirit in phytosociology. *Annali di Botanica*, 53:9–21.

PODANI, J. 2006. Braun-Blanquet's legacy and data analysis in vegetation science. *Journal of Vegetation Science,* 17:113–117.

POILECOT, P. & GAIDET, N. 2010. A quantitative study of the grass and woody layers of a Mopane (*Colophospermum mopane*) savannah in the mid-Zambezi Valley, Zimbabwe. *African Journal of Ecology,* 49:150–164.

POORE, M.E.D. 1955. The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *Journal of Ecology* 43:226–244.

RATTRAY, J.M. 1962. Vegetation types of Southern Rhodesia. *Kirkia,* 2:68–93.

RINGROSE, S., MATHESON, W., WOLSKI, P. & HUNTSMAN-MAPILA, P. 2003. Vegetation cover trends along the Botswana Kalahari transect. *Journal of Arid Environments,* 54:297–317.

RODWELL, J.S., PIGNATTI, S., MUCINA, L. & SCHAMINEE, J.H.J. 1995. European Vegetation Survey: update on progress. *Journal of Vegetation Science,* 6:759–762.

ROLEČEK, J., CHYTRÝ, M., HÁJEK, M., LVONČIK, S. & TICHÝ, L. 2007. Sampling design in large-scale vegetation studies: do not sacrifice ecological thinking to statistical purism! *Folia Geobotanica,* 42:199–208.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

RUTHERFORD, M.C., MUCINA, L., LÖTTER, M.C., BREDENKAMP, G.J., SMIT, J.H.L., SCOTT-SHAW, C.R., HOARE, D.B., GOODMAN, P.S., BEZUIDENHOUT, H., SCOTT, L., ELLIS, F., POWRIE, L.W., SIEBERT, F., MOSTERT, T.H., HENNING, B.J., VENTER, C.E., CAMP, K.G.T., SIEBERT, S.J., MATTHEWS, W.S., BURROWS, J.E., DOBSON, L., VAN ROOYEN, N., SCHMIDT, E., WINTER, P.J.D., DU PREEZ, P.J., WARD, R.A., WILLIAMSON, S. & HURTER, P.J.H. 2006. Savanna Biome (*In* Mucina, L. & Rutherford, M.C. *eds*., The vegetation of South Africa, Lesotho and Swaziland, *Strelitzia*, 19:438–538. South African National Biodiversity Institute: Pretoria). p. 439–539.

RUTHERFORD, M.C., MUCINA, M.C. & POWRIE, L.W. 2012a. The South African National Vegetation Database: History, development, applications, problems and future. South African Journal of Science, 108(1/2) Art.#629, 8 pages, DOI.org/10.4102/sajs.v108i1/2.629. Date of access: February 2012.

RUTHERFORD, M.C., POWRIE, L.W. & THOMPSON, D.I. 2012b. Are communal grazing lands necessarily degraded? Unexpected answers from the Mopane (and other) Bioregion of South Africa. 10th Annual Savanna Science Network Meeting Abstract, Skukuza, March 2012.

SCHOLES, R.J. 1990. The regrowth of *Colophospermum mopane* following clearing. *Journal of the Grassland Society of southern Africa,* 7:147–151.

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

SIEBERT, F. ECKHARDT, H.C. AND SIEBERT, S.J. 2010. The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa. *Koedoe*, 52(1): Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777. Date of access: November 2010.

SMALLIE, J.J. & O'CONNOR, T.G. 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *East African Wildlife Society, African Journal of Ecology,* 38:352–359.

SMIT, G.N., SWART, J.S. & LE ROUX, A. 1994. Root biomass, spatial distribution and relations with aboveground leaf biomass of *Colophospermum mopane*. *Bulletin of the Grassland Society of southern Africa,* 5(1):32–39.

SMIT, G.N. & RETHMAN, N.F.G. 1998a. Root biomass, depth distribution and relations with leaf biomass of *Colophospermum mopane*. *South African Journal of Botany,* 64(1):38–43.

SMIT, G.N. & RETHMAN, N.F.G. 1998b. The influence of tree thinning on the reproduction dynamics of *Colophospermum mopane*. *South African Journal of Botany,* 64(1):25–29.

SMIT, G.N. & RETHMAN, N.F.G. 2000. The influence of tree thinning on the soil water in a semi-arid savanna of southern Africa. *Journal of Arid Environments,* 44:41–59.

SMIT, G.N. 2003. The importance of Salvadora australis in relation to tree thinning in preserving herbaceous plants in a semi-arid *Colophospermum mopane* savanna. *Journal of Arid Environments,* 55:483–501.

SOLOMON, M., ZAMBATIS, N., BIGGS, H.C. & MARÉ, N. 1999. Comparison of classifications commonly used as templates for management, scientific and GIS word in the Kruger National Park. *Koedoe,* 42(2):131–142.

STALMANS, M., GERTENBACH, W.P.D. & CARVALHO-SERFONTEIN, F. 2004. Plant communities and landscapes of the Parque Nacional do Limpopo, Moçambique. *Koedoe,* 47(2):61–81.

STALMANS, M. & WISHART, M. 2005. Plant communities, wetlands and landscapes of the Parque Nacional de Banhine, Moçambique. *Koedoe,* 48(2):43–58.

STALMANS, M. & PEEL, M. 2010. Plant communities and landscapes of the Parque Nacional de Zinave, Mozambique. *Koedoe,* 52(1), Art. #703, 11pp, DOI: 10.4102/ koedoe.v52i1.703.

STEVENS, N. & SWEMMER, A.M. 2010. Comparison of *Colophospermum mopane* landscape distribution patterns at range edges and non-range edges. 8th Annual Savanna Science Network Meeting Abstract, Skukuza, March 2010.

STRAUB, A. 2002. The vegetation of Breslau Game Farm, Northern Province, Souh Africa. Pretoria: UP (Dissertation, MSc) 150p.

STRAYER, D.L., POWER, M.E., FAGAN, W.F., PICKETT, S.T.A. & BELNAP, J. 2003. A classification of ecological boundaries. *BioScience*, 53(8):723–729.

STROHBACH, B.J. 2001. Vegetation survey of Namibia. *Namibia Wissensschafrliche Gesellschaft,* 49:93–123.

THOMPSON, J.G. 1960. A description of the growth habits of mopani in relation to soil and climatic conditions. *Proceedings of the First Federal Science Congress*, 1:181–186. Rhodesia Scientific Association, Salisbury.

TICHÝ, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science,* 13(3):451–453.

TICHÝ, L., CHYTRÝ, M., HÁJEK, M., TALBOT, S. & BOTTA-DUKÁT, Z. 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science,* 21:287–299.

TIMBERLAKE, J.R., NOBANDA, N. & MAPAURE, I. 1993. Vegetation survey of the communal lands–north and west Zimbabwe. *Kirkia,* 14(2):171–270.

TIMBERLAKE, J.R. 1995. *Colophospermum mopane*: annotated bibliography and review. *The Zimbabwe Bulletin of Forestry Reseach,* 11:1–49.

TIMBERLAKE, J.R. 1996. *Colophospermum mopane* - a tree for all seasons. (*In* Mushove, P.T., Shumba, E.M. & F. Matose, F. *eds*., Sustainable Management of Indigenous Forests in the Dry Tropics, Zimbabwe Forestry Commission/SAREC: Harare. Zimbabwe). p. 201–210.

TIMBERLAKE, J.R. 1999. *Colophospermum mopane*: an overview of current knowledge. (*In* Timberlake, J.R. & Kativu, S. *eds*., African Plants: Biodiversity, Taxonomy and Uses, Royal Botanic Gardens: Kew, London). p. 565–571.

TIMBERLAKE, J. & MAPAURE, I. 2007. Bubiana conservancy vegetation. Biodiversity Foundation for Africa. *Occasional Publications in Biodiversity* 17:1–45.

TÖRÖK, K. & SZITÁR, K. 2010. Long-term changes of rock grassland communities in Hungary. *Community Ecology,* 11(1):68–76.

VAN DER MAAREL, E., ESPEJEL, I. & MORENO-CASASOLA, P. 1987. Two-step vegetation analysis based on very large data sets. *Plant Ecology,* 68(3):139–143.

VAN DER MAAREL, E. 1990. The Journal of Vegetation Science: a journal for all vegetation scientists. *Journal of Vegetation Science,* 1:1–4.

VAN DER MAAREL, E. 2005. Vegetation ecology – an overview. Blackwell: Oxford, UK.

VAN GROENEWOUD, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *Journal of Vegetation Science,* 3:239–246.

VAN VOORTHUIZEN, E.G. 1976. The mopane tree. *Botswana Notes and Records,* 8:223–230.

WALKER, B.H. 1985. Structure and function of savannas: an overview. (*In* Tothill, J.C. & Mott, J.J. *eds.*, Ecology and management of the world's savannas. Proceedings of the International Savanna Symposium, 1984. Australian Academy of Science: Canberra. p. 83–91).

WALLACE, C.S. & DALE, M.B. 2005. Hierarchical clusters of vegetation types. *Community Ecology,* 6(1) DOI:1585–8553. Date of access: January 2012.

WEARE, P.R. & YALALA, A. 1971. Provisional vegetation map of Botswana. *Botswana Notes and Records,* 3:131–147.

WEBER, H.E., MORAVEC, J. & THEURILLAT, J-P. 2000. International code of Phytosociological Nomenclature. 3rd edition. *Journal of Vegetation Science*, 11:739–768.

WERGER, M.J.A. & COETZEE, B.J. 1978. The Sudano-Zambezian Region. (*In* Biogeography and ecology of southern Africa, Werger, M.J.A. *ed*, Junk: The Hague. p. 301–462).

WESTFALL, R.H., THERON, G.K. & VAN ROOYEN. N. 1997. Objective classification and analysis of vegetation data. *Plant Ecology,* 132:137–154.

WHITE, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. *Natural Resources Research,* 20:1–356.

WILD, H. & BARBOSA, L.A.G. 1967. Vegetation map of the Flora Zambesiaca region. *Flora Zambesiac*a supplement. Harare, Zimbabwe.

WINTERBACH, R. 1998. A phytosociological synthesis of *Acacia tortilis* communities in the North-western savanna of South Africa. Pretoria: UP (Dissertation, M.Sc) 157p.

ZHANG, J.-T., LI, S. & LI., M. 2010. A comparison of Self-Organizing Feature Map clustering with TWINSPAN and fuzzy C-means clustering in the analysis of woodland communities in the Guancen Mts, China. *Community Ecology,* 11(1):120–126.

CHAPTER 3

STUDY AREA

3.1 Introduction

Heterogeneity in southern African savannas is created by different physical agents at various scales (Pickett *et al*., 2003). Considering the wide geographical distribution and size of various vegetation units associated with Mopaneveld, environmental factors that drive these vegetation patterns are expected to be extensive. Given that a detailed account on the study area was presented by Du Plessis (2001), which ultimately coincides with the study area of concern in this thesis, and since the thesis at hand is focused on re-evaluating the synthesis based on more recent methodologies, the study area and subsequent environmental factors driving the distribution of Mopaneveld will be summarized in the chapter, but will be supported by GIS-based maps.

3.2 Locality

For the purpose of this study, Mopaneveld is used to describe the demarcated areas on Figure 3-1, which was adapted from Mapaure (1994). The longitudinal boundaries of the study area lie between 11°00′ and 24°30′ E, covering approximately 550 000 km^2 over the entire distribution range of *Colophospermum mopane* (Mapaure, 1994).

Mopaneveld savannas of southern Africa can be separated into two distinct regions, which are separated by deep aeolian Kalahari sand, an unsuitable substrate for the colonization by *Colophospermum mopane.* These regions are: a) the southeast Zambezian region, which extends into South Africa, Mozambique, Botswana, Zambia, Zimbabwe, Namibia (small area along the Caprivi strip) and Malawi, and b) the southwest Angolan region, which includes the semi-arid to arid Mopaneveld in Namibia and Angola.

3.2.1 Specific study areas at the different spatial scale studies

The broader study area of interest in this thesis is the entire distribution range of Mopaneveld vegetation of southern Africa (Figure 3-1). Vegetation data across the entire distribution range of *Colophospermum mopane* would ultimately present the most rigorous presentation of the vegetation of the entire study area. It should, however, be noted that not all areas within the distribution of Mopaneveld have been covered in terms of phytosociological data and its analyses due to limited data available (see Chapter 5). Although the broad-scale synthesis of Mopaneveld vegetation (presented in Chapter 5) is often referred to as the synthesis of Mopaneveld vegetation in southern Africa, it refers to the areas in which adequate phytosociological data were available. The synthesis at the broad scale (Chapter 5), however still presents analyses of a large data set (high coverage) across environmental extremes in a large study area (wide extent). A summary of the source data for the broad-scale analysis is presented in Table 1 of Appendix 5-1 and is also highlighted in Figure 1 (Appendix 5-1).

The specific study area of the intermediate-scale synthesis (Chapter 6) comprises the Lowveld areas of the Mopane Bioregion (Mucina & Rutherford, 2006). The study area therefore stretches from the eastern end of the Soutpansberg in Venda southwards along the escarpment to its southernmost distribution south of the Olifants River in the Kruger National Park (Figure 3-2), which presents an intermediate extent.

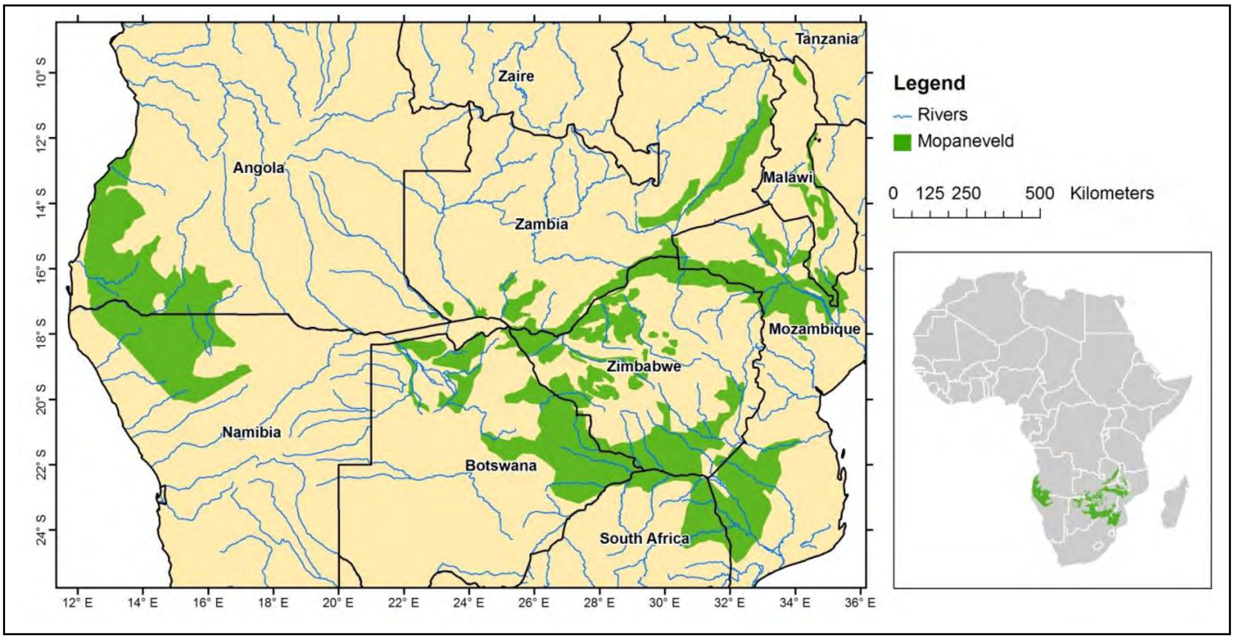


Figure 3-1. The distribution of Mopaneveld vegetation (*Colophospermum mopane*-dominated vegetation, Mapaure (1994)) across the eight different southern African countries indicating its association with large river valley bottoms in southern Africa.

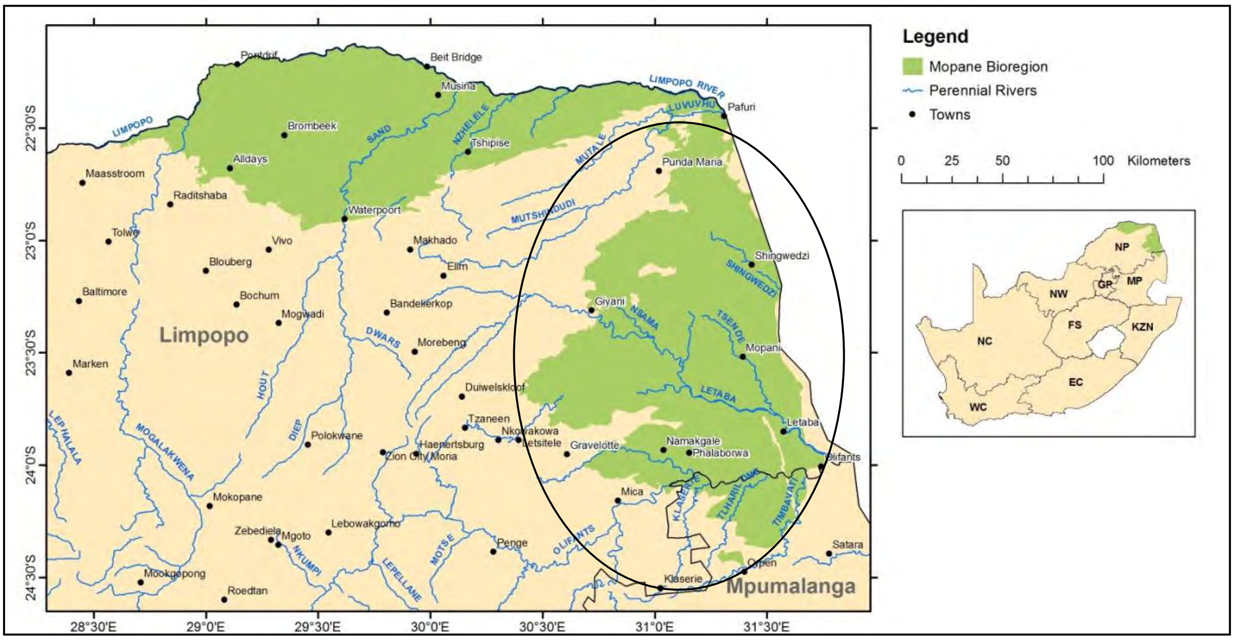


Figure 3-2. The distribution of the Mopane Bioregion (Mucina & Rutherford, 2006) in South Africa. Mopaneveld vegetation within the encircled areas represents the specific study area of the intermediate-scale synthesis of the Lowveld Mopaneveld (Chapter 7).

At the local scale vegetation classification study (Chapter 7), the specific study area of 129 ha (narrow extent) is located approximately 5 km upstream of the Mingerhout Dam along the Letaba River in the Kruger National Park (see Appendix 7-1 for detail).

3.3 Environmental factors

Various environmental factors are correlated with the distribution of savannas, including geomorphology, climate, soil, vegetation, herbivory and fire (Bourlière 1983; Cole 1986; Woodward & Williams, 1987; Shorrocks, 2007). Forming its own Bioregion in the Savanna Biome of South Africa (Mucina & Rutherford, 2006), the distribution of Mopaneveld is even so correlated to the factors mentioned above. The distribution of *Colophospermum mopane*, and therefore to a great extent the distribution of Mopaneveld (see Chapter 2) is principally influenced by moisture availability expressed through altitude, rainfall and soil texture (Mapaure, 1994). The study area will therefore be discussed according to these determinants, although others will not be neglected, for it is rather a combination of factors than a specific set of conditions that influence the distribution of the Mopaneveld (Timberlake, 1995; Okitsu, 2005).

3.3.1 Topography and Geomorphology

Mopaneveld is associated with valley bottoms of large rivers, including the Cunene, Chobe, Limpopo, Luangwa, Okavango, Shire and Zambezi (Figure 3-1) where it inhabits these broad river valleys on deep, clayey to loamy clayey soil (Werger & Coetzee, 1978; Cole, 1986; Mapaure, 1994). Areas covered by Mopaneveld are commonly associated with flat to undulating terrain on which *Colosphospermum mopane* often dominate, interrupted by scattered inselbergs (koppies or rocky outcrops) on which *Colophospermum mopane* rarely forms the dominant species in the tree layer. Apart from the large rivers dissecting the study area (Figure 3-1), other conspicuous water bodies in the Mopaneveld include the Cuvelai Delta and Etosha Pan in Namibia, the Makgadikgadi Pan and the Okavango Delta in Botswana, Lake Kariba in Zimbabwe and Zambia and Lake Malawi in Malawi.

The terrain typically associated with Mopaneveld varies from level (especially on the valley bottoms) or slightly raised terrain, to an undulating landscape characterized by the alternate dominance of Mopaneveld and Miombo in the Zambezi valley, and Mopaneveld and *Combretum* spp dominance in the Limpopo valley. Along its southern limit in Malawi, and in the Save River valley, Mopaneveld occur on stony hills (Werger & Coetzee, 1978).

The altitudinal range in which *Colophospermum mopane* dominate, i.e. 100 m to 1000 m is considerably wide, although altitude is reported a main driver for Mopaneveld distribution (Mapaure, 1994), since moisture availability is often expressed through altitude. Approximate altitudinal range for Mopaneveld in all different hosting African countries are summarised in Table 3-1.

3.3.2 Climate

3.3.2.1 Rainfall

Mopaneveld is associated with highly seasonal rainfall distribution. The warm, dry season lasts for five to eight months followed by the hot, wet season for the remainder of the year. Mopaneveld savannas are adapted to tolerate extreme environmental conditions, especially in rainfall. The drier western region receives approximately 100 mm annual precipitation versus the eastern region, which receives 1 000 mm (Figure 3-3). Disregarding these extremes, the general range of annual rainfall in which Mopaneveld predominate is approximately 250 mm – 400 mm (Table 3-1). In the savannas, high irradiance, heat and low humidity combine to create a high evaporative demand, which ensures that savannas are in net water deficit for most of the year, including much of the ‗rainy season' (Scholes & Walker, 1993).

3.3.2.2 Temperature

The entire study area has a fairly drawn-out warm summer, with a short mild to warm winter. January and February are generally the warmest months and July the coolest, but generally without frost. Namibian Mopaneveld survives most extreme mean temperatures (12 – 31°C) (Table 3-1).

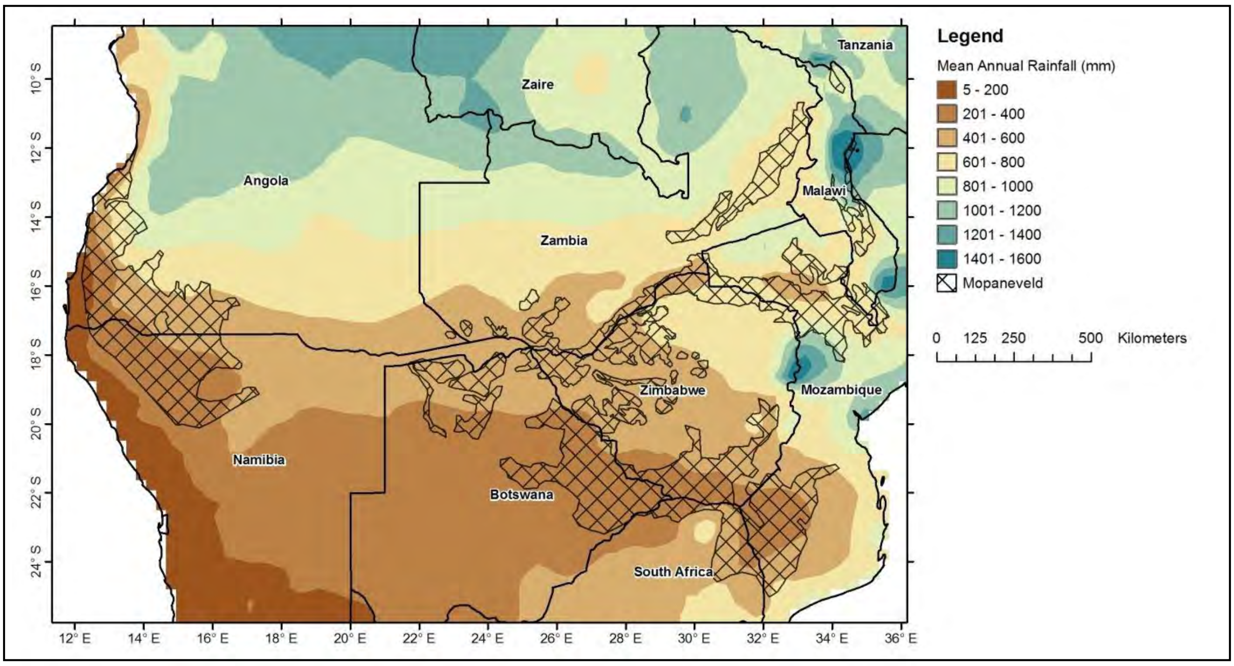


Figure 3-3. The distribution of Mopaneveld vegetation over broad rainfall patterns in southern Africa, ranging from the arid western region to the moist eastern region.

Table 3-1. A summary of mean annual rainfall, daily temperature and altitudinal range for the southern African Mopaneveld (adapted from Du Plessis, 2001).

Mopaneveld-hosting African country	Mean annual rainfall (mm)	Mean daily temperature range (°C)	Altitudinal range (m)
Angola	100 – 400	16 – 25	100 – 400
Botswana	400 – 600	13 – 30	800 – 900
Malawi	700 – 800	19 – 28	450 – 500
Mozambique	400 – 700	20 – 29	200 – 500
Namibia	100 – 550	12 – 31	150 – 1 000
South Africa	250 – 400	15 – 31	400 – 700
Zambia	700 – 1 000	14 – 30	400 – 800
Zimbabwe	500 – 700	16 – 30	400 – 950

3.3.3 Geology

Only broad geological substrates underlying southern African Mopaneveld is presented here. A simplified geology map overlain by the distribution of *Colophospermum mopane* is presented in Figure 3-4 to illustrate variation in geological parent material underlying Mopaneveld.

The majority of geological substrates underlying the study area are from the Precambrian, dissected with various intrusive, extrusive and metamorphic rocks of undetermined nature and age. Small proportions of Mopaneveld cover recent deposits, such as the Kalahari Sand from the Cenozoic (Figure 3-4). Limited areas of Mopaneveld are underlain by the Mesozoic of the Carboniferous, Jurassic to Triassic periods. Most of the Eastern Mopaneveld covers areas of alkaline black clay soil derived from Karoo (Triassic) basalt, granite and shale.

The lithology of the Mopaneveld can be divided into basic rocks, acidic rocks and recent deposits such as Kalahari Sand. Basic rocks are usually referred to as basalt. Granite and shale are acidic rocks. Granite is known for its low mineral content and shale is formed from sediments derived from weathered rocks (Krauskopf, 1967).

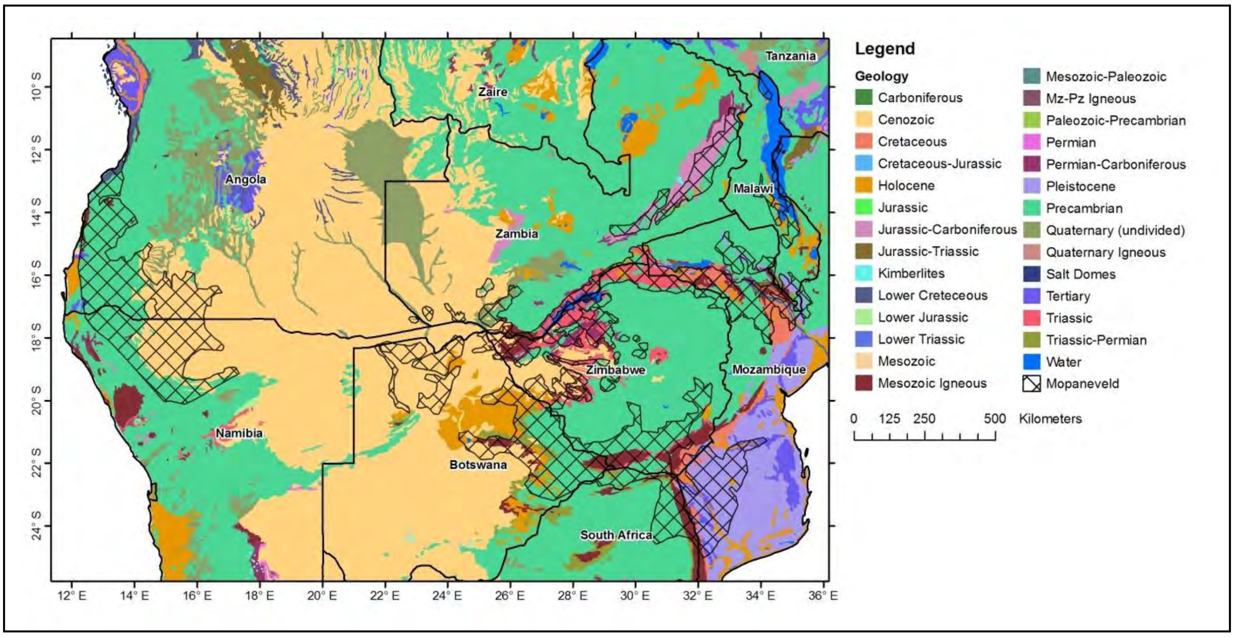


Figure 3-4. The distribution of Mopaneveld vegetation over broad geological formations in southern Africa.

3.3.4 Soil

The close relationship between soil texture and vegetation is a useful aid in studying ecosystems (Witkowski & O‘Connor, 1996) since smaller-scale variations are controlled by smaller-scale features, of which soil texture is a distinct and important factor in plant ecology (Fraser *et al*., 1987; Woodward, 1987). For a broad-scale analysis of vegetation, it is difficult to present small-scale variation in soil texture and therefore the detail on underlying soil textures presented in this thesis will depend on the scale at which the vegetation is described and discussed.

The soil of dry savannas are base-rich, especially in the Mopaneveld where large areas are underlain by basic igneous rocks such as basalt, or fine-grained sediments such as shale or mudstone. High concentration of bases in dry savannas causes alkaline soil and the accumulation of free salts in the profile. Where the parent material is basalt or related basic lavas, vertic clayey soil occur (Scholes & Walker, 1993).

Acid igneous parent materials such as granite result in a landscape with sandy, infertile uplands (typically *Combretum*-dominated vegetation) and clayey, fertile bottomlands, which are inhabited by *Colophospermum mopane*-dominated vegetation throughout large parts of the study area (Scholes & Walker, 1993).

3.4 References

BOURLIÈRE, F. 1983. Ecosystems of the world Vol. 13, Tropical savannas. Elsevier: Amsterdam, Oxford & New York.

COLE, M.M. 1986. The Savannas: biogeography and geobotany. Academic Press: London. 438 p.

DU PLESSIS, F. 2001. A Phytosociologial Synthesis of Mopaneveld. University of Pretoria. (Dissertation: M.Sc.) 193p.

FRASER, S.W., VAN ROOYEN, T.H. & VERSTER, E. 1987. Soil-plant relationships in the Central Kruger National Park. *Koedoe,* 30:19–33.

KRAUSKOPF, K.B. 1967. Introduction to geochemistry. McGraw-Hill Book Company: New York.

MAPAURE, I. 1994. The distribution of *Colophospermum mopane* (Leguminosae – Caesalpinioideae) in Africa. *Kirkia,* 15(1):1–5.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

OKITSU, S. 2005. Factors controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs*, 30:135–151.

PICKETT, S.T.A., CADENASSO, M.L. & BENNING, T. 2003. Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. (*In* Du Toit, J., Rogers K.H. & Biggs H.C. *eds.*, The Kruger Experience: ecology and management of savanna heterogeneity. Island Press: Washington. p. 22–40).

SCHOLES, R.J. & WALKER, B.H. 1993. African savannas: an overview. (*In* Scholes, R.J. & Walker, B.H. *eds.*, An African Savanna: synthesis of the Nylsvley study. Cambridge University Press: London. p.2–16).

SHORROCKS, B. 2007. The Biology of African Savannahs. The Biology of Habitat Series. Oxford University Press: 268 p.

TIMBERLAKE, J.R. 1995. *Colophospermum mopane*: annotated bibliography and review. *The Zimbabwe Bulletin of Forestry Reseach,* 11:1–49.

WERGER, M.J.A. & COETZEE, B.J. 1978. The Sudano-Zambezian Region. (*In* Biogeography and ecology of southern Africa, Werger, M.J.A. *ed*, Junk: The Hague. p. 301–462).

WITKOWSKI, E.T.F. & O'CONNOR, T.G. 1996. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Vegetatio,* 124:9–23.

WOODWARD, F.I. & WILLIAMS, B.G. 1987. Climate and plant distribution at global and local scales. *Vegetatio*, 69:189–197.

CHAPTER 4

METHODS

4.1 Introduction and background

Du Plessis (2001) was the first to conduct a synthesis on an African vegetation type, the southern African Mopaneveld, which is distributed along geographical extremes and across national borders. Due to the limitation of adequate local-scale vegetation descriptions along the distribution of this savanna type, the synthesis was based on raw floristic data, which was captured in a TURBOVEG (Hennekens & Schaminée, 2001) vegetation database, a software program designed to store, manage and export large numbers of relevés.

4.1.1 Previously used methodology

At the time when the synthesis was conducted, a typical vegetation synthesis would follow the traditional European bottom-up approach based on the culmination of local-scale vegetation descriptions (e.g. Van der Maarel *et al.*, 1987) (see also section 2.3). South African vegetation scientists followed this approach in areas with sufficient local-scale plant association descriptions, although it was later amended to present a three-step method for classifying large data sets (Bredenkamp & Bezuidenhout, 1995). None of these methods could however be followed since the Mopaneveld has not been described extensively at a local scale. A wealth of relevé data have however been accumulated by field observers but left without analyses and descriptions at the local scale. The approach followed in the *reference classification* (i.e. Siebert *et al.*, 2003) was therefore based on the application of classical classification algorithms i.e. TWINSPAN (Hill, 1979) on the entire floristic data set, and conservative measures to identify diagnostic species since it was prior to the development of improved classification technologies. This method, as well as the results obtained from this classical approach, will serve as a control against which outputs from more recently developed analytical tools in newer computer software packages and alternative algorithms will be compared.

4.1.2 Improved software tools

The computer software package JUICE (Tichý, 2002) was developed shortly after the synthesis of Mopaneveld vegetation was presented by Du Plessis (2001). JUICE enables a more comfortable treatment of large vegetation data sets in combination with various options to identify diagnostic species through non-biased statistical measures. Considering the development of such software that could treat large numbers of heterogeneous sampling plots even more objectively, a re-analysis of the complete floristic Mopaneveld data set seemed imperative.

4.1.3 Classical TWINSPAN (Hill, 1979) and an improvement on the algorithm

The classical Two-way-Indicator-Species-Analysis (TWINSPAN) algorithm (Hill, 1979) produces clusters from top to bottom that are partitioned according to all possible species in the data set. It remains a popular method in vegetation classifications, not only recently used in southern Africa (e.g. Brand *et al.*, 2010; Daemane *et al.*, 2012; Strohbach & Jancowitz, 2012), but also world-wide (e.g. Manhas *et al.*, 2009; Pajunen *et al.*, 2010; Zhang *et al.*, 2010; Cooper & McCann, 2010) despite wide criticism (Van Groenewoud, 1992; Belbin & McDonald, 1993; Dufrêne & Legendre, 1997; Ewald, 2003). A major technical limitation of TWINSPAN is that, due to its divisive character, the number of clusters increases in powers of two down the hierarchy since it cannot be adjusted manually (Rolečeck *et al.*, 2009). This ‗technical flaw‘ skews the classification hierarchy since clusters are being formed regardless their ecological strength. These limitations encouraged Rolečeck *et al.* (2009) to introduce an alternative that doesn‘t change the logic of the classical TWINSPAN algorithm, but by reducing its limitations. This improved algorithm, Modified TWINSPAN (Rolečeck *et al.*, 2009) was proposed and will be used to compare all reference classification results against for the purpose of this study.

4.1.4 Towards non-subjective selection of diagnostic species

Since Mopaneveld has a wide distribution range over ecologically distinct areas, diagnostic species identification according to subjective fidelity measures are being considered important and are therefore compared to those identified through classical classification procedures. Fidelity measures can be obtained directly in JUICE 7.0 (Tichý & Holt, 2006) and will therefore be applied at various spatial scale data sets to obtain the true probability of the occurrence of a species within a specific vegetation unit.

4.2 The methodological approach

The methodological approach discussed below will broadly apply to all analyses, although small variation to the approach will be highlighted and elaborated on in the respective chapters. An explanation on the vegetation studies that are being compared at different spatial scales is summarized in Tables 4-1 & 4-2.

Recommendations on the choice of one of these methods with respect to a phytosociological synthesis remain biased. The outcomes of the hierarchy produced by each algorithm at each different spatial scale will therefore only be presented and discussed according to their ecological significance and differences towards each other.

4.2.1 Data selection

Data were consistently selected to be analogous to the data set against which it is compared (Table 4-2), which implies that the data used in the classical TWINSPAN algorithm were the same data used in the Modified TWINSPAN algorithm. Although several vegetation classification studies were conducted after the synthesis of Mopaneveld by Du Plessis (2001) (see section 2.3.6), the data of these studies were not included in this study for the data source of the reference classification (Table 4-1) to remain analogous to the data used for the application of the modern approach.

4.2.2 Data classification approach

It is only in the broad-scale study that the classical TWINSPAN classification was repeated. The complete data set, which was used in the analysis by Du Plessis (2001) and Siebert *et al.* (2003) were re-classified in JUICE (Tichý, 2002) to test whether the use of the more recent computer software program (i.e. JUICE) would influence classification results despite the application of the same algorithm. The total data set were therefore exported directly from the master data base in TURBOVEG Version 2.28 (Hennekens & Schaminée, 2001) to JUICE version 7.0 (Tichý & Holt, 2006) after which identical classification parameters to those published by Siebert *et al.* (2003) were applied to the Mopaneveld vegetation data matrix. Since the results obtained from the classical TWINSPAN in JUICE were similar to the results obtained through the application of TWINSPAN in MEGATAB (Hennekens, 1996, see Chapter 5), it confirmed that the classical TWINSPAN algorithm does not need to be repeated in JUICE. The classical TWINSPAN classification results, which were obtained via an older software package, MEGATAB (Hennekens, 1996) and published in Du Plessis (2001), Siebert *et al.* (2003) and Siebert *et al.* (2010) could therefore be used as the references in the comparative studies, which will be referred to as the ‗*reference classifications*‘ or the ‗*reference document*‘ (Table 4-1). JUICE 7.0 (Tichý & Holt, 2006) could therefore be used as a tool to comfortably apply these respective classification algorithms.

The methods applied to compare classification results are essentially analogous for comparisons at different spatial scales. For each of the comparative studies the details and parameters used during the classification were consistent with the reference classifications (Table 4-1). Each data set, of which its content depended on the scale at which analyses were done, were independently exported from TURBOVEG (Version 2.28, Hennekens & Schaminée, 2001) to JUICE (version 7.0, Tichý, 2002) in which a unique file name was constructed for each analysis. The Modified TWINSPAN algorithm (Roleček *et al.*, 2009) was then applied to the data set at the exact parameters of the classical TWINSPAN algorithm, which was stated in the reference document. These parameters could be unique to the different studies, including pseudospecies cutlevels and number of clusters and will be stated in the respective results chapters. Since Modified TWINSPAN in JUICE allows the user to select the number of clusters that should be produced, the number of clusters selected was always consistent with the number of clusters that were produced by the classical TWINSPAN algorithm in the reference classification.

4.2.3 Diagnostic species identification approach

Since all the reference classifications used the classical, subjective approach to identify diagnostic species, these described diagnostics were compared against those identified through statistical fidelity measures. Before the application of the Modified TWINSPAN algorithm, settings in JUICE 7.0 were adjusted under ‗Options – Fidelity measures' to obtain statistically measured diagnostic species according to the Phi-coefficient distance measure. To further strengthen the uniqueness of diagnostic species to a specific cluster, Fischer's exact test was applied at p<0.001 to calculate the true probability of obtaining the observed number of occurrences of the species in the vegetation unit under the null hypothesis of independence (Tichý & Holt, 2006).

The overlap in diagnostic species is reported for each spatial scale classification.

Table 4-1. Reference classifications for each of the comparative studies at the different spatial scales.

	Reference classification	Published domain	Chapter in which comparison is presented
Broad-scale (coarse-scale) vegetation synthesis of Mopaneveld	Siebert *et al.* (2003)	*Bothalia*	5
Intermediate-scale vegetation synthesis of the South African Lowveld Mopaneveld	Du Plessis (2001)	MSc dissertation, University of Pretoria	6
Local-scale (fine-scale) vegetation classification of the Letaba herbivory and fire research exclosures	Siebert *et al.* (2010)	*Koedoe*	7

Table 4-2. Explanation and summary of the content of the different spatial scales at which vegetation classifications are being compared.

Scale of study as referred to in text	Study area	Approximate size (Scale: extent)	No of relevés (Scale: coverage)	Algorithms applied	Diagnostic spp identification approach	Chapter in which results are presented
Broad-scale (coarse-scale)	Southern African Mopaneveld	550 000 km^2	2 246	TWINSPAN (Hill, 1979) vs Modified TWINSPAN (Roleček *et al.*, 2009)	Classical, subjective approach vs Phi-coefficient statistical fidelity measure in combination with Fischer's exact test	5
Intermediate-scale	South African Lowveld Mopaneveld	13 800 km^2	877			6
Local-scale (fine-scale)	Letaba experimental exclosures	130 ha / 1.3 km^2	72			7

4.3 Presentation of results

4.3.1 Classification hierarchy

The Modified TWINSPAN algorithm (Roleček *et al.*, 2009) was essentially developed to improve the classification hierarchy produced by the classical TWINSPAN algorithm (Hill, 1979). The presentation of the different classification hierarchies therefore stands central to this thesis. The classical classification hierarchy of the reference classification will therefore be presented just as it was documented, either in a publication (e.g. Siebert *et al.*, 2003; Siebert *et al.*, 2010), or in the Master‘s dissertation (Du Plessis, 2001). Most of the traditional classification hierarchies are presented in a dendrogram in the published documentation. JUICE 7.0 provides the option to present Modified TWINSPAN classification hierarchy in a hierarchical tree as a direct output file, although these figures have no supportive information. These trees are therefore used as a basis from which the hierarchy could be explained (see Figures 5-1, 6-1, 6-2, 6-3, 7-1, 7-2, 8-2 & 8-3).

Comparisons between the different classification hierarchies are based on a few measures, which are not necessarily discussed in a fixed sequence:

a. What is the primary denominator of the first order separation of the data set, i.e. what type of vegetation is being separated at the first level of division?
b. How does separation/clustering compare down the hierachical levels?
c. Since the number of clusters is being pre-selected to be equal for both classification algorithms, to what extent do they overlap in terms of:
    a. Relevé assembly, and
    b. Species assemblages?

These measures are mainly addressed through the support of the different hierarchical presentations in dendrograms and/or hierarchical trees, although synoptic tables and summary tables are also used to compare classification results, especially when diagnostic species comparisons are also presented on the same synoptic two-way table (see Tables 5-2, 6-2 & 7-2).

4.3.2 Diagnostic species comparisons

In all the reference classifications, the classical TWINSPAN results are presented in an ordered two-way synoptic table or a phytosociological table, which were refined according to the Braun-Blanquet approach. These tables are constructed to present diagnostic species for vegetation units in respective species groups. These lists of diagnostic species, along with those identified in the descriptions of the reference documents, were considered as the ‗reference diagnostic species‘ against which the diagnostic species, identified through statistical measures were compared. Such comparisons are mainly presented in the reference synoptic table or the reference phytosociological table, or in a summary table (see Tables 5-1, 5-3, 5-4, 7-1) which facilitates comparisons between the different classification algorithms and diagnostic species identification approaches.

4.4 Presentation of the riparian vegetation classification

Results obtained through the comparative studies revealed sufficient insight into the validity of the two classification algorithms. Since the riparian zone of the Mopane Bioregion in South Africa has not been classified and described as yet, this thesis aimed at presenting such a synthesis.

The methodological approach follows the application of the Modified TWINSPAN algorithm in combination with statistical fidelity measures to identify statistically verified diagnostic species. Phi-coefficient fidelity measure along with Fischer's extact test (selected at $P<0.001$) was applied to the riparian vegetation data set to produce a classification hierarchy and subsequent descriptions of all plant communities at various hierarchical levels. For the purpose of this study, diagnostic species are distinguished from constant and dominant species.

The methods used in the riparian vegetation synthesis are more specific towards reaching specific outcomes in terms of the classification, description and floristics of the riparian zones and are therefore presented in more detail in Chapter 8.

4.5 References

BELBIN, L. & McDONALD, C. 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science,* 4:341–348.

BRAND, R.F., BROWN, L.R. & DU PREEZ, P.J. 2010. A floristic analysis of the vegetation of Platberg, eastern Free State, South Africa. *Koedoe,* 52(1):1–11.

BRAUN-BLANQUET, J. 1932. Plant Sociology. The Study of Plant Communities. Authorized English translation of 'Pflanzensoziologie' (Fuller, G.D. & Conard, H.S. *eds*. New York: McGraw-Hill).

BREDENKAMP, G.J. & BEZUIDENHOUT, H. 1995. A proposed procedure for the analysis of large phytosociological data sets in the classification of South African grasslands. *Koedoe,* 38(1):33–39.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13:79–90.

COOPER, A. & McCANN, T. 2010. Cattle exclosure and vegetation dynamics in an ancient, Irish wet oakwood. *Plant Ecology,* 212(1):79–90.

DAEMANE, M.E., CILLIERS, S.S & BEZUIDENHOUT, H. 2012. Classification and description of the vegetation in the Spitskop area in the proposed Highveld National Park, North West Province, South Africa. *Koedoe*, 54(1): Art. #1020, 7 pages. http://dx.doi.org/10.4102/koedoe. Date of access: February 2012.

DUFRÊNE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67(3):345–366.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

EWALD, J. 2003. A critique for phytosociology. *Journal of Vegetation Science,* 14:291–296.

HENNEKENS, S.M. 1996. MEGATAB: A visual editor for phytosociological tables. User's guide version October 1996. IBN-DLO: Wageningen, Lancaster University, Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

MANHAS, R.K., GAUTAM, M.K. & KUMARI, D. 2009. Two Way Indicator Species Analysis (TWINSPAN) of the herbaceous vegetation in an inland wetland ecosystem of Doon Valley, Himalaya, India. *Journal of Wetlands Ecology,* 3:23–31.

PAJUNEN, A.M., KAARLEJÄRVI, E.M., FORBES, B.C. & VIRTANEN, R. 2010. Compositional differentiation, vegetation-environment relationships and classification of willow-characterised vegetation in the western Eurasian Arctic. *Journal of Vegetation Science,* 21(1):107–119.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

SIEBERT, F. ECKHARDT, H.C. AND SIEBERT, S.J. 2010. The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa. *Koedoe*, 52(1): Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777. Date of access: November 2010.

STROHBACH, B.J. 2001. Vegetation survey of Namibia. *Namibia Wissensschafrliche Gesellschaft,* 49:93–123.

STROHBACH, B.J. & JANKOWITZ, W.J. 2012. Phytosociology of the farm Haribes in the Nama-Karoo biome of southern Namib. *Koedoe,* 54(1) Art. #1038, 13 pages. Date of access: March 2012.

TICHÝ, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science,* 13(3):451–453.

TICHÝ, L. & HOLT, J. 2006. JUICE v.7.0. Program for management, analysis and classification of ecological data. Program manual. Vegetation Science Group: Masaryk University, Brno.

VAN DER MAAREL, E., ESPEJEL, I. & MORENO-CASASOLA, P. 1987. Two-step vegetation analysis based on very large data sets. *Plant Ecology,* 68(3):139–143.

VAN GROENEWOUD, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *Journal of Vegetation Science,* 3:239–246.

ZHANG, J.-T., LI, S. & LI., M. 2010. A comparison of Self-Organizing Feature Map clustering with TWINSPAN and fuzzy C-means clustering in the analysis of woodland communities in the Guancen Mts, China. *Community Ecology,* 11(1):120–126.

CHAPTER 5

EVALUATION OF THE BROAD-SCALE VEGETATION SYNTHESIS

5.1 Introduction

The study of vegetation requires the fullest possible knowledge of the basic units, the plant communities. The study of vegetation (i.e. plant communities) is concerned with the ecology or interrelationships of plants and animals to one another, and most importantly, to their immediate environment. Classification can therefore be considered a very effective way of simplifying the complexity of vegetation (Mucina & Rutherford, 2006), since it dismantles complex ecosystems into ecological entities. Mopaneveld is even so complex in its distribution and associated vegetation and therefore needs to be simplified. A simplification of Mopaneveld vegetation at a bioregional scale was presented in a Master's dissertation (Du Plessis, 2001) through a synthesis of all compatible floristic data collected within the distribution range of this extensive vegetation type in southern Africa. Vegetation descriptions of the Mopaneveld synthesis were based on the classical approach and were published in 2003 (Siebert *et al.*, 2003; Appendix 5-1), which are also referred to in this chapter as the *reference classification*. At the highest hierarchical level, Siebert *et al*. (2003) identified and described seven vegetation types, and at a lower hierarhical level, six major plant communities were identified and described

5.2 Objectives

The main purpose of this chapter is to provide insight into different results obtained through classical versus modern approaches in vegetation classification. Due to the development of stronger computer software since Siebert *et al.* (2003), the first objective of the re-assessment of the phytosociological synthesis is to test whether traditional classification procedures applied to in JUICE (Tichý, 2002) would produce similar results to those revealed through the use of an older software package, MEGATAB (Hennekens, 1996).

The more specific objectives that will be targeted in this chapter are consistent with the main objectives of the thesis, although they are presented here in context of a broad-scale analysis only, i.e. to evaluate the credibility of (i) the classical TWINSPAN algorithm and (ii) classical measures to identify diagnostic species in a broad-scale vegetation synthesis.

From the above, it is envisaged that the research presented in this chapter would provide insight on the importance of the selection of a classification method in obtaining rigorous results for a broad-scale phytosociological synthesis based on extensive raw vegetation data across heterogeneous landscapes.

Please note that this study is not aimed at presenting an improved synthesis and revised descriptions of Mopaneveld vegetation in southern Africa. To enable this, all available data (including more recent data) from all the Mopaneveld-hosting countries need to be included, which is not the aim of this study. This chapter is primarily aimed at comparing the outcomes of different numerical-analytical tools applied to the exact similar data set from which a detailed, published discussion on the vegetation is based (i.e. Siebert *et al.*, 2003).

5.3 Methods

5.3.1 Classification approaches

Details and background on the methodological approach can be viewed in Chapter 4 (Methods, section 4.1.1) as well as in the reference documents (i.e. Du Plessis, 2001; Siebert *et al.*, 2003). Only the methods that are unique to the comparative study presented in this chapter will be reported here.

The Mopaneveld data set is made up by relevé data from various authors and different countries within which *Colophospermum mopane* dominate. A large proportion of this data has not been published, and others never analyzed (see Du Plessis, 2001). Du Plessis (2001) amalgamated all the available floristic data in Mopaneveld and applied the classical TWINSPAN algorithm (Hill, 1979) to the complete set of raw data (i.e. 2 298 relevés) to obtain the best possible clustering of Mopaneveld vegetation in southern Africa. It was anticipated that, by repeatedly applying TWINSPAN at a single level of division to identify and omit the azonal vegetation relevés, the final data set would represent vegetation that is considered faithful to the Mopaneveld vegetation type. TWINSPAN classification with pseudospecies cutlevels of 0-5-25-50 was applied to this delimited data set at six levels of division, an option directly available in MEGATAB (Hennekens, 1996). The refinement of this phytosociological table was done in a percentage frequency synoptic table. Although refinement of two-way tables remains subjective, Du Plessis (2001) proposed an alternative, less subjective approach to refine large two-way tables to identify diagnostic species groups. According to this approach, species are considered diagnostic if they are either totally faithful to a cluster with a frequency of higher than 10 %, or at least twice as frequent in a specific cluster. Based on the results and subsequent refinement, seven different vegetation types were identified and described for Mopaneveld vegetation. For the purpose of a comparison between the classification outputs, a brief summary of the vegetation as described in the reference document (i.e. Siebert *et al*., 2003) is presented in Table 5-1.

Since the computer software package, JUICE (Tichý, 2002) allows for data analyses and table arrangement of large data sets in particular, its suitability for performing data analyses for the purpose of this comparative study was tested. The equivalent, complete Mopaneveld data set used by Siebert *et al*. (2003) was therefore analyzed in JUICE version 7.0 (Tichý & Holt, 2006), following the exact parameters that were used in the reference classification. The classification results are however not presented in table format, although the results and how they compare to Siebert *et al*. (2003) will be discussed briefly in section 5.4.1 of this chapter.

The Modified TWINSPAN algorithm is developed specifically to enable the construction of a more objective classification hierarchy (Roleček *et al*., 2009). The first objective of this study (i.e. to evaluate the credibility of the classical TWINSPAN algorithm towards a broad-scale synthesis) is addressed through the application of the Modified TWINSPAN algorithm to the exact Mopaneveld data set that was used in the classical classification approach. A *post hoc* comparison of the respective classification hierarchies is done.

5.3.2 Measures of diagnostic species identification

Prior to the development of a non-biased approach to identify diagnostic species (e.g. Chytrý *et al*., 2002), most vegetation classifications followed a classical, subjective approach in which diagnostic species were identified and selected for plant community descriptions. In the reference classification, the method used for diagnostic species identification was claimed to limit subjectivity, although the selection remains rather subjective since it involves human bias and no statistical measures. This chapter is aimed at presenting the disparity of vegetation classification end-products when different measures of diagnostic species identification are being used. First, the classical TWINSPAN algorithm is performed in JUICE, version 7.0 in combination with fidelity measures to identify diagnostic species. The Phi-coefficient was applied to the classical TWINSPAN classification table to reveal a two-way table in which only species with the strongest fidelity to each cluster is presented. Fidelity diagnostics were set in JUICE 7.0 (Tichý & Holt, 2006) at the lower threshold value of 20, similar to the 20% threshold value of diagnostics in Siebert *et al*. (2003). To present these results in comparison with the published diagnostics from Siebert *et al*. (2003), the species that are considered true diagnostic species according to the statistical measures are indicated on the published syntable (Table 5-2).

In combination with the application of the Modified TWINSPAN algorithm to the Mopaneveld data set, statistical measures of fidelity were again applied to objectively identify diagnostic species for each hierarchical cluster produced by the more recent algorithm. These lists of diagnostic species are compared with the diagnostic species identified through the classical approach, and new names for vegetation types within the Mopaneveld are proposed according to the modern approach (Figure 1-1).

Table 5-1. An abbreviated description of all the vegetation units that were identified and described in the first synthesis of Mopaneveld vegetation by Siebert *et al*. (2003).

Name of vegetation type / major plant community as in Siebert *et al*. (2003)	**Origin of vegetation unit**	**Diagnostic characteristics**
1. *Digitaria milanjana – Colophospermum mopane* vegetation type	Zimbabwe, Save River valley	Mopane woodlands.
1.1 *Justicia flava – Colophospermum mopane* major plant community	Zimbabwe, Save River valley	Deep alluvium and clayey bottomlands of the Save River valley; Tall valley bushveld with occasional cathedral mopane.
1.2 *Setaria sphacelata – Colophospermum mopane* major plant community	Zimbabwe, Save River valley	Disturbed land, rocky outcrops and inselbergs on shallow, coarse sandy soil; Closed woodland with well-developed shrublayer
2. *Croton megalobotrys – Colophospermum mopane* vegetation type	Riparian zones from Zimbabwe and South Africa	Elevated riverbank woodlands; *Colophospermum mopane* abundant in tree layer.
3. *Cissus cornifolia – Colophospermum mopane* vegetation type	South African Lowveld Mopaneveld	Vegetation structure is dependent on the underlying geology, e.g. tall woodlands on shale, and multi-stemmed short shrubland on basalt and gabbro.
4. *Ptycholobium contortum – Colophospermum mopane* vegetation type	Limpopo River valley, north of the Soutpansberg	Low open to closed woodland on sandy soil overlying clay derived from the Archaean Complex.
5. *Enneapogon scoparius – Colophospermum mopane* vegetation type	Disturbed, semi-arid Mopaneveld	Seral community; Shrubland to woodland on varying soil texture; unpalatable grass species and several annual forb species characterize this vegetation type.

6. *Boscia foetida – Colophospermum mopane* vegetation type	Semi-arid to arid Namibian Mopaneveld	Shrubveld to open tree savanna on sand, gravel and calcrete of the Kalahari Group, and limestone, shale, conglomerate and quartzite of the Damara Sequence.
6.1 *Eragrostis viscosa – Colophospermum mopane* major plant community	Cuvelai delta, Owamboland, Namibia and arid Kaokoland	Shrubveld (Owamboland) or open treeveld (Kaokoland) on sandy soil with clayey or calcareous subsoil.
6.2 *Leucosphaera bainesii – Colophospermum mopane* major plant community	Etosha National Park, Namibia and surrounding areas	Shrubveld or low treeveld on calcareous ridges and plains of the Kalahari Group; herbaceous layer is poorly developed.
7. *Bauhinia petersiana – Colophospermum mopane* vegetation type	Namibia	Mopane srubveld on deep, aeolian Kalahari sands overlaying clay.
7.1 *Philenoptera nelsii – Colophospermum mopane* major plant community	Deep sandy substrates of the arid section of Etosha National Park	Shrubveld on deep, aeolian Kalahari Sand overlying clay.
7.2 *Asparagus nelsii – Colophospermum mopane* major plant community	Moister northeastern Namibian Mopaneveld bordering the Caprivi	Mopane woodlands on sand overlying alluvium of ancient floodplains.

5.4 Results

5.4.1 Comparison of computer software outputs

The classification hierarchy that was obtained from the more recent software program JUICE, version 7.0 turned out to be equivalent to the published hierarchy (i.e. Siebert *et al*., 2003), except for the *Enneapogon scoparius – Colophospermum mopane* vegetation type (vegetation type 5, Table 5-1), which was only vaguely presented in the JUICE output. The justification of this vegetation type remains fuzzy, since it could not clearly be fitted into a biogeographical region or an environmental entity. It was eventually proposed to present a disturbed, seral vegetation type (Du Plessis, 2001). The use of JUICE, version 7.0 therefore seems to eliminate fuzzy clustering and can therefore be considered a reliable tool in which classification algorithms could be applied.

5.4.2 Comparison of classification hierarchies

Two separate dendrograms were constructed to compare the hierarchy produced by each classification algorithm respectively (Figure 5-1). The classical TWINSPAN classification hierarchy is adapted from Siebert *et al*. (2003) and presented in Figure 5-1a, whereas the

Modified TWINSPAN hierarchy is presented in Figure 5-1b. Each dendrogram is supported with habitat information for the different clusters made up by a specific set of relevé assemblages. Detailed explanations on the hierarchy produced by the classical TWINSPAN algorithm have been covered in the reference document (Siebert *et al.*, 2003) and will therefore only be presented here in the context of a comparison with the Modified TWINSPAN hierarchy.

Similar to the classical TWINSPAN, the Modified TWINSPAN algorithm separated eastern and western Mopaneveld at the first hierarchical level. A number of relevés (i.e. 68) from South Africa, Botswana and Zimbabwe that were originally clustered with the western Mopaneveld after the application of the classical TWINSPAN algorithm are clustered with the eastern Mopaneveld after the Modified TWINSPAN algorithm was applied, which produced a more sensible clustering.

The classical TWINSPAN algorithm produced a hierarchy that is mostly consistent with biogeographical regions. After the western Mopaneveld was separated from the eastern Mopaneveld, the classical TWINSPAN algorithm separated the moister Zimbabwean and South African Lowveld Mopaneveld from the semi-arid South African Mopaneveld of the Limpopo River Valley (2nd level of division, Figure 5-1a). The western Mopaneveld, however, was separated according to predominant soil where the Kalahari Sand of aeolian origin was separated from the semi-arid to arid Kaokoland and Etosha regions (2nd level of division). The latter were then separated into vegetation units on shallow sandy soil overlaying clay (i.e. Cuvelai Delta, Owamboland) and vegetation typically found on shallow, coarse sandy soil or calcareous soil (Etosha and Kaokoland) (3rd level of division, Figure 5-1a). At the third level of division, the eastern Mopaneveld separated the moist southeastern Zimbabwean Mopaneveld of the Save River from the South African Mopaneveld on bottomlands, and the semi-arid Limpopo River valley was separated from the seral, degraded vegetation unit (Figure 5-1a). The fourth level of division disentangled the eastern Mopaneveld even further by separating the Save River valley into alluvium bottomlands and rocky outcrops, and the moist bottomlands of South African Mopaneveld into the riparian zone Mopaneveld and the South African Lowveld Mopaneveld (Figure 5-1a, 4th level of division).

Differences between the respective classification hierarchies are most pronounced in the clustering of the western Mopaneveld (Figure 5-1). The western Mopaneveld was separated by the Modified TWINSPAN algorithm at the second level of division according to Mopaneveld vegetation on shallow, physiologically dry, calcareous lithosols of Etosha, which is not subdivided any further, versus the deeper clayey soil overlain by sand of the Cuvelai

delta (Owamboland) and Kaokoland depressions in which *Colophospermum mopane* dominate (Figure 5-1b). No Namibian Sandveld Mopaneveld (i.e. the *Bauhinia petersiana – Colophospermum mopane* vegetation type, Table 5-1) is assembled through this algorithm.
The second level of division of the eastern Mopaneveld, produced by the Modified TWINSPAN algorithm, revealed two distinct groups. The Mopaneveld vegetation associated with mostly gneiss of the northern areas of South Africa, i.e. stretching from Musina, north of the Soutpansberg to Phalaborwa in the south, is the most distinct and no further subdivisions of this type were revealed through the Modified TWINSPAN hierarchy (Figure 5-1b). The other group is combined by various data sets stretching from Zimbabwe into the Kruger National Park. The latter is more associated with granite and basalt of which soil texture varies from heavy clay to deep, sandy substrates. This second level of division is similar to the classical TWINSPAN clustering. Although consistent with its nature to increase the number of clusters down the hierarchy, the classical TWINSPAN clustered the semi-arid Mopaneveld on gneiss into more units down the hierarchy, of which the *Enneapogon scoparius – Colophospermum mopane* major vegetation type (5) (Siebert *et al.*, 2003) is weakly justified.

According to the Modified TWINSPAN hierarchy, the western Mopaneveld is separated at the third level of division into the arid Kaokoland Mopaneveld and the semi-arid Owamboland (i.e. Cuvelai Delta) Mopaneveld. This is not similar to the classical TWINSPAN hierarchy, in which the Cuvelai Delta and Kaokoland vegetation were still clustered at the third hierarchical level. In the classical TWINSPAN hierarchy, the combined Cuvelai Delta and Kaokoland vegetation (i.e. the *Eragrostis viscosa – Colophospermum mopane* major plant community (6.1), Table 5-1) were separated from the vegetation typical of calcareous substrates, which was separated as a unique vegetation type after the second hierarchical level in the clustering formed through the Modified TWINSPAN (Figure 5-1).

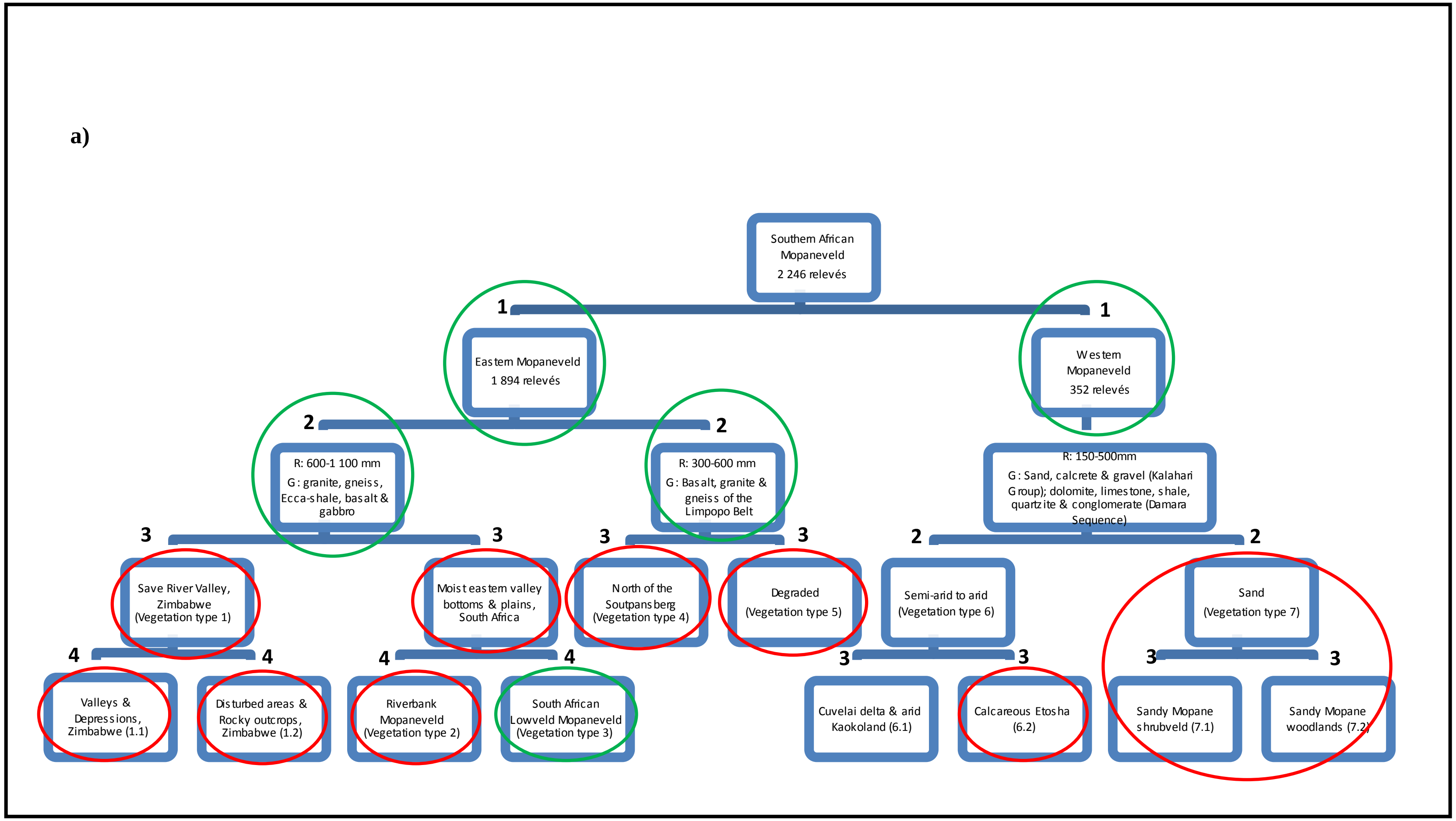


Figure 5-1(a). Classification hierarchy produced by the classical TWINSPAN algorithm according to Siebert *et al*. (2003). Red circles illustrate different clustering, whereas green circles represent clusters that are similarly formed through the two respective applications. The numbers represent the hierarchical levels, or levels of division. R = rainfall; G = geology.

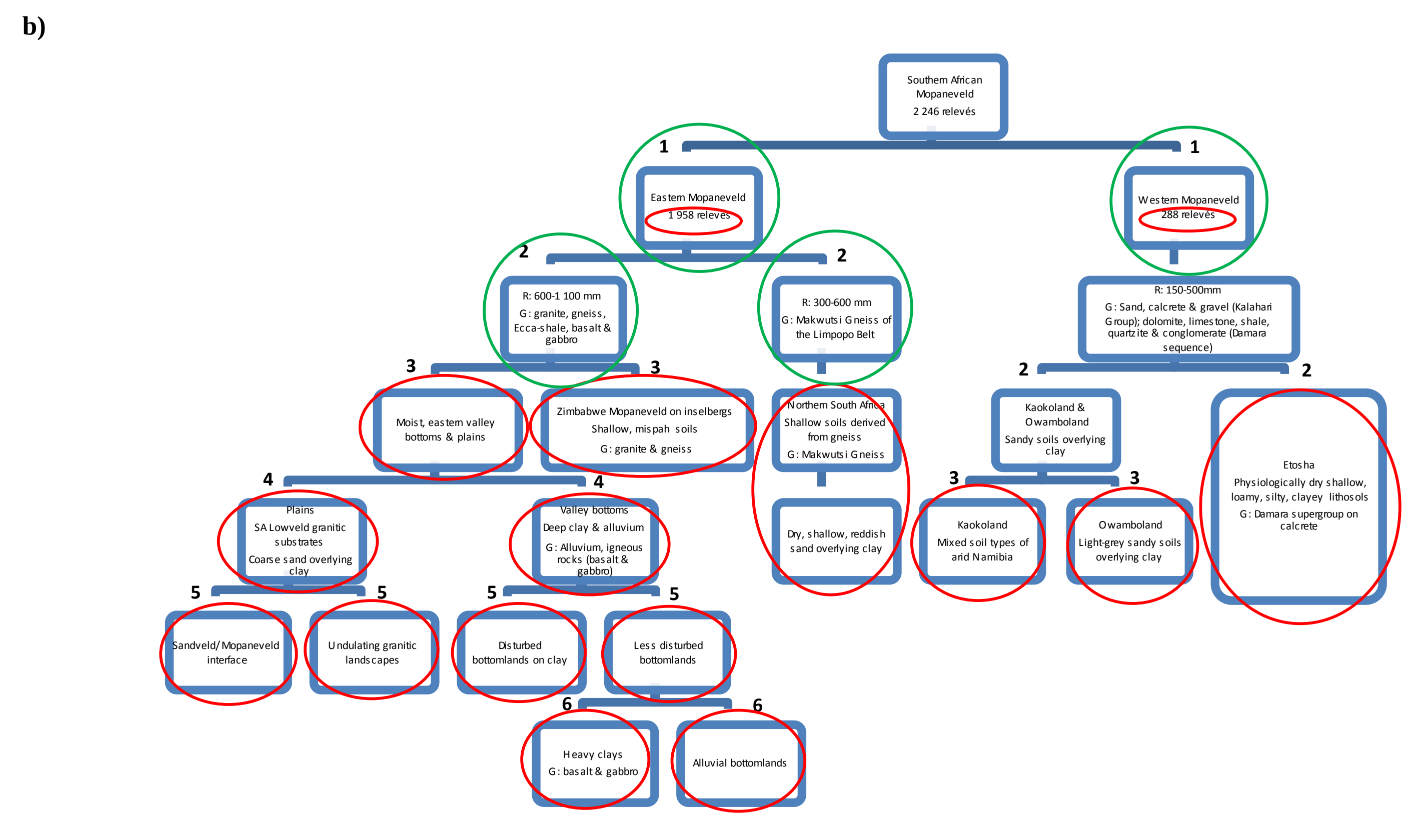


Figure 5-1(b). Classification hierarchy produced by the Modified TWINSPAN algorithm. Red circles illustrate different clustering, whereas green circles represent clusters that are similarly formed through the two respective applications. The numbers represent the hierarchical levels, or levels of division. R = rainfall; G = geology.

In the eastern Mopaneveld, clustering at the third level of division also revealed differences between the two classification algorithms. The Zimbabwean Mopaneveld on shallow soil and inselbergs is separated from Zimbabwean and South African valley bottoms and plains according to the Modified TWINSPAN algorithm, although the third level of division produced by the classical TWINSPAN suggested the division of the Save River valley vegetation from the South African Lowveld vegetation. According to the Modified TWINSPAN algorithm, clustering at this level is more clearly associated with soil texture opposed to the classical TWINSPAN clustering, which is stronger related to biogeographical regions (Figure 5-1).

Clustering below the third level of division is significantly different between the two classification hierarchies (Figure 5-1). According to the Modified TWINSPAN algorithm, the two Zimbabwean major plant communities (1.1 and 1.2) is not justified, as well as the *Croton megalobotrys* – *Colophospermum mopane* vegetation type of riparian zones (vegetation type 2, Table 5-1). Its closest relative is the cluster which was formed after the sixth level of division in the Modified TWINSPAN hierarchy, i.e. the so-called ‗Alluvial bottomlands‘ (Figure 5-1). The South African Lowveld Mopaneveld (i.e. the *Cissus cornifolia* – *Colophospermum mopane* vegetation type, Table 5-1) is weakly represented in a single cluster in the Modified TWINSPAN hierarchy. In this hierarchical presentation, this vegetation type is combined with the valley bottoms and plains of the Save River Mopaneveld. It is only the vegetation on granitic substrates from the South African Lowveld Mopaneveld that is distinctly separated through the Modified TWINSPAN algorithm.

Furthermore, the Modified TWINSPAN algorithm proposed a hierarchy in which the Zimbabwean Mopaneveld on shallow, rocky soil and inselbergs is not further separated, although the eastern valley bottoms and plains represent five vegetation units down the hierarchy (Figure 5-1).

5.4.3 Comparison of diagnostic species

5.4.3.1 Statistical measures of fidelity applied to the classical TWINSPAN algorithm

The first step was to compare diagnostic species identified through the classical approach against statistical measures of fidelity. The abbreviated synoptic table (Table 5-2) was used to demonstrate the similarity and differences between percentage frequency diagnostics, and fidelity diagnostics when the algorithm remained the classical TWINSPAN (Hill, 1979).

TABLE 5-2–Abbreviated synoptic table of Mopaneveld vegetation types in the study area

(Diagnostic species of both %Frequency and Fidelity are shaded in light grey. Dark grey spp indicate fidelity diagnostics from groups other than was published

Major vegetation type	**1.1**	**1.2**	**2**	**3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Number of relevés	***71***	***131***	***92***	***1375***	***157***	***68***	***144***	***147***	***51***	***10***
Species group A										
Colophospermum mopane	69	20	55	58	91	75	67	61	45	80
Dichrostachys cinerea	25	29	22	52	53	57	19	41	71	10
Tragus berteronianus	68	5	2	50	79	43	21	15	2	20
Grewia bicolor	40	11		59	84		23	40	39	30
Commiphora africana	9	4		22	9	13	7	6	29	10
Grewia flavescens	7	37	1	14		30	12	4	10	40
Evolvulus alsinoides	8	5		34	70		12	6	8	10
Species group B										
Cyathula uncinulata	70	48								
Indigofera varia	45	20	2			1	6	2	2	
Cucumis zeyheri	44	31								
Digitaria milanjiana	44	75					1			
Diospyros quiloensis	35	33								
Dactylocteni giganteum	34	11	1	3						
Abutilon grandiflorum	27	11			1					
Species group C										
Justicia flava	61	4	2	10	1		1			
Sporobolus nitens	52	8		10					2	
Oropetium capense	52	1		11	33			13		
Cissus rotundifolia	40	6		1						
Aristida junciformis	34	9					2	1		
Hemizygia bracteosa	27	8		4						
Thilachium africanum	24	4		1						
Zanthoxylum capense	21	1		1						
Boscia mossambicensis	20	8	1							
Enteropogon monostachys	20	8								
Stylochiton natalensis	18	6		3						
Plectranthus neochilus	18	1								
Plectranthus caninus	14	3								
Dactyloctenium australe	11	2								
Species group D										
Setaria sphacelata	3	24	2	1	1					
Vigna frutescens	1	18								
Cucumis metuliferus	7	17							2	
Phyllanthus reticulatus	3	14	1	1						
Species group E										
Sporobolus fimbriatus			64	7	1	22	1			
Spirostachys africana			40	5		6	1	8		
Croton megalobotrys		1	34							
Ficus sycomorus			21							
Flaveria bidentis			20							
Panicum deustum			20	2		6				
Phragmites australis			19							
Hyphaene coriacea			8		3					
Phoenix reclinata			8							
Species group F										
Cissus cornifolia				54						
Tephrosia polystachya				48			1			
Corchorus asplenifolius				34				2		
Aristida congesta s. congeta			2	32	2		8			
Melhania forbesii	14	8	3	28			4	6	16	
Waltheria indica				28			2			
Solanum panduriforme		5	7	28			10			
Dalbergia melanoxylon		9	1	27						
Clerodendrum ternatum				27			1	7	16	
Acacia exuvialis				25						
Limeum fenestratum				24			2		4	
Ruellia patula				24						
Themeda triandra			4	23						
Indigofera vicioides				22						
Bothriochloa radicans			1	22				12		
Acalypha indica			4	21	1			3		
Flueggea virosa		2	2	20	7		2	9		
Asparagus setaceus				20	1		1			
Lantana rugosa	3	1		20			3			
Chamaecrista mimosoides				19						
Ceratotheca triloba				16			1			
Indigofera rhytidocarpa				16						
Bothriochloa insculpta			2	16	2	1				
Tragia dioica				16						
Endostemon tereticauli				16						

TABLE 5-2–(cont.)

Major vegetation type	**1.1**	**1.2**	**2**	**3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Number of relevés	***71***	***131***	***92***	***1375***	***157***	***68***	***144***	***147***	***51***	***10***
Ormocarpum trichocarpum			1	16						
Cyperus rupestris				15						
Kohautia virgata				15						
Maytenus heterophylla		2		15		1		1		
Vernonia fastigiata				15						
Sesamum alatum				15						
Blepharis integrifolia				14				1		
Talinum caffrum				14			2			
Ipomoea crassipes				14						
Vigna unguiculata				13						
Chamaesyce neopolycnemoides				13			2			
Crabbea velutina				13						
Indigofera bainesii				13					2	
Grewia hexamita				12	1	1	3			
Sida dregei			1	12			1			
Andropogon gayanus				12						
Species group G										
Combretum hereroense		4	45	21	1	5	5	8		
Euclea divinorum		1	23	18			2	6		
Cymbopogon plurinodis			20	18	1	32		1		
Cassia abbreviata		1	15	11	2	3				
Species group H										
Eragrostis rigidior	38	32	5	36		3	1		2	
Species group I										
Ptycholobium contortum					78					
Tephrosia purpurea					73		1	2	6	
Commicarpus fallacissimus					68			1		
Acalypha villicaulis					63		8			
Achyranthes aspera			5	7	63	1	8	5	6	
Amaranthus schinzianus					61					
Cleome angustifolia				3	51		1			
Calostephane divaricata			1	4	47	1		4	2	
Indigofera heterotricha				6	44					
Kirkia acuminata		10		2	40	1	1	4		
Neuracanthus africanus			1	5	34					
Monechma debile				5	33				4	
Asparagus suaveolens					33					
Kohautia cynanchica					33					
Indigofera nebrowniana					33					
Indigofera trita					32			2	2	
Limeum sulcatum				2	28		1	4		
Ocimum americanum				7	28		7			
Jatropha spicata					27					
Grewia villosa	3	1		9	26		3	16		
Solanum coccineum			1	9	25		1			
Geigeria acaulis					25		3	8		
Justicia protracta				4	25					
Commiphora tenuipetiolata					23					
Sesamum triphyllum		1			22		2	1		
Commiphora edulis		9			21					
Leucas sexdentata					21					
Sterculia rogersii		1		2	21					
Pavonia columella			1	1	18					
Gardenia resiniflua		10		1	18		1			
Eragrostis biflora					16			1		
Digitaria velutina					15	1	1			
Adansonia digitata	1				15					
Acacia erubescens	1	7		2	15		1			
Blepharis diversispina					13				6	
Megalochlamys kenyensis					13					
Priva africana					12					
Species group J										
Bulbostylis hispidula				14	39		10		4	10
Hibiscus micranthus				47	69			12	12	
Aristida congesta s. barbicollis			1	43	50	1	1			
Heliotropium steudneri	7	3	1	29	28		1			
Dicoma tomentosa				25	69		8	7	2	
Hermannia boraginiflora				23	59		1			
Seddera capensis				22	65					
Leucas glabrata			2	19	33					
Abutilon austro-africanum			4	19	12					
Phyllanthus maderaspatensis				19	26			10	4	
Commiphora mollis		8	2	18	58	2	4	3		

TABLE 5-2–(cont.)

Major vegetation type	**1.1**	**1.2**	**2**	**3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Number of relevés	***71***	***131***	***92***	***1375***	***157***	***68***	***144***	***147***	***51***	***10***
Pavonia burchellii				16	30		6	4	2	
Pupalia lappacea			3	15	14		1	7	2	
Chamaecrista absus				15	30			2	4	
Mariscus rehmannianus				14	21					
Ipomoea magnusiana				13	54				2	
Hermbstaedtia odorata			1	12	21		9			
Corbichonia decumbens				10	22					
Combretum mossambicense		5	3	13	11		7	1		
Species group K										
Urochloa mosambicensis	66	67	15	54	2				2	
Maerua parvifolia	37	17	2	26	25					
Commelina benghalensis	48	39	3	26	43		1	3	4	
Kyllinga alba	37	3		9	27		3	1	6	
Grewia monticola	30	45		11	32		2			
Lannea schweinfurthii	3	13	3	22	30	6				
Lonchocarpus capassa	3	8	70	17	4	3				
Setaria sagittifolia	3	18	4	1	12					
Species group L										
Panicum natalense			8			29				
Sansevieria hyacinthoides			17	5	2	29				
Dicoma anomala						13	5			
Thesium utile						13	3		2	
Species group M										
Acacia nigrescens		17	45	41	30	53	1			
Eragrostis superba	1	6	15	26		25	1	4	2	
Sclerocarya birrea		3	23	32	39	28	3	2		10
Albizia harveyi		3	18	23	2	5				
Acacia gerrardii	1	2	22	8	1	44			2	
Species group N										
Triraphis purpurea						1	17	26		
Acacia nilotica			9	4			22	14	2	
Anthephora schinzii							13	21	6	
Boscia foetida			2		1		10	13	2	
Species group O										
Abutilon angulatum			3		1		15	6	4	
Eragrostis viscosa							15			
Willkommia sarmentosa							12	1		
Species group P										
Leucosphaera bainesii								62		
Enneapogon desvauxii								39	4	
Eragrostis nindensis							7	36	2	
Eragrostis echinochloidea							3	34		
Monelytrum luederitziana								25		
Hibiscus caesius								23	2	
Chascanum pinnatifidum				1			1	22	8	
Abutilon fruticosum				2	1		1	20		
Seddera suffruticosa				4			1	18	2	
Indigofera charlieriana					1		1	18	4	
Chamaesyce inaequilatera							3	17	2	
Aristida rhiniochloa				6		1	6	16		
Eragrostis porosa							5	16		
Stipagrostis hirtigluma s. patula							1	15		
Helichrysum tomentosulum								15	2	
Pegolettia senegalensis			1	2			1	15	4	
Stipagrostis hirtigluma s. pearsonii								15		
Petalidium engleranum								14	8	
Monechma genistifolium								14	4	
Gossypium triphyllum								13		
Ruelliopsis setosa								13		
Eragrostis annulata							2	13		
Hirpicium gazanioides							1	12	2	
Acacia nebrownii								12		
Species group Q										
Acacia senegal				1	11		8	11	2	
Species group R										
Combretum apiculatum	4	44	27	64	85	84	9	33	6	
Cenchrus ciliaris		1	28	11	11	24	6	50		
Enneapogon scoparius			49	10	3	52	6	10		
Combretum imberbe	3	5	56	14	5	6	9	7		
Species group S										
Terminalia sericea			1	12		5	5	1	47	100
Tephrosia dregeana							2	3	25	40
Rhus tenuinervis							3	1	20	50

TABLE 5-2–(cont.)

Major vegetation type	**1.1**	**1.2**	**2**	**3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Number of relevés	***71***	***131***	***92***	***1375***	***157***	***68***	***144***	***147***	***51***	***10***
Bauhinia petersiana							0		19	20
Combretum collinum				6			1		10	60
Species group T										
Acacia fleckii							3	7	49	
Lonchocarpus nelsii								4	49	
Merremia tridentata				7				1	49	
Elephantorrhiza suffruticosa								6	45	
Acanthosicyos naudinianus							3		43	
Requienia sphaerosperma							1		41	
Acacia ataxacantha							3	1	31	
Commiphora angolensis							1	7	31	
Albizia anthelmintica	8			1			7	7	31	
Maerua juncea			3	1			1	8	29	
Indigofera colutea								2	23	
Merremia palmata				3			2	4	22	
Harpagophytum procumbens									18	
Ipomoea verbascoidea								1	18	
Kohautia caespitosa				1			1	1	17	
Clerodendrum dekindtii								1	16	
Petalidium coccineum								1	14	
Triraphis schinzii								4	14	
Vernonia poskeana				5			3	6	14	
Oxygonum dregeanum									12	
Eragrostis dinteri							1	4	12	
Melinis nerviglumis	3	5					1	5	12	
Species group U										
Catophractes alexandri						1	5	45	16	
Anthephora pubescens							3	34	57	
Acacia reficiens							3	26	44	
Montinia caryophyllacea							1	25	25	
Otoptera burchellii							1	25	57	
Helinus integrifolius								23	12	
Heliotropium ovalifolium							3	17	18	
Cephalocroton mollis				1				16	10	
Hermannia modesta				2			3	15	22	
Blepharis obmitrata								15	10	
Grewia retinervis							3	15	49	
Acacia mellifera							1	14	35	
Ehretia rigida			1	9			1	13	26	
Barleria lancifolia				3	18		1	13	20	
Species group V										
Schmidtia pappophoroides				54	11	5	15	15	75	
Brachiaria deflexa			4	30	93	18	3	1	2	
Stipagrostis uniplumis			1	2	58	35	24	48	78	
Boscia albitrunca	1			5	67	3	22	30	61	
Grewia flava	3				77	6	5	19	49	
Monechma divaricatum				2	12	1	19	27	16	
Commiphora pyracanthoides				5	6	5	6	33	26	
Species group W										
Enneapogon cenchroides		6	30	52	97	71	40	61	31	
Terminalia prunioides	1		25	18	81	18	43	41	24	
Eragrostis lehmanniana			36	6	55	25	26	7	76	
Melinis repens			15	29	49	43	9	47	30	
Digitaria eriantha			12	62	10	21	1		6	
Ozoroa paniculosa			7	2	1	18	2	1	22	
Species group X										
Panicum maximum	26	72	36	68	19	21	5		14	
Acacia tortilis	20	22	10	10	20	6	10	3	4	
Species group Y										
Asparagus nelsii							6			60
Dicoma schinzii							3		4	60
Ozoroa schinzii							1			50
Requienia pseudosphaerosperma							1			40
Talinum arnotii							3		2	40
Aristida stipoides							15		6	40
Stipagrostis uniplumis v. uniplumis							6			30
Ochna pulchra							0		4	30
Hyphaene petersiana							5		2	20
Peltophorum africanum			4	12			2		4	20
Harpagophytum zeyheri				1			3			20
Tragus racemosus							6			20
Dichapetalum cymosum										20
Cyperus margaritaceus							1			20

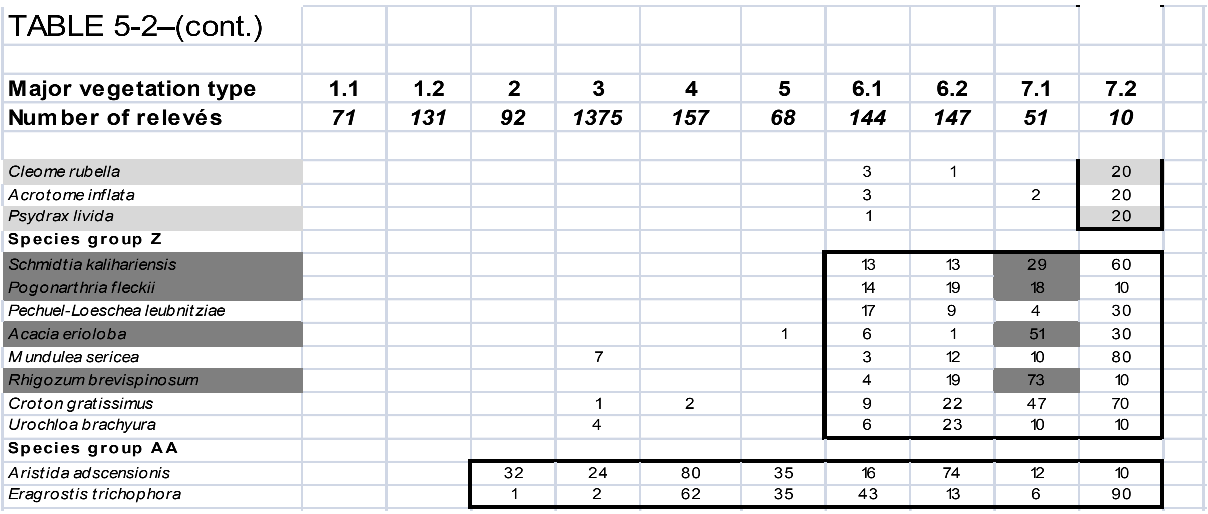


TABLE 5-2–(cont.)

Major vegetation type	1.1	1.2	2	3	4	5	6.1	6.2	7.1	7.2
Number of relevés	*71*	*131*	*92*	*1375*	*157*	*68*	*144*	*147*	*51*	*10*
Cleome rubella							3	1		20
Acrotome inflata							3		2	20
Psydrax livida							1			20
Species group Z										
Schmidtia kalihariensis							13	13	29	60
Pogonarthria fleckii							14	19	18	10
Pechuel-Loeschea leubnitziae							17	9	4	30
Acacia erioloba						1	6	1	51	30
Mundulea sericea				7			3	12	10	80
Rhigozum brevispinosum							4	19	73	10
Croton gratissimus				1	2		9	22	47	70
Urochloa brachyura				4			6	23	10	10
Species group AA										
Aristida adscensionis			32	24	80	35	16	74	12	10
Eragrostis trichophora			1	2	62	35	43	13	6	90

Overall, most (i.e. 84%, Table 5-3) of the percentage frequency diagnostic species retain its diagnostic disposition when fidelity measures are applied. There is, however, only a 31% resemblance with the published diagnostics when all fidelity diagnostics are considered as true diagnostics (Table 5-3). A total of 339 species were added to the list of diagnostics after fidelity measures were applied. These species, although low in percentage frequency, are faithful to specific clusters and can therefore be considered as ecologically specialized species, which have been inadvertently denied by previous attempts to describe the vegetation units of the Mopaneveld.

Table 5-3. Quantitative comparison between fidelity diagnostics produced in JUICE 7.0 (Tichý & Holt, 2006) and percentage frequency diagnostics for each of the vegetation types described by Siebert *et al*. (2003) respectively, and overall. Numbers in brackets correspond to the vegetation type number in Siebert *et al*, (2003) and Table 5-1. Please note that vegetation type 5 is not included due to its indistinguishable clustering in JUICE.

	No.of diagnostic species			% Matching diagnostics	
	Frequency	**Fidelity**	**Matching diagnostics**	**Frequency match**	**Fidelity match**
Zimbabwean Mopaneveld (1)	14	17	12	86	71
Riparian Mopaneveld (2)	9	30	8	89	27
South African Lowveld Mopaneveld (3)	41	190	38	93	20
Mopaneveld north of the Soutpansberg (4)	37	53	30	81	57
Namibian Mopaneveld (6)	28	96	18	64	19
Kalahari Sand Mopaneveld (7)	44	79	39	89	49
Overall	173	465	145	84	31

At a bioregional scale, there is little resemblance in traditionally identified diagnostics and fidelity diagnostics, although most of the diagnostics identified through classical procedures retain their ‗diagnostic status' after fidelity measures were applied. The differences between diagnostics identified through classical approaches and those identified through statistical fidelity measures are mainly articulated in the higher number of diagnostic species identified through statistical fidelity measures (Table 5-3).

5.4.3.2 Statistical measures of fidelity applied to the Modified TWINSPAN algorithm

A complete synoptic table produced through the application of the Modified TWINSPAN algorithm and fidelity measures for diagnostic species identification, is presented in Appendix 5-2. Since the classification hierarchy produced by the Modified TWINSPAN algorithm is dissimilar to the classical TWINSPAN hierarchy, diagnostic species are also expected to be widely divergent. These differences ultimately suggest alternative names for vegetation types and major plant communities at the bioregional scale of Mopaneveld vegetation. The revised names are constituted from diagnostic species that were identified through Phi-coefficient fidelity measures in the Modified TWINSPAN classification (Appendix 5-2) and are presented as:

1. *Leucosphaera bainesii – Eragrostis echinochloidea* Mopane savanna on calcareous soil of Etosha
2. *Croton gratissimus – Pogonarthria fleckii* Mopane savanna of arid regions
2.1 *Acacia nilotica – Eragrostis trichophora* dry Mopane savanna on clay overlain by sand
2.2 *Rhigozum brevispinosum – Antephora pubescens* dry Mopane savanna on mixed, gravelly soil
3 *Commiphora mollis – Brachiaria deflexa* semi-arid Mopane savanna on shallow, stony soil
4 *Cucumis zeyheri – Setaria sphacelata* Mopane savanna on Zimbabwean hills and disturbed areas
5 *Acacia nigrescens – Eragrostis rigidior* Mopane savanna on valley bottoms
5.1 *Philenoptera violacea – Combretum imberbe* Mopane savanna on deep alluvium and clay
5.1.1 *Tephrosia multijuga – Setaria incrassata* Mopane savanna on heavy clays
5.1.2 *Croton megalobotrys – Sporobolus fimbriatus* riparian zone Mopaneveld
5.2 *Acacia tortilis – Sporobolus nitens* disturbed Mopane savanna on Zimbabwean bottomlands

6 *Crotalaria sphaerocarpa – Digitaria eriantha* Mopane savanna of the South African Lowveld

6.1 *Pseudolachnostylis maprouneifolia – Perotis patens* Mopane savanna – Punda Maria (Makuleke) Sandveld interface

6.2 *Acacia exuvialis – Tephrosia polystachya* Mopane savanna on undulating granitic landscapes

Since the data from which this synthesis is conducted only include limited habitat data, the relationship between habitat and vegetation clustering could not be tested through indirect gradient analyses. The importance of environmental factors as drivers of vegetation clustering is, however, recognized. Therefore, diagnostic species with highest fidelity values within each cluster (i.e. representing either a vegetation type or major plant community) were related to environmental factors that are associated with the distribution of these species according to field guides (e.g. Gibbs-Russel *et al*., 1991; Retief & Herman, 1997; Van Wyk & Van Wyk, 1997; Mannheimer *et al*., 2008). These habitat features associated with the diagnostic species for each cluster is summarized in Table 5-4. All the diagnostic species with highest fidelity (i.e. >40), shared similar habitat features, more typically geology and soil texture, which is consistent with the outcomes typified by the Modified TWINSPAN hierarchy (Figure 5-1).

Despite the significant differences between the two classification hierarchies, there are some similarities between the diagnostic species identified through the different measures, which are summarized in Table 5-4. The largest proportion of diagnostic species shared between the modern approach and the classical approach is between the *Leucosphaera bainesii – Eragrostis echinochloidea* Mopane savanna on calcareous soil of Etosha, which shares twenty statistically-identified diagnostic species with the *Leucosphaera bainesii – Colophospermum mopane* major plant community of Siebert *et al*. (2003). Most of the other vegetation types and major plant communities also share a number of diagnostics of which the strongest ones are highlighted in Table 5-4.

Table 5-4. A complete summary of the Modified TWINSPAN classification output highlighting the vegetation types and major plant community clusters that show some affinity to the classical TWINSPAN classification descriptions. Habitat preferences of diagnostic species are summarized to provide insight into the ecologically distinctiveness of each cluster produced by the Modified TWINSPAN algorithm.

Vegetation types and major plant community clusters following the Modified TWINSPAN classification	**Five strongest diagnostic species** (Phi-coeff fidelity; Fischer's exact test p>0.001; Fidelity>40%) **Spp in **bold** is identified as diagnostic in both measures	**No of all diagnostics**	**Common habitat features of the diagnostic species**	**Closest floristic relative in Siebert *et al*. (2003) (see Table 5-1)**	**No of diagnostics shared by different classification algorithms**
1. *Leucosphaera bainesii – Eragrostis echinochloidea* Mopane savanna on calcareous soil of Etosha	***Eragrostis echinochloidea*** ***Leucosphaera bainesii*** ***Enneapogon desvauxii*** ***Eragrostis annulata*** ***Monelytrum leuderitzianum***	34	Shallow, calcareous soil; shallow, sandy limestone	6.2 *Leucosphaera bainesii – Colophospermum mopane* major plant community	20
2.1 *Acacia nilotica – Eragrostis trichophora* dry Mopane savanna on clay overlain by sand	*Eragrostis trichophora* *Eragrostis viscosa* ***Aristida stipoides*** *Willkommia sarmentosa* ***Hyphaene petersiana***	25	Sandy or sandy loam substrates	7. 2 *Asparagus nelsii – Colophospermum mopane* major plant community	10
2.2 *Rhigozum brevispinosum – Antephora pubescens* dry Mopane savanna on mixed, gravelly soil	*Antephora pubescens* *Rhigozum brevispinosum* *Otoptera burchellii* *Grewia retinervis* ***Acacia fleckii***	29	Shallow, sandy and/or stony soil in arid lands	7.1 *Philenoptera nelsii – Colophospermum mopane* major plant community	9
3. *Commiphora mollis – Brachiaria deflexa* semi-arid Mopane savanna on shallow, stony soil	*Aristida congesta* *Brachiaria deflexa* ***Ptycholobium contortum*** *Commiphora mollis* ***Tephrosia purpurea***	32	Shallow, sandy and/or stony soil. Often associated with disturbance	4. *Ptycholobium contortum – Colophospermum mopane* vegetation type	17
4. *Cucumis zeyheri – Setaria sphacelata* Mopane savanna on Zimbabwean hills and disturbed areas	*Cucumis zeyheri* ***Vigna frutescens*** ***Setaria spacelata*** *Setaria sagittifolia* *Millettia sutherlandii*	11	Sandy soil in shade. Riparian habitats	1.2 *Setaria sphacelata – Colophospermum mopane* major plant community	3
5.1.1 *Tephrosia multijuga – Setaria incrassata* Mopane savanna on heavy clays	*Setaria incrassata* *Tephrosia multijuga* *Panicum coloratum* *Neorautanenia amboensis* *Sorghum versicolor*	15	Heavy, deep clayey soil	NONE	0

5.1.2 *Croton megalobotrys – Sporobolus fimbriatus* riparian zone Mopaneveld	***Croton megalobotrys*** ***Sporobolus fimbriatus*** ***Ficus sycomorus*** ***Flaveria bidentis*** ***Spirostachys africanus***	15	Alluvial substrates along riparian zones	2. *Croton megalobotrys – Colophospermum mopane* vegetation type	7
5.2 *Acacia tortilis – Sporobolus nitens* disturbed Mopane savanna on Zimbabwean bottomlands	***Sporobolus nitens*** *Acacia tortilis* ***Boscia mossambicensis*** *Albizia anthelmintica* *Kalanchoe lanceolata*	5 (relatively weak, <40% fidelity)	Bare patches, overgrazed veld; disturbed patches	1.1 *Justicia flava – Colophospermum mopane* major plant community	2
6.1 *Pseudolachnostylis maprouneifolia – Perotis patens* Mopane savanna – Punda Maria Sandveld interface	*Pseudolachnostylis maprouneifolia* *Strychnos madagascariensis* *Combretum zeyheri* *Pteleopsis myrtifolia* *Guibourtia conjugata*	71	Deep, sandy substrates	NONE	0
6.2 *Acacia exuvialis – Tephrosia polystachya* Mopane savanna on undulating granitic landscapes	***Tephrosia polystachya*** ***Acacia exuvialis*** *Hibiscus micranthus* ***Cissus cornifolia*** ***Ruellia patula***	102	Granitic Lowveld; course sandy substrates; overgrazed veld	Partially included in: 3. *Cissus cornifolia – Colophopermum mopane* vegetation type	36

5.5 Discussion

A combination of classical and modern approaches has been considered in this chapter to perform a comparison of results obtained through different numerical-analytical approaches for a broad-scale synthesis of heterogeneous vegetation.

When statistical measures for diagnostic species identification is considered without changing the classification algorithm, therefore keeping to the classical TWINSPAN algorithm (Hill, 1979), there is a considerable overlap in diagnostic species between the original synthesis and the revised approach to identify diagnostics. Using statistical fidelity measures for diagnostic species identification revealed a number of additional diagnostic species. Procedures performed by the original synthesis (Siebert *et al.*, 2003), regarded these species too sparsely distributed to be considered as diagnostic.

Changing the algorithm used for classification hierarchy however, produced more variance in the end-results when the two approaches are being compared. The Modified TWINSPAN algorithm (Roleček *et al.*, 2009) classified the data set into ten clusters, which were formed without any subjective intervention. Contrary to the relationship between clusters and biogeographical regions produced by the classical classification hierarchy, the non-biased classification hierarchy produced by the Modified TWINSPAN algorithm revealed clusters that are more evidently associated with habitat, more specifically geology and soil (see Table 5-4).

The application of the Modified TWINSPAN algorithm in combination with statistical fidelity measures to identify diagnostic species produced results that are even more dissimilar to the originally published synthesis (Siebert *et al.*, 2003). Although these algorithms and statistical measures weren‘t developed at the time when the original synthesis was performed, the contrasting results obtained from revised methodologies underline the importance of numerical-analytical technique selection for any broad-scale vegetation classification.

For a broad-scale phytosociological synthesis of vegetation data that are sampled across wide environmental extremes and also across a geographically wide distribution range, the classical TWINSPAN algorithm combined with classical frequency diagnostic identifications seem to be inadequate to reveal ecologically expressive vegetation units. Whether the Modified TWINSPAN algorithm is the most reliable method for such synthesis however, remains unclear until all possible combinations of recent numerical-analytical methods and associated software packages (e.g. Belbin, 1993; Belbin and McDonald, 1993; Podani, 2001; Tichý *et al*., 2009; Kindt & Coe, 2005; McCune & Mefford, 2006; Schmidtlein *et al*., 2010) have been performed on the same data set.

5.6 References

BELBIN, L. 1993. PATN Pattern Analysis Package. Users Guide. Division of Wildlife and Ecology: CSIRO.

BELBIN, L. & McDONALD, C. 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science,* 4:341–348.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13:79–90.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

GIBBS-RUSSEL, G.E., WATSON, L., KOEKEMOER, M., SMOOK, L., BARKER, N.P., ANDERSON, H.M. & DALLWITZ, M.J. 1991. Grasses of southern Africa. *Memoirs of the Botanical Survey of South Africa* 58.

HENNEKENS, S.M. 1996. MEGATAB: A visual editor for phytosociological tables. User's guide. Version October 1996. IBN-DLO, Wageningen, and Lancaster University, Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

KINDT, R. & COE, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (CRAF): Nairobi, Kenya.

MANNHEIMER, C., MAGGS-KÖLLING, G., KOLBERG, H. & RÜGHEIMER, S. 2008. Wildflowers of the southern Namib.Macmillan, Namibia.

McCUNE, B. & MEFFORD, M.J. 2006. PC-ORD v.5.2. Multivariate analysis of ecological data. MJM Software: Gleneden Beach, OR.

MOSTERT, T.H.C., BREDENKAMP, G.J., KLOPPER, H.L., VERWEY, C., MOSTERT, R.E. & HAHN, N. 2008. Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *Koedoe,* 50(1):32–48.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland*.* Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

PODANI, J. 2001. SYN-TAX 2000. Computer Programs for Data Analysis in Ecology and Systematics. User‘s Manual. Scientia Publishing: Budapest.

RETIEF, E. & HERMAN, P.P.J. 1997. Plants of the northern Provinces of South Africa: keys and diagnostic characters. *Strelitzia*, 6:1–681.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

SCHMIDTLEIN, S., TICHÝ, L., FEILHAUER, H. & FAUDE, U. 2010. A brute-force approach to vegetation classification. *Journal of Vegetation Science,* 21:1162–1171.

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

STRAUB, A. 2002. The vegetation of Breslau Game Farm, Northern Province, Souh Africa. Pretoria: UP (Dissertation, MSc) 150p.

TICHÝ, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science,* 13(3):451–453.

TICHÝ, L. & HOLT, J. 2006. JUICE v.7.0. Program for management, analysis and classification of ecological data. Program manual. Vegetation Science Group: Masaryk University, Brno.

TICHÝ, L., CHYTRÝ, M., HÁJEK, M., TALBOT, S. & BOTTA-DUKÁT, Z. 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science,* 21:287–299.

VAN WYK, A.E. & VAN WYK, 1997. P. Field guide to trees of southern Africa. Struik: Cape Town.

CHAPTER 6

EVALUATION OF THE INTERMEDIATE-SCALE VEGETATION SYNTHESIS:

A RE-ASSESSMENT OF THE LOWVELD MOPANEVELD IN SOUTH AFRICA

6.1 Introduction

A synthesis of Mopaneveld vegetation in several countries of southern Africa (Siebert *et al.*, 2003) revealed the identification of the *Cissus cornifolia – Colophospermum mopane* vegetation type, which is particularly associated with the South African Lowveld Mopaneveld savanna. A re-assessment of Mopaneveld vegetation with the application of more recent algorithms also revealed a Mopaneveld vegetation unit that is associated with the South African Lowveld, namely the *Crotalaria sphaerocarpa – Digitaria eriantha* Mopane savanna of the South African Lowveld (see Chapter 5). It covers all vegetation units in the Mopane Bioregion (Mucina & Rutherford, 2006), except for SVmp1 (Musina Mopane Bushveld) and SVmp2 (Limpopo Ridge Bushveld). Due to its large biogeographical range, but yet narrower than the entire Mopaneveld of southern Africa, the classification of this data set is considered to present a synthesis at an intermediate scale.

6.2 Objectives

Since the thesis is aimed at evaluating the credibility of the classical approach at various spatial scales, the main objective that will be targeted in this chapter is to evaluate the credibility of the classical approach at an intermediate-scale.

The more specific objective of the intermediate-scale synthesis presented in this chapter is to analyze vegetation data sampled across the entire South African Lowveld Mopaneveld (SALM) according to the different classification approaches. Comparisons of results obtained through the application of the classical and modern approach respectively are envisaged to present insight into the importance of the selection of a classification method in obtaining rigorous results for an intermediate-scale phytosociological synthesis.

6.3 Methodology

Since the vegetation of the SALM is only documented in a Master's dissertation (i.e. Du Plessis, 2001), there is no published reference document, although the results described in Du Plessis (2001) will frequently be referred to. A reclassification of the SALM was therefore considered, which started off with the selection of data that was considered representative of Mopaneveld vegetation in the savanna landscapes of the South African Lowveld.

6.3.1 Data selection

A data set similar to the one used by Du Plessis (2001) were used for analyses. However, the data that were used by Du Plessis (2001) contained relevés from vegetation types that are believed not to be representative of Mopaneveld, such as the Punda Maria (Makuleke) Sandveld vegetation. Relevés that were sampled in the Makuleke Sandy Bushveld (SVI1, Mucina & Rutherford, 2006) in the Punda-Maria/Wambiya area in the northern parts of the Kruger National Park were therefore omitted (total of 45 relevés), but only if they did not contain *Colophospermum mopane*. A considerable number of these relevés were classified under the *Terminalia sericea* – *Colophospermum mopane* major plant community (Du Plessis, 2001), although the floristic justification of this major plant community is being questioned due to the low frequency of *Colophospermum mopane* in this community. Furthermore, data were selected to ensure that no azonal vegetation data disrupts the classification results and therefore all relevés sampled in, or close to rivers, streams and pans, were omitted from the data base (total of 189 relevés), similar to the procedures followed by Du Plessis (2001). These azonal relevés were pooled with even more data from riparian ecosystems in the Mopaneveld to present a first classification of riparian zone vegetation in the Mopane Bioregion of South Africa (see Chapter 8). A total of 877 relevés (i.e. the refined data set) that were sampled across the Mopaneveld of the South African Lowveld, were consequently considered for further analyses. A TURBOVEG (Hennekens & Schaminée, 2001) database was constructed to host all relevés sampled within the study area.

6.3.2 Classification procedures

During the first step to evaluate the classical synthesis of Mopaneveld vegetation (Chapter 5), the JUICE version 7.0 software package (Tichý & Holt, 2006) was tested and proved to be an adequate computer software program to apply classification algorithms and different statistical measures of species fidelity. All selected relevé data of the SALM were imported in JUICE, version 7.0 (Tichý & Holt, 2006) in which the classical and modern approaches were tested independently.

The first step of this intermediate-scale synthesis is to compare the classification results of the refined SALM data set (total of 877 relevés) produced through the application of the classical TWINSPAN algorithm in JUICE, and to compare these results to the synthesis of Du Plessis (2001) (total of 1 111 relevés). Since Du Plessis (2001) identified and described four distinctly different vegetation units in the SALM, two levels of division were again applied in the classical TWINSPAN algorithm (Hill, 1979) among default parameters (i.e. 0-5-50 cutlevels; minimum group size: 6), similar to Du Plessis (2001), but in JUICE to ultimately produce four clusters.

Differences in diagnostic species when statistical measures of fidelity are applied to the classical TWINSPAN classification are also examined. Fischer‘s exact test was therefore applied in combination with the Phi-coefficient fidelity measure to assist in identifying true diagnostic species per vegetation unit. These diagnostic species are tabulated and presented against the percentage frequency table to compare diagnostic species selections (Table 6-1 and Table 6-2).

To ultimately test for differences among classification algorithms, the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) was applied on the refined SALM data set with similar parameters to the above. Since the Modified TWINSPAN algorithm produced more rigorous results in the broad-scale synthesis (see Chapter 5), it is considered to be applied and tested against classical approaches at an intermediate-scale synthesis. Diagnostic species were again selected according to the Phi-coefficient statistical fidelity measures in combination with Fischer‘s exact test ($p<0.001$) to calculate the true probability of obtaining the observed number of occurrences of the species in the vegetation unit under the null hypothesis of independence (Tichý & Holt, 2006).

6.4 Results

6.4.1 Comparison between the classification of Du Plessis (2001) and the refined data set from SALM

In the earlier synthesis of the SALM, Du Plessis (2001) identified four major plant communities through the application of the classical TWINSPAN algorithm. These four major plant communities are linked to most prominent geological substrates and soil underlying Mopaneveld in the SALM. These major communities were informally named as:

1. The *Terminalia sericea – Colophospermum mopane* communities on sandy soil
2. The *Acacia nigrescens – Colophospermum mopane* communities on clayey soil

3. The *Euclea divinorum – Colophospermum mopane* communities on deep clayey soil, mainly derived from Ecca-shale
4. The *Combretum apiculatum – Colophospermum mopane* communities on granite and gneiss

Table 6-1 Vegetation units of the classified major plant communities identified by Du Plessis (2001) and their corresponding units identified through the classification of the refined SALM data set.

Major plant communities Du Plessis (2001)	**Corresponding vegetation units from the refined SALM data set**
The *Terminalia sericea – Colophospermum mopane* communities on sandy soil (Cluster 1, Figure 6-1a)	Mopaneveld on sandy transitions and uplands (Cluster 3, Figure 6-1b)
The *Acacia nigrescens – Colophospermum mopane* communities on clayey soil (Cluster 2, Figure 6-1a)	Mopane shrubveld on clayey bottomlands (Cluster 2, Figure 6-1b)
The *Euclea divinorum – Colophospermum mopane* communities on deep clayey soil, mainly derived from Ecca-shale (Cluster 3, Figure 6-1a)	Bottomlands with nutrient-rich soil (Cluster 4, Figure 6-1b)
The *Combretum apiculatum – Colophospermum mopane* communities on granite and gneiss (Cluster 4, Figure 6-1a)	Combretum-mopane woodland on shallow, coarse sandy soil (Cluster 1, Figure 6-1b)

The results obtained from the application of the classical TWINSPAN algorithm in JUICE version 7.0 (Tichý & Holt, 2006) on the refined SALM data set (see 6.2.1) are similar to Du Plessis (2001) (Table 6-1; Figure 6-1). Each major plant community of Du Plessis (2001) corresponds to a vegetation unit that was clustered through the classification of the refined SALM data set (Table 6-1). The main difference between the two classifications is the less explicit clustering of a Sandveld major community, which was proposed by Du Plessis (2001) (Figure 6-1).

6.4.2 Diagnostic species comparisons

Diagnostic species identified through classical measures and through the application of statistical fidelity measures to identify true diagnostic species for the classification of the refined SALM data set revealed differences in diagnostic species groups. A visual illustration of the differences between traditionally selected diagnostic species (according to subjective measures using percentage frequency per cluster) and statistical measures of diagnostic species identification for the same classification algorithm of the refined SALM data set are presented in Table 6-2. The percentage overlap in diagnostic species between the two different approaches varies between 38 and 63 (Table 6-2).

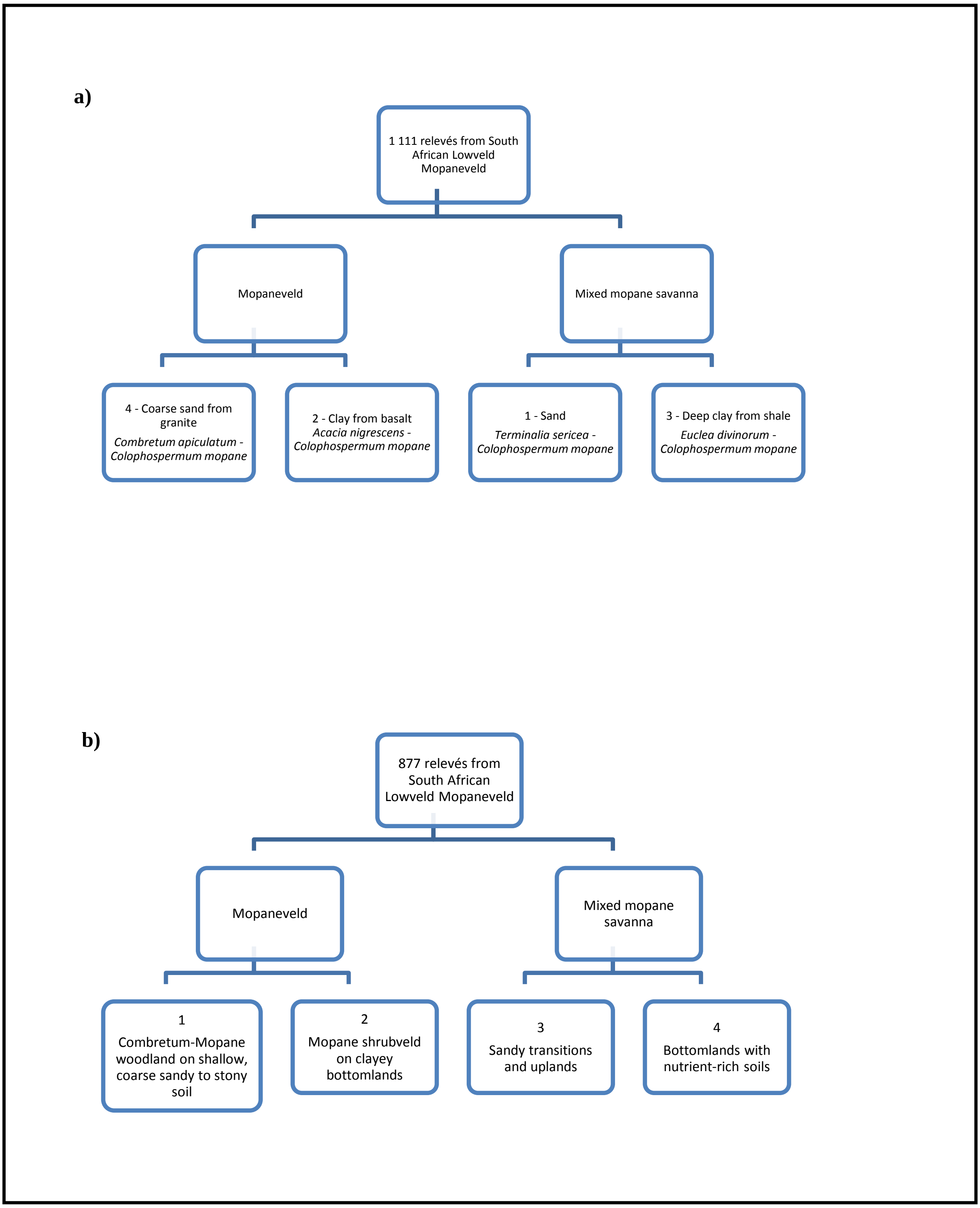


Figure 6-1. Classical TWINSPAN hierarchy of the four major plant communities based on a) Du Plessis (2001) produced through the application of the classification algorithm in MEGATAB (Hennekens, 1996) and b) a refined data set of SALM produced through the application of the classification algorithm in JUICE (Tichý & Holt, 2006).

As a result of different diagnostic species, plant community names will change indisputably, although it will not be presented here since the revision of major plant community names will follow the results obtained from the Modified TWINSPAN classification in combination with statistical measures for diagnostic species selection.

6.4.3 Classification algorithm comparisons

Results obtained from the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) applied to the refined data set of SALM are much different from the classification produced by the classical TWINSPAN algorithm (Figure 6-2), especially in terms of classification hierarchy. A fidelity syntable of the Modified TWINSPAN classification is presented in Table 6-3.

When the classical TWINSPAN algorithm (Hill, 1979) is applied to a data set for hierarchical classification, the number of clusters increases in powers of two down the hierarchy due to its divisive character that cannot be adjusted manually (Roleček *et al.*, 2009). This nature of the classical algorithm is clearly observed in the divisive results of the SALM. Four vegetation groups were produced through the second division of each major cluster (Figure 6-1a) regardless whether the vegetation of each of the two clusters truly represents heterogeneous entities that credit separation. The modified TWINSPAN algorithm however, produced four clusters without any further division of the so-called ‗Mixed mopane savanna‘ (Figure 6-1b). The four vegetation units were formed by the division of the remaining clusters into three distinctly different units, of which units 2 and 3 were formed through a third level of division of the ‗Mopaneveld‘ cluster. The Modified TWINSPAN algorithm acknowledges the difference between the mopane shrubveld on heavy clays and that on Nitrogen-rich bottomlands.

To test the distinctive character of the ‗Mixed mopane savanna‘ cluster, the modified TWINSPAN was repeatedly applied to the data set up to 8 clusters with the assumption that the ‗Mixed mopane savanna‘ cluster would at least subdivide into more units as the numbers of clusters to produce by the algorithm increase. Even after performing a classification to reveal 8 clusters, the ‗Mixed Mopane savanna‘ did not separate, whilst the ‗Mopaneveld‘ cluster (cluster 1, Figure 6-1b) was subdivided into many different smaller units of lowest hierarchy (Figure 6-3). The ‗Mixed Mopane savanna‘ could therefore be considered a significant, but less heterogenous vegetation unit of the Mopaneveld of the South African Lowveld and needs some further investigation.

Table 6-2. A visual comparison of diagnostic species selection between the classical, subjective selection of diagnostics based on % frequency (LEFT column), and non-biased, statistically measured diagnostics (RIGHT). Similarly identified diagnostics between the different approaches are coloured correspondingly and is expressed as a percentage overlap.

Classical TWINSPAN **Classical approach**					**% Overlap**	**Classical TWINSPAN** **Statistical approach**				
Cluster number	**1**	**2**	**3**	**4**		Cluster number	**1**	**2**	**3**	**4**
Diagnostic spp for community 1										
Pterocarpus rotundifolius	20	5	2	0	**38**	*Pterocarpus rotundifolius*	31	---	---	---
Brachiaria nigropedata	34	5	18	2		*Brachiaria nigropedata*	31	---	---	---
Vigna unguiculata	42	10	29	3		*Vigna unguiculata*	30	---	12	---
Urochloa brachyura	20	7	1	0		*Urochloa brachyura*	30	---	---	---
Combretum collinum	18	4	2	0		*Combretum collinum*	29	---	---	---
Digitaria eriantha	96	72	81	49		*Digitaria eriantha*	29	---	8.3	---
Albizia harveyi	48	15	27	16		*Albizia harveyi*	28	---	---	---
Mundulea sericea	22	2	13	1		*Mundulea sericea*	25	---	6.5	---
Oxalis semiloba	11	2	0	1		*Oxalis semiloba*	24	---	---	---
Dalbergia melanoxylon	48	34	32	13		*Dalbergia melanoxylon*	20	---	---	---
Ximenia caffra	13	1	7	4		*Ximenia caffra*	16	---	---	---
Ziziphus mucronata	25	5	18	11		*Ziziphus mucronata*	16	---	---	---
Ipomoea crassipes	29	15	25	11		*Ipomoea crassipes*	13	---	---	---
Diagnostic spp for community 2										
Cenchrus ciliaris	3	35	1	8	**50**	*Cenchrus ciliaris*	---	42	---	---
Setaria incrassata	3	22	1	1		*Setaria incrassata*	---	35	---	---
Sorghum versicolor	0	16	0	2		*Sorghum versicolor*	---	33	---	---
Bothriochloa insculpta	24	42	6	9		*Bothriochloa insculpta*	---	31	---	---
Themeda triandra	34	53	12	17		*Themeda triandra*	---	30	---	---
Neorautanenia amboensis	11	15	0	0		*Neorautanenia amboensis*	---	20	---	---
Panicum coloratum	14	35	9	15		*Panicum coloratum*	---	25	---	---
Sericorema remotiflora	0	11	0	1		*Sericorema remotiflora*	---	27	---	---
Combretum imberbe	14	33	5	10		*Combretum imberbe*	---	27	---	---
Neuracanthus africanus	2	14	1	5		*Neuracanthus africanus*	---	22	---	---
Tephrosia multijuga	0	13	0	1		*Tephrosia multijuga*	---	30	---	---
Fingerhuthia africana	2	25	2	16		*Fingerhuthia africana*	---	25	---	---
Species diagnostic to 1 and 2										
Heteropogon contortus	70	57	41	19		*Heteropogon contortus*	27	12	---	---
Eragrostis superba	48	47	26	16		*Eragrostis superba*	17	15	---	---
Diagnostic spp for community 3										
Waltheria indica	24	2	64	33	**45**	*Waltheria indica*	---	---	42	---
Tricholaena monachne	30	6	68	18		*Tricholaena monachne*	---	---	48	---
Perotis patens	13	1	30	1		*Perotis patens*	---	---	35	---
Indigofera filipes	6	1	26	5		*Indigofera filipes*	---	---	34	---
Leucas glabrata	9	6	46	27		*Leucas glabrata*	---	---	33	---
Terminalia sericea	28	1	39	1		*Terminalia sericea*	16	---	33	---
Polygala sphenoptera	9	6	32	7		*Polygala sphenoptera*	---	---	31	---
Trichoneura grandiglumis	16	1	28	2		*Trichoneura grandiglumis*	---	---	30	---
Helichrysum candolleanum	0	0	13	1		*Helichrysum candolleanum*	---	---	30	---
Evolvulus alsinoides	33	11	63	52		*Evolvulus alsinoides*	---	---	28	14
Andropogon gayanus	32	5	38	7		*Andropogon gayanus*	17	---	25	---
Hermannia boraginiflora	12	9	42	33		*Hermannia boraginiflora*	---	---	25	12
Cyperus rupestris	14	1	35	18		*Cyperus rupestris*	---	---	27	---
Xerophyta retinervis	2	1	18	7		*Xerophyta retinervis*	---	---	26	---

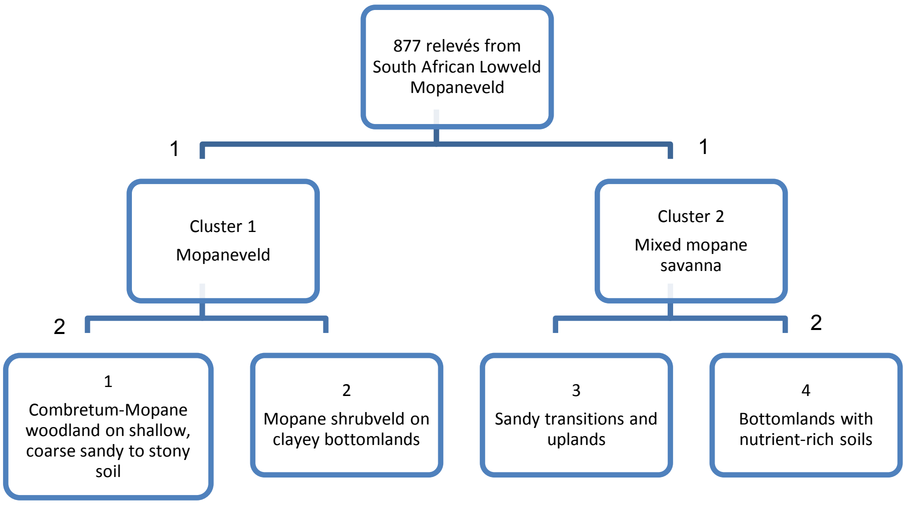
Melinis repens	32	11	59	30		*Melinis repens*	---	---	32	---
Crotalaria schinzii	6	0	20	5		*Crotalaria schinzii*	---	---	26	---
Aristida stipitata	0	0	12	2		*Aristida stipitata*	---	---	26	---
Tephrosia polystachya	46	42	74	58		*Tephrosia polystachya*	---	---	22	---
Indigofera bainesii	11	10	35	15		*Indigofera bainesii*	---	---	26	---
Hemizygia bracteosa	5	0	14	4		*Hemizygia bracteosa*	---	---	21	---
Kyllinga alba	9	3	25	9		*Kyllinga alba*	---	---	24	---
Ipomoea magnusiana	15	4	34	12		*Ipomoea magnusiana*	---	---	28	---
Ornithogalum seineri	11	4	26	7		*Ornithogalum seineri*	---	---	25	---
Aristida meridionalis	7	0	13	0		*Aristida meridionalis*	---	---	22	---
Aristida mollissima	10	1	21	0		*Aristida mollissima*	---	---	29	---
Brachiaria serrata	5	1	14	0		*Brachiaria serrata*	---	---	25	---
Hemizygia elliottii	2	1	12	2		*Hemizygia elliottii*	---	---	23	---
Chascanum hederaceum	2	1	11	1		*Chascanum hederaceum*	---	---	22	---
Gnidia sericea	1	0	8	0		*Gnidia sericea*	---	---	23	---
Emilia transvaalensis	0	0	6	1		*Emilia transvaalensis*	---	---	20	---
Ceratotheca triloba	4	7	34	23		*Ceratotheca triloba*	---	---	26	---
Chamaesyce neopolycnemoides	14	5	36	21		*Chamaesyce neopolycnemoides*	---	---	25	---
Species diagnostic to 1 and 3						**Species group E**				
Pogonarthria squarrosa	72	4	85	19		*Pogonarthria squarrosa*	31	---	46	---
Combretum apiculatum	98	40	93	54		*Combretum apiculatum*	34	---	28	---
Chamaecrista absus	34	2	37	5		*Chamaecrista absus*	20	---	25	---
Cissus cornifolia	84	39	80	50		*Cissus cornifolia*	25	---	20	---
Kohautia virgata	40	7	41	5		*Kohautia virgata*	23	---	25	---
Fimbristylis companulata	18	0	25	1		*Fimbristylis companulata*	13	---	27	---
Strychnos madagascariensis	18	1	22	1		*Strychnos madagascariensis*	13	---	21	---
Eragrostis rigidior	58	17	64	37		*Eragrostis rigidior*	16	---	24	---
Agathesanthemum bojeri	22	1	22	1		*Agathesanthemum bojeri*	20	---	20	---
Merremia tridentata	18	1	17	1		*Merremia tridentata*	19	---	15	---
Combretum zeyheri	13	1	9	0		*Combretum zeyheri*	18	---	8.9	---
Ozoroa engleri	29	10	26	5		*Ozoroa engleri*	17	---	13	---
Sclerocarya birrea	46	25	47	25		*Sclerocarya birrea*	13	---	13	---
Diagnostic spp for community 4										
Pupalia lappacea	0	3	5	36	**63**	*Pupalia lappacea*	---	---	---	45
Endostemon terecaulis	0	1	13	36		*Endostemon terecaulis*	---	---	---	41
Abutilon austro-africanum	2	7	11	42		*Abutilon austro-africanum*	---	---	---	42
Tragus berteronianus	10	15	45	69		*Tragus berteronianus*	---	---	---	42
Aristida adscensionis	0	6	25	45		*Aristida adscensionis*	---	---	---	38
Bothriochloa radicans	2	21	9	45		*Bothriochloa radicans*	---	---	---	38
Grewia villosa	0	3	3	24		*Grewia villosa*	---	---	---	37
Brachiaria deflexa	0	3	12	32		*Brachiaria deflexa*	---	---	---	37
Sporobolus nitens	1	4	4	27		*Sporobolus nitens*	---	---	---	36
Terminalia prunoides	2	14	12	39		*Terminalia prunoides*	---	---	---	34
Acalypha indica	2	8	30	46		*Acalypha indica*	---	---	---	34
Maerua parvifolia	19	19	20	55		*Maerua parvifolia*	---	---	---	34
Portulaca kermisina	0	0	9	24		*Portulaca kermisina*	---	---	---	34
Leucas neuflizeana	0	0	11	19		*Leucas neuflizeana*	---	---	---	26
Aristida scabrivalvis	0	1	7	23		*Aristida scabrivalvis*	---	---	---	33
Grewia subspathulata	0	1	5	20		*Grewia subspathulata*	---	---	---	31
Seddera suffruticosa	0	1	1	14		*Seddera suffruticosa*	---	---	---	30
Melhania prostrata	2	0	6	20		*Melhania prostrata*	---	---	---	29
Commiphora pyracanthoides	0	0	6	16		*Commiphora pyracanthoides*	---	---	---	27
Mehania forbesii	22	10	40	51		*Mehania forbesii*	---	---	---	25
Asparagus setaceus	8	8	29	43		*Asparagus setaceus*	---	---	---	29
Phyllanthus asperulatus	0	1	6	16		*Phyllanthus asperulatus*	---	---	---	26
Solanum coccineum	3	2	9	23		*Solanum coccineum*	---	---	---	27
Grewia flavescens	2	1	10	20		*Grewia flavescens*	---	---	---	25
Sporobolus panicoides	0	1	4	12		*Sporobolus panicoides*	---	---	---	24
Ruellia patula	25	9	27	46		*Ruellia patula*	---	---	---	25
Phyllanthus incurvus	0	1	4	12		*Phyllanthus incurvus*	---	---	---	23

Crabbea velutina	3	5	23	28
Greiwa hexamita	2	2	6	18
Commelina africana	0	2	6	21
Sida chrysantha	0	1	2	11
Euclea divinorum	24	7	10	34
Indigofera rhytidocarpa	5	11	18	31
Gisekia africana	0	2	7	14
Justicia anagalloides	2	1	6	14
Tribulus terrestris	0	3	2	17
Pavonia burchellii	10	12	10	36
Heliotropium steudneri	3	38	34	49
Melhania rehmannii	0	10	10	26
Enneapogon cenchroides	23	48	59	71
Oropetium capense	6	4	17	26
Hibiscus micranthus	42	35	61	80
Grewia bicolor	47	43	62	82
Achyranthes aspera	0	2	4	17
Boerhavia diffusa	0	6	2	19
Commelina eckloniana	4	1	3	18
Ehretia amoena	0	5	3	19
Justicia flava	2	5	2	19
Chloris virgata	3	5	7	19
Amaranthus thunbergii	0	2	3	14
Enteropogon macrostachyus	1	1	2	13
Barleria elegans	0	1	0	7
Eragrostis lehmanniana	0	1	4	12
Sansevieria hyacynthoides	0	1	5	13
Species diagnostic to 3 and 4				
Kyphocarpa angustifolia	5	5	79	67
Aptosimum lineare	5	4	30	26
Dicoma tomentosa	2	10	41	33
Commelina benghalensis	22	12	45	37

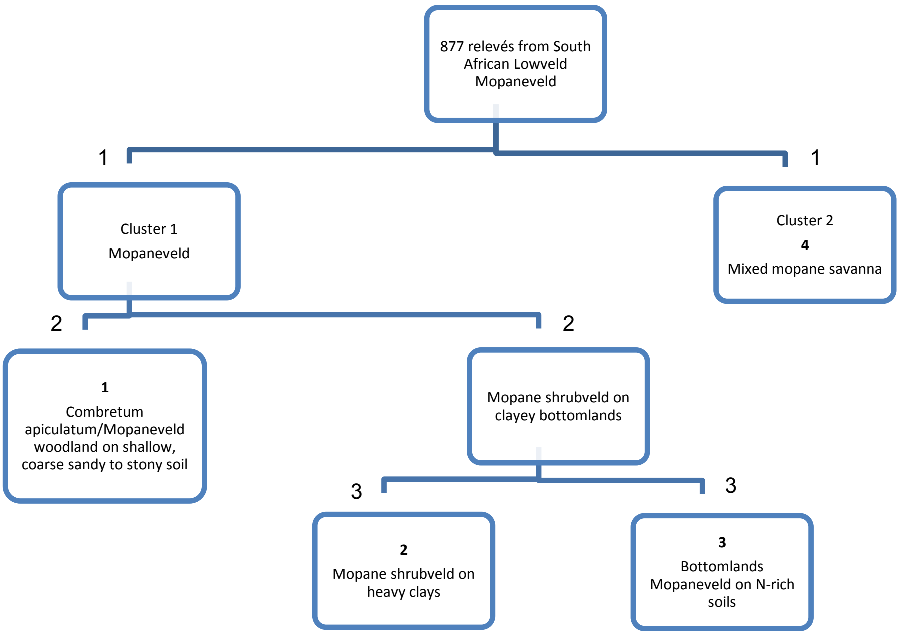
Crabbea velutina	---	---	---	22
Greiwa hexamita	---	---	---	24
Commelina africana	---	---	---	30
Sida chrysantha	---	---	---	25
Euclea divinorum	---	---	---	23
Indigofera rhytidocarpa	---	---	---	23
Gisekia africana	---	---	---	21
Justicia anagalloides	---	---	---	20
Tribulus terrestris	---	---	---	30
Pavonia burchellii	---	---	---	29
Heliotropium steudneri	---	---	---	23
Melhania rehmannii	---	---	---	27
Enneapogon cenchroides	---	---	---	24
Oropetium capense	---	---	---	21
Hibiscus micranthus	---	---	---	30
Grewia bicolor	---	---	---	28
Achyranthes aspera	---	---	---	28
Boerhavia diffusa	---	---	---	29
Commelina eckloniana	---	---	---	26
Ehretia amoena	---	---	---	28
Justicia flava	---	---	---	27
Chloris virgata	---	---	---	21
Amaranthus thunbergii	---	---	---	26
Enteropogon macrostachyus	---	---	---	25
Barleria elegans	---	---	---	22
Eragrostis lehmanniana	---	---	---	21
Sansevieria hyacynthoides	---	---	---	22
Kyphocarpa angustifolia	---	---	47	34
Aptosimum lineare	---	---	22	15
Dicoma tomentosa	---	---	27	17
Commelina benghalensis	---	---	20	10

Another conspicuous difference between the two classification hierarchies is the absence of a ‗Sandy transitions and uplands‘ vegetation unit in the Modified TWINSPAN hierarchy (Figure 6-1). The relevés that constituted this unit in the classical TWINSPAN output are grouped with either the ‗Mixed Mopane savanna‘ or the ‗Combretum/Mopane woodland‘ in the Modified TWINSPAN output. This result evidently reveals that the classical TWINSPAN algorithm produces clusters of which their ecological justification is indistinct.

The dissimilar classification results that were revealed from the different algorithms encouraged a re-assessment of the vegetation of the SALM according to the Modified TWINSPAN algorithm and statistical measures of species diagnostics. Short descriptions of these units are presented as a revision of the major plant communities identified and described by Du Plessis (2001).



a) Classical TWINSPAN classification hierarchy



b) Modified TWINSPAN classification hierarchy

Figure 6-2. Classification hierarchy of the SALM for a) the classical TWINSPAN (Hill, 1979), and b) the Modified TWINSPAN algorithm (Roleček *et al.*, 2009). Numbers outside boxes refer to the level of division.

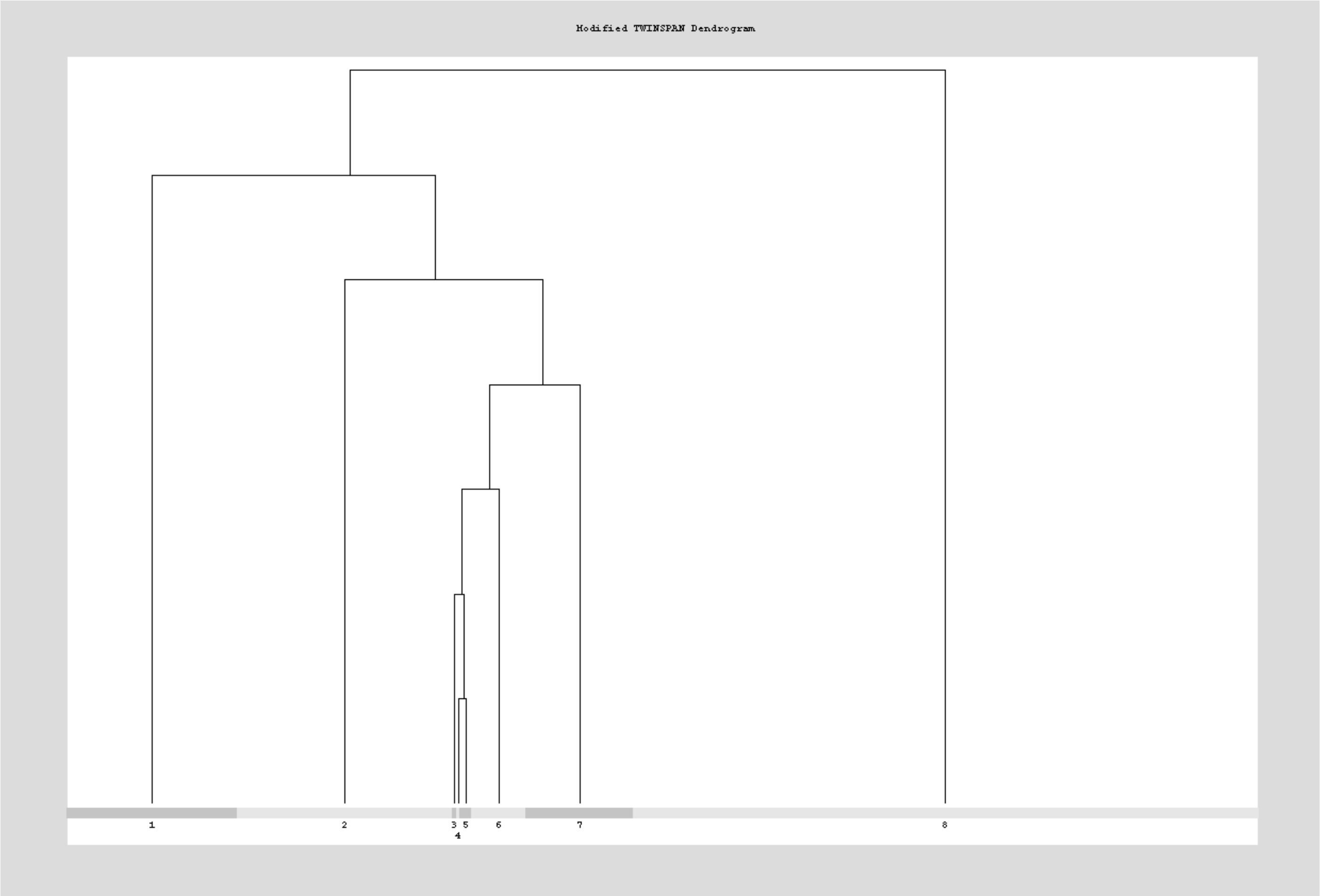


Figure 6-3. The application of the Modified TWINSPAN algorithm to the refined SALM data set producing eight clusters to test whether the ‗Mixed mopane savanna' (cluster 8) is more homogeneous than the Mopane savanna (clusters 1 – 7). This hierarchical tree was obtained as an output file directly from JUICE, version 7.0 (Tichý & Holt, 2006).

Table 6-3. A percentage Phi-coefficient fidelity syntable of the SALM produced through the application of the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) to the vegetation data set.

	1	**2**	**3**	**4**
	Combretum/ Mopane	**Clay**	**Bottomland Mopane**	**Mixed mopane Savanna**
Number of relevés	**124**	**162**	**130**	**461**
Species group A				
Combretum apiculatum	41.9	---	---	8.8
Vigna unguiculata	35.3	---	---	---
Brachiaria nigropedata	35.1	---	---	---
Chamaecrista absus	32.8	---	---	---
Kohautia virgata	32.8	---	---	---
Cissus cornifolia	32	---	---	---
Mundulea sericea	31.3	---	---	---
Albizia harveyi	31.1	---	---	---
Agathesanthemum bojeri	30.1	---	---	---
Terminalia sericea	29.7	---	---	9
Pterocarpus rotundifolius	28.3	---	---	---
Digitaria eriantha	27.7	---	---	---
Merremia tridentata	27.4	---	---	---
Combretum collinum	27	---	---	---
Andropogon gayanus	26.9	---	---	---
Urochloa brachyura	25.5	6.3	---	---
Combretum zeyheri	24.5	---	---	---
Fimbristylis companulata	24.2	---	---	---
Strychnos madagascariensis	22.1	---	---	---
Ozoroa engleri	21.9	---	---	---
Oxalis semiloba	21.7	---	---	---
Heteropogon contortus	21.5	15.8	---	---
Ziziphus mucronata	20.6	---	---	---
Litogyne gariepina	19.2	---	---	---
Ximenia caffra	19.1	---	---	---
Sclerocarya birrea	18.5	---	---	---
Species group B				
Themeda triandra	---	62	---	---
Setaria incrassata	---	40.2	---	---
Neorautanenia amboensis	---	32.4	---	---
Panicum coloratum	---	30.3	---	---
Eragrostis superba	9.7	28.6	---	---
Combretum imberbe	---	27.5	---	---
Chamaecrista mimosoides	---	27.2	---	---
Sericorema remotiflora	---	25.2	---	---
Merremia palmata	---	21.3	---	---

Ormocarpum trichocarpum	---	17	---	---
Cymbopogon excavatus	---	15.7	---	---
Ipomoea eriocarpa	---	15.3	---	---
Rhynchosia densiflora	---	14.3	---	---
Rhynchosia minima	---	14	---	---
Species group C				
Dalbergia melanoxylon	17.3	14.9	---	---
Philenoptera violacea	14.3	13.2	---	---
Species group D				
Neuracanthus africanus	---	---	36.6	---
Fingerhuthia africana	---	---	33.6	---
Aristida congesta	---	---	32.1	---
Bothriochloa insculpta	---	3.9	31.6	---
Seddera capensis	---	---	31.5	---
Barleria lanceolata	---	---	21.9	---
Colophospermum mopane	**8.3**	**---**	**26.9**	**---**
Commiphora glandulosa	---	---	21.7	---
Combretum mossambicense	---	---	19.6	---
Becium obovatum	---	---	17.7	---
Chamaesyce tettensis	---	---	15.2	---
Boscia foetida	---	---	15.2	---
Euphorbia guenzi	---	---	14.7	---
Indigofera hermannioides	---	---	13.7	---
Species group E				
Cenchrus ciliaris	---	26.3	18.5	---
Sorghum versicolor	---	19.8	12.9	---
Tephrosia multijuga	---	18.6	10.5	---
Species group F				
Kyphocarpa angustifolia	---	---	---	70.1
Endestemon terecaulis	---	---	---	44
Tragus berteronianus	---	---	---	46
Aristida adscensionis	---	---	---	42.9
Acalypha indica	---	---	---	41.1
Waltheria indica	---	---	---	40.2
Portulaca kermesina	---	---	---	37.4
Evolvulus alsinoides	---	---	---	36.9
Brachiaria deflexa	---	---	---	36.3
Asparagus setaceus	---	---	---	35.5
Leucas neuflizeana	---	---	---	35.4
Pupalia lappacea	---	---	---	34.5
Leucas glabrata	---	---	---	34.8
Dicoma tomentosa	---	---	---	34.4
Abutilon austro-africanum	---	---	---	34.1
Melhania forbesii	---	---	---	33.4

Aristida scabrivavlis	---	---	---	33.3
Aptosimum lineare	---	---	---	32.8
Hermannia boraginiflora	---	---	---	31
Crabbea velutina	---	---	---	30.7
Grewia flavescens	---	---	---	30.6
Melhania prostrata	---	---	---	30.5
Commiphora pyracanthoides	---	---	---	30.4
Grewia subspathulata	---	---	---	30.1
Hibiscus micranthus	---	---	---	29.7
Cyperus rupestris	---	---	---	28.7
Ceratotheca triloba	---	---	---	28.4
Commelina africana	---	---	---	28.3
Phyllanthus asperulatus	---	---	---	27.7
Rhinacanthus xerophilus	---	---	---	26.5
Grewia villosa	---	---	---	26.5
Oropetium capense	---	---	---	26.3
Sporobolus nitens	---	---	---	26.1
Ruellia patula	---	---	---	26
Tricholaena monchne	---	---	---	26
Solanum coccineum	---	---	---	25.7
Commelina benghalensis	---	---	---	25.5
Grewia bicolor	---	---	---	24.5
Sansevieria hyacynthoides	---	---	---	24.2
Sporobolus panicoides	---	---	---	24
Chamaesyce neopolycnemoides	---	---	---	23.9
Xerophyta retinervis	---	---	---	23.7
Phyllanthus incurvus	---	---	---	23.7
Achyranthes aspera	---	---	---	23.3
Melinis repens	---	---	---	23.1
Seddera suffruticosa	---	---	---	22.8
Bulbostylis hispidula	---	---	---	22.6
Gisekia africana	---	---	---	22.5
Indigofera rhytidocarpa	---	---	---	22.2
Indigofera filipes	---	---	---	22
Grewia hexamita	---	---	---	21.8
Limeum viscosum	---	---	---	21.8
Sida chrysantha	---	---	---	21.8
Justicia anagalloides	---	---	---	21.7
Helichrysum candolleanum	---	---	---	21.5
Aristida stipitata	---	---	---	21.5
Corchorus asplenifolius	---	---	---	21.4
Limeum fenestratum	---	---	---	21.4
Sesamum alatum	---	---	---	21.2
Maerua parvifolia	---	---	---	20.8

Crotalaria schinzii	---	---	---	20.2
Terminalia prunioides	---	---	---	20.1
Tribulus terrestris	---	---	---	20
Eragrostis lehmanniana	---	---	---	19.9
Amaranthus thunbergii	---	---	---	19.8
Mariscus rehmannianus	---	---	---	19.6
Enteropogon macrostachyus	---	---	---	19.2
Commelina erecta	---	---	---	18.9
Enneapogon scoparius	---	---	---	18.4
Coccinia rehmannii	---	---	---	18.3
Vernonia poskeana	---	---	---	18.4
Dactyloctenium aegyptium	---	---	---	18.3
Tephrosia polystachya	---	---	---	18.2
Euclea undulata	---	---	---	18.1
Melhania didyma	---	---	---	18
Melhania rehmannii	---	---	---	17.9
Hermstaedtia odorata	---	---	---	17.8
Bothriochloa radicans	---	---	---	17.7
Tricleceras laceratum	---	---	---	17.7
Talinum caffrum	---	---	---	17.1
Pavonia burchelli	---	---	---	17.1
Ipomoea magnusiana	---	---	---	17.1
Asparagus buchananii	---	---	---	17.1
Chloris virgata	---	---	---	16.8
Kyllinga alba	---	---	---	16.2
Ehretia amoena	---	---	---	16.2
Hemizygia bracteosa	---	---	---	16.1
Indigofera bainesii	---	---	---	16
Heliotropium steudneri	---	---	---	15.7
Geigeria ornativa	---	---	---	15.5
Perotis patens	---	---	---	15.1
Hemizygia elliotti	---	---	---	15.1
Cucumis africanus	---	---	---	15.1
Boerhavia diffusa	---	---	---	14.6
Pappea capensis	---	---	---	14.6
Monechma divaricata	---	---	---	14.6
Justicia flava	---	---	---	14.6
Ocimum americanum	---	---	---	14.2
Euclea divinorum	---	---	---	14.3
Fockea angustifolia	---	---	---	14
Spirostachys africana	---	---	---	13.4
Cordia monoica	---	---	---	13.4
Acacia grandicornuta	---	---	---	13.4
Hermannia modesta	---	---	---	13

Panicum maximum	---	---	---	13.1
Phyllanthus pentandrus	---	---	---	12.7
Acacia burkei	---	---	---	12.7
Gymnosporia senegalensis	---	---	---	12.5
Aristida mollissima	---	---	---	10.5
Blepharis integrifolia	---	---	---	10.1
Species group G				
Enneapogon cenchroides	---	---	28.6	21
Species group H				
Pogonarthria squarrosa	50.6	---	---	17.1
Eragrostis rigidior	27.5	---	---	16.2

6.4.4 A revision of the four SALM major plant communities (Du Plessis, 2001)

Descriptions of the SALM vegetation will follow the numbering of clusters, which present major plant communities identified by the Modified TWINSPAN classification hierarchy (Figure 6-2b).

1. The *Brachiaria nigropedata – Combretum apiculatum* Lowveld Mopane woodland

This open mopane woodland community is commonly associated with *Combretum apiculatum* and other species that are typically found on crests on shallow, coarse sandy to stony soil overlaying clays on granite and gneiss. It is widespread in the Kruger National Park and adjacent areas on undulating granitic plains where *Colophospermum mopane* frequently dominates the more clayey bottomlands and species associated with well-drained soil dominate the crests, such as *Combretum apiculatum, C. zeyheri* and *Terminalia sericea*.

A detailed description of this major plant community is presented by Rutherford *et al.* (2006) as the Phalaborwa-Timbavati Mopaneveld (SVmp7) in the Mopane Bioregion (Mucina & Rutherford, 2006).

Diagnostic species for the *Brachiaria nigropedata – Combretum apiculatum* Lowveld Mopane woodland are listed under species group A of Table 6-3 and include the following:

Trees and shrubs: *Combretum apiculatum*, *C. collinum*, *C. zeyheri*, *Mundulea sericea*, *Albizia harveyi*, *Terminalia sericea*, *Pterocarpus rotundifolius*, *Sclerocarya birrea* and *Strychnos madagascariensis*, and the common strangling shrub *Cissus cornifolia*.

Forbs: *Vigna unguiculata*, *Chamaecrista absus*, *Kohautia virgata*, *Agathesanthemum bojeri* and *Merremia tridentata*.

<u>Graminoids</u>: Grasses such as *Brachiaria nigropedata*, *Digitaria eriantha*, *Andropogon gayanus*, *Urochloa brachyura* and the sedge *Fimbristylis companulata*.

According to the Modified TWINSPAN classification hierarchy, the following two major plant communities (i.e. clusters 2 and 3, Figure 6-2b) are floristically related, mainly due to the similar habitat they occupy, namely deep, dark, clayey soil texture. The vertic clayey soil derived from gabbro are less suitable for *Colophospermum mopane*, therefore the separation of the two groups, of which the basaltic clays (i.e. the *Themeda triandra – Combretum imberbe* shrubveld, major community no 3) host the highest fidelity of *Colophospermum mopane* (species group D, Table 6-3).

2. The *Themeda triandra – Combretum imberbe* Lowveld Mopane shrubveld

This community is restricted to soil texture with a high clay content, mostly associated with gabbro intrusions. The landscape is irregular or even slightly undulating which is dominated by a short shubveld of *Colophospermum mopane* and other woodies, which are only found in low abundances. Soil texture is dark vertisols in areas with a concave topography. The Timbavati gabbro intrusions are mostly responsible for higher grass cover and stunted *Colophospermum mopane* shrubs. This shrubveld community covers the Mopane gabbro shrubland (SVmp8, Rutherford *et al.* (2006)).

Diagnostic species are listed in species group B of Table 6-3 and include the following:

<u>Trees and shrubs</u> (poorly-developed woody diagnostics): *Combretum imberbe* and *Ormocarpum trichocarpum*.

<u>Forbs</u>: *Neorautanenia amboensis*, *Chamaecrista mimosoides*, *Merremia palmata* and *Sericorema remotiflora.*

<u>Grasses</u> (grasses are well presented as diagnostics in high abundances): *Themeda triandra*, *Setaria incrassata*, *Panicum coloratum* and *Eragrostis superba*.

3. *Fingerhuthia africana – Commiphora glandulosa* Lowveld Mopane vegetation unit

This community can be considered the most typical Mopane community in the SALM and also has the highest fidelity of *Colophospermum mopane* (species group D, Table 6-3). According to the Modified TWINSPAN results in combination with fidelity measures to identify diagnostic species, it is the only community in which *Colophospermum mopane* is considered a true diagnostic species. Although it is also associated with common geological substrates of the Lowveld region, including basalt from the Letaba Formation of the Lebombo Group in the Karoo Supergroup, the landscape is less irregular with *Colophospermum mopane* forming the dominant woody species on deep clayey soil on bottomlands and shallow, reddish, gravelly soil overlaying clays in the midslopes. This community stretches along the basaltic plains in the Kruger National Park, where *Colophospermum mopane* dominance is replaced by scattered *Acacia nigrescens* and *Sclerocarya birrea* trees to the south outside the distribution range of *Colophospermum mopane*. This community is similar to the Mopane basalt shrubland vegetation unit (SVmp4, Rutherford *et al.*, 2006).

Diagnostic species are listed under species group D in Table 6-3, and include the following:

Trees and shrubs: Due to the dominance of *Colophospermum mopane* in this community, the only other woody species that are diagnostic to this community are *Commiphora glandulosa* and *Combretum mossambicense*.

Forbs: *Neuracanthus africanus*, *Seddera capensis* and *Barleria lancifolia*.

Grasses: *Fingerhuthia africana*, *Aristida congesta* and *Bothriochloa insculpta*.

4. *Tragus berteronianus – Terminalia prunioides* Mixed Lowveld Mopane woodland

This community is widespread in the SALM where *Colophospermum mopane* does not exclusively dominate the woody layer. It is generally associated with bottomlands of granitic landscapes and also on ancient floodplains and sodium-rich soil. This community is strongly assembled in its species since the re-application of the Modified TWINSPAN algorithm to produce more clusters never resulted in the division of this vegetation unit. It is also the vegetation unit that contains the highest number of vegetation relevés, and the highest number of diagnostic species (Table 6-3). There is no vegetation type within the Mopane Bioregion (Mucina & Rutherford, 2006) that is explicitly related to this community since this community is constituted by many relevés (a total of 461) in which *Colophospermum mopane* is not strongly presented. This community is floristically linked, although weakly, to the Tsende Mopaneveld (SVmp5) and Phalaborwa-Timbavati Mopaneveld (SVmp7, Rutherford *et al.*, 2006).

Diagnostic species are listed under species group F in Table 6-3.

Trees and shrubs: *Grewia* species characterize this community of which *Grewia bicolor*, *G. flavescens* and *G. villosa* are the most conspicuous. Other diagnostic woody species include *Commiphora pyracanthoides*, *Maerua parvifolia* and *Terminalia prunioides*. On sodic soil diagnostic woody species include *Euclea divinorum*, *Spirostachys africana* and *Acacia grandicornuta*.

Forbs: Most diagnostic species are forbs, of which the species with the highest percentage fidelity include *Kyphocarpa angustifolia*, *Endostemon tereticaulis*, *Acalypha indica*, *Waltheria indica*, *Portulaca kermesina*, *Evolvulus alsinoides*, *Asparagus setaceus*, *Leucas glabrata*, *Pupalia lappacea*, *Dicoma tomentosa*, *Abutilon austro-africanum*, *Melhania forbesii*, *M. prostrata*, *Aptosimum lineare*, *Hermannia boraginiflora*, *Crabbea velutina* and *Hibiscus micranthus*.

Grasses: The grass layer is usually overgrazed and dominated by annuals. Common grasses include *Tragus berteronianus*, *Aristida adscensionis*, *Brachiaria deflexa* and *Aristida scabrivalvis*.

6.5 Discussion

Mopaneveld vegetation of the South African Lowveld extends across large areas in the northern parts of the savanna biome. Due to its wide distribution range, the SALM data set was considered to represent an intermediate-scale synthesis of vegetation data. The vegetation data set that was used for analysis in this comparative study was refined from the original data set from which Du Plessis (2001) identified the major plant communities. The classification of this refined data revealed vegetation units that are strongly related to the units described by Du Plessis (2001), despite differences in the source data used for analyses. Diagnostic species identifications are, however, only 50 % analogous between the two approaches of diagnostic species selection. Similar to the outcomes of the broad-scale synthesis, there is a higher number of diagnostic species that are being identified through statistical fidelity measures than through classical approaches.

The comparison of results obtained from the classical approach versus results obtained through the modern approach of the same data source (i.e. the use of the refined data set), revealed certain discrepancies. Although there are similarities in the classification outputs, e.g. both algorithms revealed groups that are typically associated with clays and coarse sands derived from granitic substrates, the Modified TWINSPAN algorithm produced clusters (i.e. vegetation units) at various hierarchical levels, which are ecologically more pronounced.

The application of statistical fidelity measures to aid in the identification of diagnostic species resulted in diagnostic species that are more closely related to the habitat which underlies the respective vegetation unit, i.e. the major plant community.

Based on field observations and knowledge on savanna vegetation, one would expect the Mixed mopane woodland (i.e. the *Tragus berteronianus – Terminalia prunioides* Mixed Lowveld Mopane woodland) to be separated into distinct vegetation entities, but since Modified TWINSPAN did not separate this community, even at high hierarchical levels, this woodland is less heterogeneous than previously reported (Du Plessis, 2001). These findings support the need for further research on the heterogeneity within Mopaneveld vegetation in the Lowveld savanna of South Africa.

The selection of classification algorithms and measures to identify diagnostic species for a phytosociological synthesis at an intermediate spatial scale is considered important to present objective classification hierarchies and diagnostic species that are ecologically meaningful. Until other numerical-analytical techniques are applied to the data set for an intermediate-scale synthesis, the Modified TWINSPAN algorithm could be considered to present a more ecologically meaningful classification. In combination with statistical measures of species diagnostic selection, the four major plant communities that are briefly described here are believed to present a more rigorous synthesis of the Mopaneveld of the South African Lowveld.

6.6 References

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

HENNEKENS, S.M. 1996. MEGATAB: A visual editor for phytosociological tables. User's guide. Version October 1996. IBN-DLO, Wageningen, and Lancaster University, Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

RUTHERFORD, M.C., MUCINA, L., LÖTTER, M.C., BREDENKAMP, G.J., SMIT, J.H.L., SCOTT-SHAW, C.R., HOARE, D.B., GOODMAN, P.S., BEZUIDENHOUT, H., SCOTT, L., ELLIS, F., POWRIE, L.W., SIEBERT, F., MOSTERT, T.H., HENNING, B.J., VENTER, C.E., CAMP, K.G.T., SIEBERT, S.J., MATTHEWS, W.S., BURROWS, J.E., DOBSON, L., VAN ROOYEN, N., SCHMIDT, E., WINTER, P.J.D., DU PREEZ, P.J., WARD, R.A., WILLIAMSON, S. & HURTER, P.J.H. 2006. Savanna Biome. (*In* Mucina, L. & Rutherford, M.C. *eds*., The vegetation of South Africa, Lesotho and Swaziland, *Strelitzia* 19. South African National Biodiversity Institute: Pretoria. p. 438–538).

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

TICHÝ, L. & HOLT, J. 2006. JUICE v.7.0. Program for management, analysis and classification of ecological data. Program manual. Vegetation Science Group: Masaryk University, Brno.

RESULTS

CHAPTER 7

EVALUATION OF THE LOCAL-SCALE VEGETATION SYNTHESIS:

AN ASSESSMENT OF THE MOPANEVELD VEGETATION ALONG A SECTION OF THE LETABA RIVER IN SOUTH AFRICA

7.1 Introduction

The importance of selecting the most objective classification algorithm for broad-scale and intermediate-scale phytosociological syntheses was presented in previous chapters. Most plant community descriptions in South Africa are however based on local-scale classifications (e.g. Eckhardt *et al.,* 1997; Morgenthal & Cilliers, 1999; Gotze *et al.*, 2003; Brown *et al.*, 2005; Cleaver *et al.*, 2005; Daemane *et al.*, 2012) and are mostly focused on vegetation mapping and descriptions of plant communities as management units.

Southern Africa hosts one of the richest floras in the world, especially when endemic plant taxa are also being considered (Cowling *et al.*, 1989). Despite this floristic wealth, many areas in South Africa remain unknown with regards to vegetation classifications. Large quantities of vegetation data have been accumulated over time (Rutherford *et al.*, 2012), although only a limited number of the accumulated data are presented in formal classifications or plant community descriptions in published format. Local-scale vegetation descriptions serve as important reference documents for environmental managers. The selection of a reliable classification algorithm for such local-scale vegetation studies are therefore considered in this chapter.

7.2 Objectives

Consistent with the aims of the broad-scale and intermediate-scale syntheses to present a comparison between results obtained through the classical approach and the modern approach respectively, this chapter aims to present insight on the importance of the selection of a classification algorithm and the use of alternative methods to identify diagnostic species at the local-scale.

The more specific objective that will be targeted in this chapter is to compare results obtained from the modern approach with the classical approach when a local-scale vegetation classification within a small section of Mopaneveld vegetation along the Letaba River in the Kruger National Park is being investigated.

7.3 Methodology

7.3.1 Study area

The local-scale study that is being investigated here is the long-term exclosures monitoring site along a section of the Letaba River in the Kruger National Park, which falls within the Lowveld Rugged Mopaneveld (SVmp6, Rutherford *et al*., 2006) of the Mopane Bioregion (Mucina & Rutherford, 2006). The rationale behind the establishment of the exclosures is to monitor the effects of fire and herbivory along semi-arid savanna riparian ecosystems by excluding these from the system (O‘Keefe & Alard, 2002). Vegetation and floristic surveys were conducted in 2007 after which a vegetation map with subsequent plant community descriptions and floristic comparisons were published by Siebert *et al.* (2010).

7.3.2 Analyses

Vegetation data input was done in TURBOVEG (Hennekens & Schaminée, 2001). The classification was based on the application of the classical TWINSPAN algorithm (Hill, 1979) in MEGATAB (Hennekens, 1996). Although the study was undertaken at a local scale, the study area represents a heterogeneous savanna landscape, which includes a riparian zone, footslope, midslope and crest, as well as a non-perennial stream that dissects the landscape (Siebert *et al.*, 2010). Diagnostic species that were used in the plant community descriptions were identified through the classical, subjective approach, which are consistent with the Zurich Montpellier (Braun-Blanquet) School of subjective classification (Kent, 2012).

Similar to the approach followed in Chapters 5 and 6 to investigate and compare this classical approach of vegetation classification and descriptions with novel approaches, the same data set were used to apply the more recent Modified TWINSPAN algorithm (Roleček *et al.*, 2009) in JUICE 7.0 (Tichý & Holt, 2006). For the purpose of comparing classification results, the Modified TWINSPAN algorithm was set to produce 11 clusters in JUICE, which are equivalent to the number of clusters produced by the classical TWINSPAN approach followed by Siebert *et al.* (2010). *Post hoc* comparisons between classification hierarchies are presented in dendrograms and in discussions on differences and resemblances at various hierarchical levels.

The published diagnostic species (Siebert *et al.*, 2010) were compared to the diagnostic species that were identified through statistical fidelity measures, more particular the Phi-coefficient fidelity measure in combination with Fischer‘s exact test (Tichý and Holt, 2006), which were applied to the data set to aid in a more objective identification of diagnostic species. Comparisons of diagnostic species are presented directly on the published phytosociological table (Table 7-2) for optimal visual interpretation of results.

7.4 Results

The classical approach of vegetation classification followed by Siebert *et al.* (2010) revealed the identification of the following plant communities at the Letaba exclosures study site (see Appendix 7-1 for the full publication), of which the classification hierarchy is presented in Figure 7-1:

1. *Hemizygia bracteosa – Acacia exuvialis* crest savanna
1.1 *Xerophyta humilis – Oldenlandia herbacea* seepage
1.2 *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld
1.2.1 *Senna italica* variant
1.2.2 Typical variant
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 *Philenoptera violacea – Jasminum fluminense* riverbank woodland
4.1.1 *Hyphaene coriacea* variant
4.1.2 *Nuxia oppositifolia* variant
4.2 *Combretum imberbe – Enneapogon cenchroides* open woodland.

Detailed descriptions on each of these plant communities could be viewed in Siebert *et al.* (2010) (see Appendix 7-1).

7.4.1 Comparison of classification hierarchy

Classification hierarchy results obtained from the two respectively applied classification algorithms revealed very similar results. Although presented at different hierarchical levels, all plant communities, sub-communities and variants described by Siebert *et al.* (2010) are similarly clustered after the application of the Modified TWINSPAN algorithm (Figure 7-2).

At the highest hierarchical level, both algorithms separated the azonal, riparian-type vegetation from savanna vegetation, although the Modified TWINSPAN considered the seasonally wet savanna (community 3, Siebert *et al.*, (2010)) as being floristically more related to the savanna vegetation than to the azonal riparian-type vegetation (Figure 7-2). This clustering is different than what was revealed by the classical TWINSPAN output (Figure 7-1). From the Modified TWINSPAN output, the Riverine woodland community (community 4, Siebert *et al.* (2010)) is considered distinctly different from the Mopaneveld savanna and seasonally wet savanna by separating them at the first level of division. The seasonally wet savanna (community 3) is separated from the other savanna communities at the second hierarchical level (Figure 7-2). Similarly to the classical TWINSPAN hierarchy, both the Riverine woodland community (community 4) and the seasonally wet savanna community (community 3) were separated into two sub-communities (Figure 7-1; Figure 7-2). According to the Modified TWINSPAN hierarchy, the crest savanna community (community 1) and the lowland savanna community (community 2) are ranked lower than proposed by Siebert *et al.* (2010) forming only after the third level of division from the uplands savanna (Figure 7-2). These communities could floristically be considered as sub-communities of a community of higher rank, probably presenting the upland savannas of the Letaba exclosures (Figure 7-2). Clustering beyond these hierarchical levels are very similar between the two different classification algorithms (compare Figures 7-1 and 7-2).

When hierarchical ranking are not being considered, the two classification algorithms revealed almost identical assemblages of relevés up to sub-community level. Table 7-1 summarizes the clustering of relevés in the two respective classifications. Due to the distinctively different hierarchical rank of the Riverine woodland community revealed by the Modified TWINSPAN classification, it was expected that more clusters would form through classification procedures (Table 7-1), which is evident in the ‗newly-formed' cluesters (i.e. variants, Figure 7-2). Results from the Modified TWINSPAN output (Figure 7-2; Table 7-1) furthermore suggest that the *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld (1.2) is floristically less heterogeneous than previously reported (Siebert *et al.*, 2010).

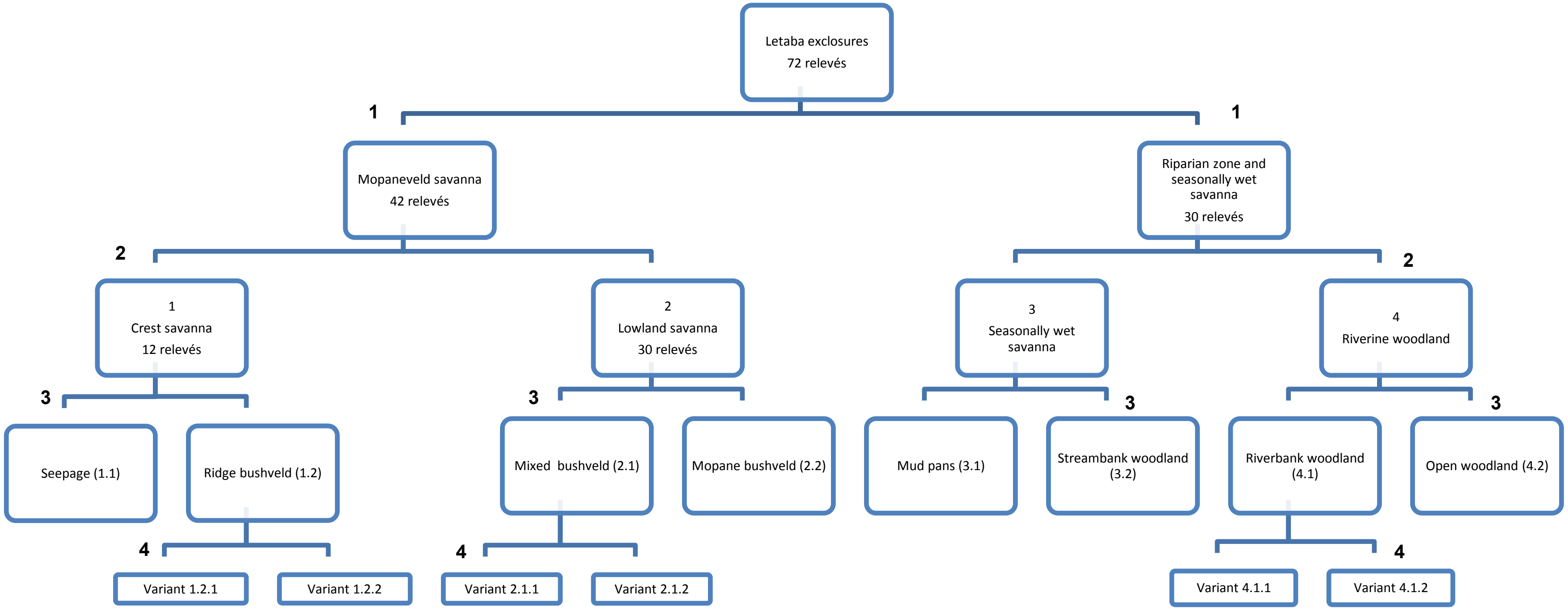


Figure 7-1. Detailed classification hierarchy presented through the application of the classical TWINSPAN algorithm (Hill, 1979) in MEGATAB (Hennekens, 1996). Community numbers are in accordance with the published numbers (Siebert *et al.*, 2010). Numbers outside boxes represent levels of division.

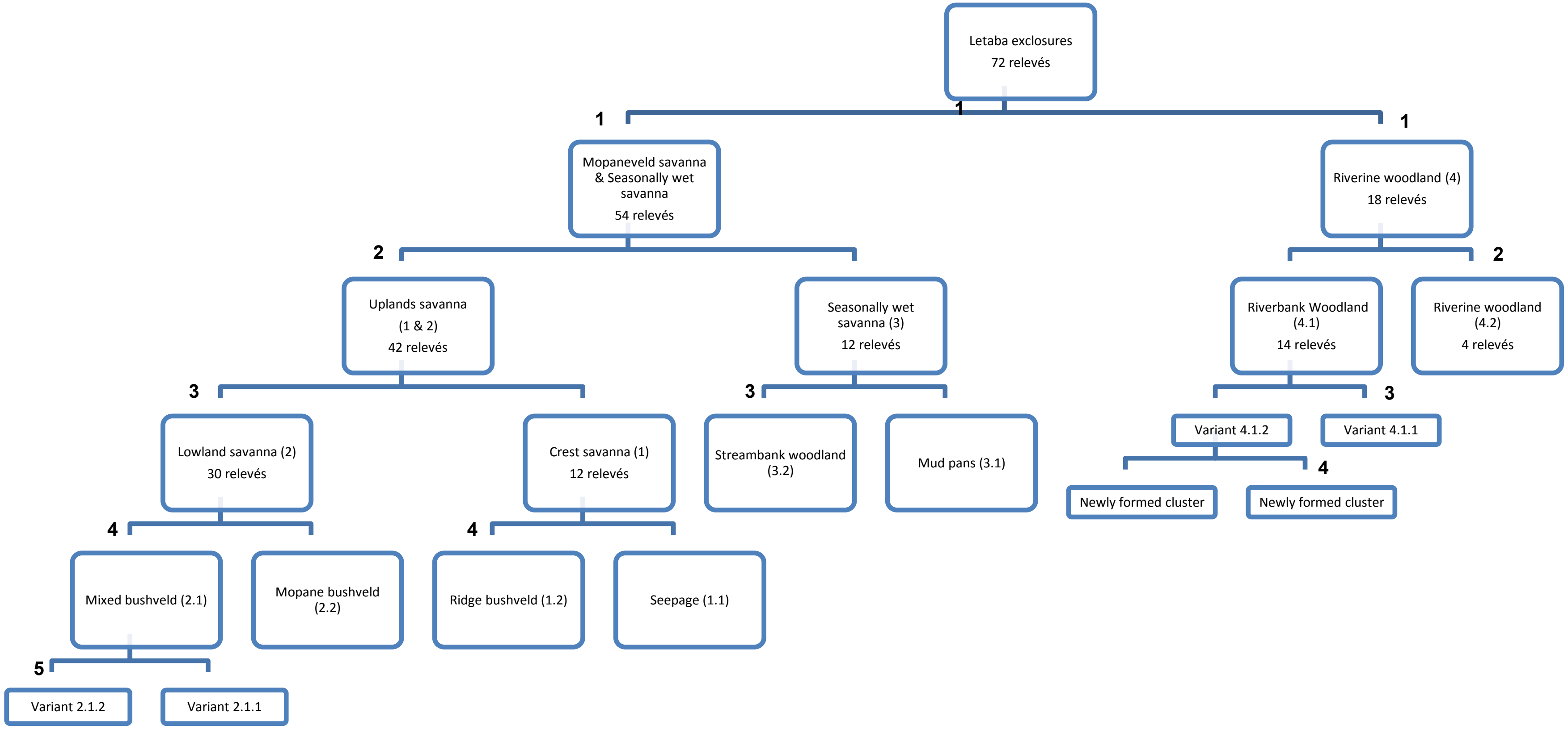


Figure 7-2. Detailed classification hierarchy (i.e. Figure 7.2a explained in more detail) presented through the application of the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) in JUICE 7.0 (Tichý & Holt, 2006). Numbers outside boxes represent levels of division.

7.4.2 Comparison of diagnostic species

Diagnostic species were compared across the eleven pre-identified clusters (i.e. all the clusters of different hierarchy published by Siebert *et al*. (2010)), which present levels lower than the plant community.

Table 7-1. Comparison of relevé assemblages between the two classification algorithm outputs up to the lowest hierarchical level. Differences are indicated as shaded numbers or text.

Community name according to Siebert *et al.* (2010)		**Relevé assemblage under this community for the two respective classifications**	
		Classical TWINSPAN	**Modified TWINSPAN**
1.1	*Xerophyta humilis – Oldenlandia herbacea* seepage	12	12, 31
1.2	*Sclerocarya birrea – Bothriochloa radicans* ridge bushveld	5, 6, 22, 26, 31, 32, 58, 59, 62, 63, 70	5, 6, 22, 26, 32, 58, 59, 62, 63, 70
1.2.1	*Senna italica* variant	5, 6, 32, 59, 63	No subdivision of this cluster resulted from the Modified TWINSPAN
1.2.2	Typical variant	22, 26, 58, 62, 70	No subdivision
2.1	*Melhania rehmannii – Enneapogon scoparius* mixed bushveld	11, 13, 14, 16, 23, 24, 25, 28, 52, 61, 64, 65, 67, 68, 69, 71, 72, 73, 77, 78, 81	11, 13, 14, 16, 23, 24, 25, 28, 52, 61, 64, 65, 67, 68, 69, 71, 72, 73, 77, 78, 81
2.1.1	*Lannea schweinfurthii* variant	11, 14, 16, 52, 64, 65, 68, 69, 72, 73, 77, 81	11, 14, 16, 24, 52, 64, 65, 68, 69, 72, 73, 77, 81
2.1.2	*Aristida canescens* variant	13, 23, 24, 25, 28, 61, 67, 71, 78	13, 23, 25, 28, 61, 67, 71, 78
2.2	*Maerua parvifolia – Agathisanthemum bojeri* mopane bushveld	3, 4, 10, 17, 19, 29, 51, 74, 79	3, 4, 10, 17, 19, 29, 51, 74, 79
3.1	*Eragrostis trichophora – Sporobolus stapfianus* mud pans	7, 18, 33, 34, 35, 36	7, 18, 33, 34, 35, 36
3.2	*Barleria elegans – Acacia karroo* streambank woodland	15, 27, 50, 53, 54, 56	15, 27, 50, 53, 54, 56
4.1	*Philenoptera violacea – Jasminum fluminense* riverbank woodland	1, 2, 8, 9, 20, 21, 30, 38, 40, 46, 47, 48, 49, 83	1, 2, 8, 9, 20, 21, 30, 38, 40, 46, 47, 48, 49, 83
4.1.1	*Hyphaene coriacea* variant	2, 9, 21, 30, 38, 47, 49	2, 9, 21, 30, 38, 47, 49
4.1.2	*Nuxia oppositifolia* variant	1, 8, 20, 40, 46, 48, 83 No subdivision	1, 46, 83 separated from 8, 20, 40, 48
4.2	*Combretum imberbe – Enneapogon cenchroides* open woodland	41, 42, 44, 82	41, 42, 44, 82

Table 7-2 Phytosociological table of the Letaba exclosures derived from classical TWINSPAN classification procesures (Siebert *et al.*, 2010). Diagnostic species identified through statistical measures of fidelity (Phi-coefficient in combination with Fischer‘s exact test) are indicated on the original phytosociological table to indicate differences and resemblances in diagnostic species selection using different measures. Species that are identified as diagnostics through both measures are shaded in light grey, whereas dark grey shaded species are fidelity diagnostics that differ from the published diagnostics. Letters in brackets represent growth form, e.g. (a)=annual, (s)=succulent, (d)=dwarf.

			Crest Savanna												Lowland Savanna																														Seasonally wet Savanna												Riverine Woodland																	
			1												2																														3												4																	
			1.1	1.2											2.1																					2.2									3.1						3.2						4.1														4.2			
				1.2.1					1.2.2						2.1.1												2.1.2																														4.1.1							4.1.2										
242 species			1	2	2	5	6	7			5	6	3	3	1	1	1	5	6	6	6	6	7	7	7	8	1	2	2	2	2	6	6	7	7			1	1	1	2	5	7	7		1	3	3	3	3	1	2	5	5	5	5			2	3	3	4	4			2	4	4	4	8	4	4	4	8
			2	2	6	8	2	0	5	6	9	3	1	2	1	4	6	2	4	5	8	9	2	3	7	1	3	3	4	5	8	1	7	1	8	3	4	0	7	9	9	1	4	9	7	8	3	4	5	6	5	7	0	3	4	6	2	9	1	0	8	7	9	1	8	0	0	6	8	3	1	2	4	2
Species group 1																																																																										
Hemizygia elliottii	Lamiaceae	Herb	1	+	3	3	a	b	+	.	r	.	1	a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tricliceras laceratum	Turneraceae	Annual	+	.	+	+	.	.	.	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acacia exuvialis	Fabaceae	Tree/Shrub	+	1	+	.	+	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 2																																																																										
Xerophyta humilis	Velloziaceae	Herb	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oldenlandia herbacea	Rubiaceae	Annual	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melinis repens	Poaceae	Gram (a)**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 3																																																																										
Tragus berteronianus	Poaceae	Gram (a)	.	.	+	+	.	.	+	+	+	+	+	1	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+
Bothriochloa radicans	Poaceae	Gram	.	.	+	.	+	+	+	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sclerocarya birrea	Anacardiaceae	Tree	.	+	+	+	.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 4																																																																										
Senna italica	Fabaceae	Herb	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Heliotropium ovalifolium	Boraginaceae	Annual	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Boerhavia diffusa*	Nyctaginaceae	Herb	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Corbichonia decumbens	Molluginaceae	Annual	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pterodiscus speciosus	Pedaliaceae	Suffrutex	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 5																																																																										
Schmidtia pappophoroides	Poaceae	Gram	+	.	.	.	+	a	+	+	+	+	.	.	1	+	3	+	a	.	.	.	+	1	.	1	a	3	1	+	+	1	+	+	1	+	a	+	a	4	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crabbea velutina	Acanthaceae	Herb	.	.	.	.	+	.	.	+	.	.	.	+	1	+	+	+	+	+	+	1	+	+	1	+	+	+	+	+	.	+	+	+	+	+	.	+	+	.	.	+	+	.	.	+	.	.	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cissus cornifolia	Vitaceae	Climber (s)	.	.	.	.	.	.	+	+	.	.	.	+	.	.	.	.	+	+	+	+	+	+	.	+	+	+	.	+	.	.	1	+	+	.	.	.	+	+	+	.	.	.	+	.	.	.	+	.	+	+	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hibiscus praeteritus	Malvaceae	Annual	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	+	+	+	.	.	.	.	.	+	.	.	.	+	.	+	1	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ruellia cordata	Acanthaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	+	.	+	+	+	.	+	+	.	+	.	.	.	+	.	.	.	+	+	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Species group 6																																																																										
Melhania rehmannii	Sterculiaceae	Shrub (d)	.	+	.	+	.	.	.	.	+	.	.	+	+	.	+	.	+	.	+	.	+	.	.	.	+	1	+	.	+	.	.	.	+	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aptosimum lineare	Scrophulariacea	Shrub (d)	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+	+	+	.	+	+	.	.	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asparagus setaceus	Asparagaceae	Shrub	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	+	.	+	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Abutilon angulatum	Malvaceae	Shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ocimum filamentosum	Lamiaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dumasia villosa	Fabaceae	Climber	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	+	.	.	+	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coccinia adoensis	Cucurbitaceae	Climber	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 7																																																																										
Vigna luteola	Fabaceae	Climber	.	.	.	.	.	+	+	.	.	.	.	.	+	+	+	+	.	+	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lannea schweinfurthii	Anacardiaceae	Tree	.	.	.	.	.	+	.	.	.	.	.	.	+	.	r	r	.	+	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Indigofera nebrowniana	Fabaceae	Shrub (d)	.	.	.	+	+	+	.	.	+	+	.	.	.	+	.	.	+	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Commiphora africana	Burseraceae	Tree/Shrub	.	.	.	+	.	+	.	.	.	.	.	+	.	+	.	+	.	.	r	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Indigofera cryptantha	Fabaceae	Shrub (d)	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ocimum gratissimum	Lamiaceae	Herb	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 8																																																																										
Rhynchosia totta	Fabaceae	Climber	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aristida canescens	Poaceae	Gram	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cleome monophylla	Cleomaceae	Annual	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+	.	.	+	+	+	.	+	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mariscus sumatrensis	Cyperaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	+	.	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.

Species group 9																																																																										
Acalypha indica	Euphorbiaceae	Annual	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	+	.	.	.	.	1	+	+	+	+	+	+	1	+	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	+	.	+	+	+	.	.	.	+	.	+	.	.	.	+
Heliotropium steudneri	Boraginaceae	Annual	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	1	+	.	+	+	1	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Maerua parvifolia	Capparaceae	Shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	1	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	1	.	.	+	+	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agathisanthemum bojeri	Rubiaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	+	.	+	+	+	1	1	.	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Kohautia virgata	Rubiaceae	Annual	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	1	+	+	.	.	+	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eragrostis rigidior	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+	.	.	.	.	.	.	.	+	.	.	+	+	+	.	.	+	a	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Cyperus obtusiflorus	Cyperaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eragrostis micrantha	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Commelina benghalensis	Commelinaceae	Annual	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Pogonarthria squarrosa	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 10																																																																										
Evolvulus alsinoides	Convolvulaceae	Annual	+	+	.	+	+	.	.	.	+	+	+	.	+	+	+	+	.	.	+	+	+	+	+	+	+	.	+	.	.	+	+	+	.	+	.	+	.	+	+	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Enneapogon scoparius	Poaceae	Gram	.	.	.	+	.	a	.	1	1	+	.	.	+	a	.	+	1	3	1	a	a	b	.	a	.	1	+	+	.	.	+	3	+	.	.	.	+	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Commelina africana	Commelinaceae	Herb	.	.	.	+	.	.	+	+	.	.	.	+	.	m	+	.	+	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	+	+	+	.	.	+	+	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+
Limeum fenestratum	Limeaceae	Annual	.	.	.	.	.	.	+	+	.	.	+	+	.	.	+	.	+	+	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Dicoma tomentosa	Asteraceae	Annual	.	.	.	+	+	+	+	.	.	+	.	.	.	+	.	+	+	.	.	.	.	+	.	+	+	.	.	.	.	.	.	1	1	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
Talinum caffrum	Portulacaceae	Annual	.	+	.	+	+	.	+	.	+	.	.	.	.	.	+	+	.	+	+	.	+	+	.	+	+	.	.	.	.	.	+	.	.	.	.	+	+	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Clerodendrum ternatum	Lamiaceae	Herb	.	.	.	+	+	.	.	+	+	+	.	+	.	+	+	.	+	.	.	.	.	+	+	+	+	+	.	+	.	+	.	+	.	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamaecrista absus	Fabaceae	Annual	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+	+	+	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhigozum zambesiacum	Bignoniaceae	Shrub	.	+	.	+	.	+	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucas glabrata	Lamiaceae	Herb	.	.	.	.	.	.	+	.	.	+	+	.	.	.	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 11																																																																										
Sporobolus fimbriatus	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	1	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Justicia flava	Acanthaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	+	+	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Grewia bicolor	Tiliaceae	Shrub	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hibiscus calyphyllus	Malvaceae	Shrub (d)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilanthes viridis	Pteridaceae	Geophyte	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 12																																																																										
Eragrostis trichophora	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	3	3	3	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxalis species	Oxalidaceae	Geophyte	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	a	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cyperus esculentus	Cyperaceae	Geophyte	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sporobolus stapfianus	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Sporobolus africanus	Poaceae	Gram	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hemizygia bracteosa	Lamiaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urochloa panicoides	Poaceae	Annual	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.
Sesbania bispinosa*	Fabaceae	Shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala sphenoptera	Fabaceae	Annual	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 13																																																																										
Barleria elegans	Acanthaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.
Vigna frutescens	Fabaceae	Climber	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	+	+	+	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Manilkara mochisia	Sapotaceae	Tree	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnosporia buxifolia	Celastraceae	Shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acacia karroo	Fabaceae	Tree	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Cardiospermum corindum	Sapindaceae	Climber	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tricalysia lanceolata	Rubiaceae	Shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euclea divinorum	Ebenaceae	Shrub	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Species group 14																																																																										
Colophospermum mopane	Fabaceae	Tree/Shrub	1	b	1	+	a	b	3	3	1	1	a	1	3	3	b	3	3	3	3	3	3	b	3	a	a	b	3	a	b	1	3	a	b	3	3	3	a	a	a	3	3	a	1	.	1	1	a	1	1	+	1	+	1	1	a	+	.	.	.	.	+	.	.	.	.	.	.	.	1	1	.	+
Terminalia prunioides	Combretaceae	Tree/Shrub	.	+	+	+	+	+	a	1	a	a	+	+	1	1	+	1	+	+	+	+	+	r	a	.	+	.	a	1	1	+	a	1	+	+	+	.	+	.	r	+	+	+	.	.	+	+	.	+	1	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretum apiculatum	Combretaceae	Tree/Shrub	r	+	1	+	1	+	+	.	+	+	1	a	.	.	+	.	+	+	1	1	+	+	+	.	+	+	1	a	+	a	1	.	1	+	.	+	.	.	.	.	.	.	.	.	.	+	.	+	+	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Panicum coloratum	Poaceae	Gram	+	+	+	.	.	.	a	a	+	+	1	a	a	+	+	1	.	.	a	1	+	.	1	.	+	+	a	+	1	.	a	+	a	1	a	+	+	+	1	.	1	+	+	.	+	+	.	.	+	+	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Ocimum americanum	Lamiaceae	Herb	.	+	.	+	+	+	+	+	+	+	.	+	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	.	+	.	+	+	+	+	+	+	.	.	+	1	+	+	+	.	+	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyllanthus maderaspatensis	Phyllanthaceae	Herb	.	+	+	.	+	.	+	+	+	+	+	.	.	.	+	+	.	.	.	.	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Lantana rugosa	Verbenaceae	Herb	.	+	.	.	+	+	+	+	+	+	+	+	1	+	.	+	.	+	+	+	+	+	+	.	+	+	+	.	+	+	.	.	.	.	.	+	.	+	+	+	+	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tephrosia purpurea	Fabaceae	Shrub (d)	+	.	+	.	.	+	+	+	.	.	.	+	+	+	.	.	.	.	+	+	.	+	.	.	.	+	.	+	.	.	.	+	+	.	+	.	.	.	+	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solanum panduriforme	Solanaceae	Herb	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	+	+	+	.	.	.	+	.	.	+	.	.	.	1	.	+	.	1	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Ceratotheca triloba	Pedaliaceae	Annual	+	+	+	+	+	+	+	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	.	+	+	+	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Melhania acuminata	Sterculiaceae	Shrub (d)	.	.	.	.	+	+	+	+	+	+	.	+	+	+	.	+	+	+	+	+	.	+	.	+	+	+	+	.	.	.	+	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyllanthus incurvus	Phyllanthaceae	Herb	.	+	.	+	.	1	+	+	.	.	.	+	+	+	.	.	+	.	.	.	+	.	+	+	+	+	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Dichrostachys cinerea	Fabaceae	Shrub	+	+ . . + +	+ . . . + .	. + . r + . . . + . + +	+ + . . + . + . .	. . + ... + .	+	+ + + + . +	+ + ...	. . . .	. . . .
Pavonia burchellii	Malvaceae	Herb	.	+ . . . +	. + + + + +	+ . + . + . . . + . + .	. . + + . . + + .	+ . . + + . + + .	. + ...	+ . + . + +	. . . + . + +	. . . .	. . . .
Hibiscus micranthus	Malvaceae	Herb	.	+ . + . .	+ + . . + .	+ . . + + + . + + + + +	. + ... + . +	. . + . . + . . .	. . + . + .	. . + + . .	. . . . . . +	. . . .	+ . . .
Acacia nigrescens	Fabaceae	Tree	.	+ + . + .	+ . + . r .	. . + . . + + + + . . .	. . . + ...	. . . .	. . . . . .	+ + + + . .	+ . . + . . .	. . . .	. . . .
Jasminum stenolobum	Oleaceae	Climber	.	+	. . . . . .	+ + . . . + ... + .	. . . . . . + . .	. . + + + . . + +	. + . + . +	. + + . + +	. . . .	. . . .	. . . .
Tragia dioica	Euphorbiaceae	Herb	.	. . . . +	. . . . . .	+ + . . + + + + . + . +	+ . + + + + . . +	. . . . . . + . .	. . + . . .	. . . + . +	. . . + . . .	. . . .	. + . +
Cyperus rupestris	Cyperaceae	Herb	.	. . . . +	+ . + . . .	. . . . +	. . . . + .	. . . . . . + . .	. . . . . .	. . . + + .	. . . .	. . . .	. . . .
Species group 15													
Croton megalobotrys	Euphorbiaceae	Tree	.	. . . . .	. . . . . .	. . . .	. . . .	r . r	. . . . . .	. . . . . .	+ + 1 + a + 1	1 3 1 a + 1 1	+ + + +
Gymnosporia senegalensis	Celastraceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. + + + . .	+ + 1 + + . +	+ + + . 1 a +	. . + +
Panicum deustum	Poaceae	Gram	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . + . . .	. . + . . .	. . + . a b 1	. . . a + . +	+ + . +
Indigofera tinctoria	Fabaceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . a	. . . . . .	. . . . . .	. . + . . . +	+ . . . + . +	. . + +
Species group 16													
Philenoptera violacea	Fabaceae	Tree	.	. . . . .	. . . + . .	. . . . + + . + . . . +	. . . . + ...	. . . .	. . . . . .	+ 1 + + . +	1 . + 1 a a 1	+ 1 + + + + +	. . + 1
Diospyros mespiliformis	Ebenaceae	Tree	.	. r . . .	. . . . . .	. . . .	. . . .	. . . .	+	. + . + + .	+ + + 1 + + +	1 1 . . + . .	. . . .
Combretum microphyllum	Combretaceae	Climber	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	+ . + . + . +	+ + . 1 + + 1	. . . .
Jasminum fluminense	Oleaceae	Climber	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . + . . .	+ . . . . +	+ . + + + . +	+ 1 . + . + .	. . . .
Trichilia emetica	Meliaceae	Tree	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . + . + + .	+ + . . . a .	. . . .
Lippia javanica	Verbenaceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	+ . . . + . .	. + ...	. . . .
Species group 17													
Gardenia volkensii	Rubiaceae	Tree/Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	+ + . . + + +	+ . . . + . .	. . . .
Hyphaene coriacea	Arecaceae	Tree	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	+ + + . . + .	. . . .	. . . .
Euclea natalensis	Ebenaceae	Tree/Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . + + + +	. . . .	. . . .
Thunbergia neglecta	Acanthaceae	Climber	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. + ...	+ . . + . + .	. . . .	. . . .
Sida cordifolia	Malvaceae	Shrub (d)	.	. . . . .	+	. . . + ...	. . . .	. . . .	. + ...	. . . + . .	. + ... +	+	. . . .
Tragia glabrata	Euphorbiaceae	Shrub (d)	.	+	. . . . . .	. . . .	. . . .	. . . .	+ + ...	. . . . . .	+ . . . . + +	+	. . . .
Abutilon austro-africanum	Malvaceae	Shrub (d)	.	. . . . .	. . . . . .	. . . . . . + ...	. . . .	. . . .	. . . . . .	. . . . . .	+ . . . . + .	. . . .	. . . .
Kedrostis africana	Cucurbitaceae	Climber	.	. . . . .	. . . . . +	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. + + ...	. . . .	. . . .
Pupalia lappacea	Amaranthaceae	Annual	.	. . + . .	. . . . . .	. . . .	. . . .	. . . . . . + . .	. . . . . .	. . . + . .	. . . + + . .	. . . . . + .	. . . .
Species group 18													
Cynodon dactylon	Poaceae	Gram	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. + . + . . .	1 a 3 . a 1 3	. . a a
Nuxia oppositifolia	Buddlejaceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . + . .	. . 1 . + . .	3 + + a b + 1	. . . .
Cyperus sexangularis	Cyperaceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . + . .	. . . .	+ + + + . + +	. . . .
Phragmites mauritianus	Poaceae	Gram	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	+ . 1 . . r .	. . . .
Leonotis ocymifolia	Lamiaceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . + . + . +	. . + .
Commelina erecta	Commelinaceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . . . . + . .	. . . . . .	. + . . . +	. . . . . . +	. . . . + + +	. . . .
Vernonia glabra	Asteraceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . . + + . .	. . . .
Cleome angustifolia	Cleomaceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	+ . + ...	. . . .
Cynoglossum lanceolatum	Boraginaceae	Herb	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . . . + . +	. . . .
Urochloa oligotricha	Poaceae	Gram	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	+ . . . b . +	. . . .
Diospyros lycioides	Ebenaceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . . . . +	r . . . . . +	. . . .
Species group 19													
Enneapogon cenchroides	Poaceae	Gram	.	+ . . + .	. . . . + .	. . . .	. . . . 1	. . . .	1 . . . + .	. . . . . .	. . . .	. . . .	a 3 . +
Combretum imberbe	Combretaceae	Tree	.	. . . . .	. . . . . .	. . . . + . . .	. . . .	. . . .	. . . . . .	. . . . . .	. 1 + ...	. . . + . . .	+ 1 1 1
Ledebouria revoluta	Hyacinthaceae	Geophyte	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . . .	+ 1 + .
Ornithogalum setosum	Hyacinthaceae	Geophyte	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . . .	. + + .
Pechuel-Loeschea leubnitziae	Asteraceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	. . . . . .	. . . .	. . . .	+ . . .
Species group 20													
Phyllanthus reticulatus	Phyllanthaceae	Shrub	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	+ . + + + +	. . . + . + +	1 . . . + + .	. + . .
Combretum mossambicense	Combretaceae	Climber	.	. . . . .	. . . . . .	. . . . + .	. . . .	. . . . r .	. . . . . .	. . 1 . + .	+ + . + . . .	+ . . + . + .	+ + . .
Cassia abbreviata	Fabaceae	Tree	.	. . . . .	+	. + . + + . . . + . + .	. . + . + ...	. . . . . + . . .	. . . . . .	+ . + . . +	+ + + + . + .	. . . . . + .	. + + .
Cocculus hirsutus	Menispermacea	Climber	.	. . . . .	. . . . . .	+	. . . .	. . . .	. . . . . .	+ + . + + .	. . . + + . .	. . + . . . +	. . + .
Momordica foetida	Cucurbitaceae	Climber	.	. . . . .	. . . . . .	. . . .	. . . .	. . . .	. . . . . .	+ + ...	. . . . . + .	. . + + . . .	. . . .
Species group 21													
Panicum maximum	Poaceae	Gram	.	+ + + + .	. + ...	+ . 1 . . + 1 1 . + . .	+ + + + + 1 . + +	. + 3 + + . a . .	1 3 a a . a	1 1 + 1 a a	1 3 4 + a + 1	1 a a 3 . 1 +	. . + +
Waltheria indica	Sterculiaceae	Annual	.	+ . a + +	+ . + + + +	+ . + + + + + + + + . +	+ + . . . + + + +	. + . + + + + + .	+ . . . + +	. + . + . .	. + . . . + +	+ . . . + . .	+ + + .
Eragrostis superba	Poaceae	Gram	.	+ . + . +	. . + + . .	+ . + ... +	+ + . + . + + + +	+ 1 + . 1 . + + 1	+ + . 1 + +	1 + + . . +	+ + ... +	+ + + ...	. . . .
Kyllinga alba	Cyperaceae	Herb	.	+ . . + .	+ + + + + +	+ . + a + . + 1 + + . .	+ + + . + . . + +	+ + + + + + . + .	. . + . . .	. + ...	+	. . . .	+ + + .
Melhania forbesii	Sterculiaceae	Shrub (d)	.	+ . + + .	+	. + . + . . + + + . . +	. . . . . . + + .	+ . + + 1 + 1 + +	. . 1 . . .	. . . . . .	+ + . + . . +	+ . . . . + .	+ + . .
Urochloa mosambicensis	Poaceae	Gram	.	. . + . .	. . . . . .	. . . + ...	+ + . . + + + + +	. . . + ...	. . . . . .	. . . . . .	. . + . . + .	. . . .	+ + + 3
Flueggea virosa	Phyllanthaceae	Shrub	.	. . . . .	. . . . + .	. + . + . . + + . . . +	. . . .	. + + + . + + + .	. . + + . +	. + . + . .	. . . . + . .	+ + 1 + . + .	. + . .
Commelina eckloniana	Commelinaceae	Herb	.	. . . . .	+ . + + . .	. . . . + . . .	+ . . . . . + . +	. . + + ...	. . . . . .	. . + . . .	+	. . . .	. . + +
Combretum hereroense	Combretaceae	Shrub/Tree	.	+	. . . . . .	a + . + . . + + . + + .	. . + . . + . . .	+	. . . . . .	. a . 1 + .	1 1 . + . + .	. . . .	+ . + 1
Solanum lichtensteinii	Solanaceae	Shrub (d)	.	. . . . .	. . + . . +	+ . . . . . + + ...	+ + ... + . .	. . . .	+ + ...	. . . . . .	+	. . . .	+ . . +

Considering the comparison between the published diagnostic species (Table 7-2) and diagnostic species identified through more objective statistical fidelity measures, results revealed some resemblance in diagnostic species identification (Table 7-2). It is, however also evident that in some diagnostic species groups, not a single species is measured as diagnostic when fidelity measures are applied (e.g. species group 4, Table 7-2). To quantify the differences between diagnostic species identification, a summary of the number of overlapping diagnostic species, ‗new' diagnostics revealed from fidelity measures, and the number of published diagnostics ‗lost' after statistical fidelity measures are summarized in Table 7-3. Siebert *et al.* (2010) identified 86 diagnostic species in the 11 vegetation clusters, which presents vegetation descriptions from the plant community up to the variant level. Of these published diagnostic species, only 30 species are considered diagnostic species after the application of statistical fidelity measures (Table 7-3). Fifteen ‗new' diagnostic species were identified, which were not considered as diagnostic species through the classical approach of identifying diagnostics, whereas a total of 56 published diagnostic species are not typically diagnostic to a particular cluster after statistical measures of fidelity were applied (Table 7-3).

The absence of fidelity diagnostics from the two variants of the *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld sub-community strengthens the results obtained from the Modified TWINSPAN classification, which revealed no sub-division of this sub-community (Figure 7-2b). The published vegetation units in which there is a considerable overlap in classical identified diagnostics and statistically measured diagnostics include the *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld sub-community (community 1.2, Siebert *et al*. (2010), the *Aristida canescens* variant (community 2.1.2) of the *Melhania rehmannii – Enneapogon scoparius* mixed bushveld and the *Eragrostis trichophora – Sporobolus stapfianus* mud pans (community 3.1) (Table 7-3). Certain vegetation units have been named after diagnostic species that are not considered as diagnostics after the application of fidelity measures. They include the *Xerophyta humilis – Oldenlandia herbacea* seepage (community 1.1), the *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld (community 1.2), in which *Sclerocarya birrea* lost its diagnostic value (species group 3, Table 7-2), the *Melhania rehmannii – Enneapogon scoparius* mixed bushveld (community 2.1) and its *Lannea schweinfurthii* variant (community 2.1.1), which lost *Lannea schweinfurthii* as a diagnostic species (species group 7, Table 7-2), the *Philenoptera violacea – Jasminum fluminense* riverbank woodland (community 4.1), of which *Philenoptera violacea* are not considered a diagnostic species (species group 16, Table 7-2), and the *Combretum imberbe – Enneapogon cenchroides* open woodland (community 4.2), of which *Enneapogon* *cenchroides* lost its diagnostic value after the application of statistical fidelity measures (species group 19, Table 7-2).

Some fidelity diagnostic species were listed in the published phytosociological table (Table 7-2) under species groups that contain species that are considered ‗general' species. Such species include *Schmidtia pappophoroides* (species group 5, Table 7-2), a diagnostic species of the *Aristida canescens* variant (community 2.1.2) of the *Melhania rehmannii – Enneapogon scoparius* mixed bushveld sub-community. Others include *Crabbea velutina* (species group 5), *Evolvulus alsinoides* and *Enneapogon scoparius* (species group 10), which are all fidelity diagnostic species of the *Lannea schweinfurthii* variant (community 2.1.1) of the latter sub-community.

7.5 Discussion

Although the selection of classification algorithms was shown to be important for both intermediate and large-scale syntheses of vegetation data, a resemblance in classification results is evident when the two classification algorithm outputs are being compared in a local-scale vegetation classification. Contrary to the results obtained from larger scale vegetation syntheses (see Chapters 5 and 6), results from this local-scale classification comparison could not confirm that the classical TWINSPAN algorithm is unreliable and should be avoided in local-scale vegetation descriptions. Despite the difference in classification hierarchy, all communities, sub-communities and even variants could be identified in similar relevé groups.

There is, however, little overlap in diagnostic species between the classical approach of identifying diagnostics and the more objective approach in which statistical measures are being used to calculate the fidelity of a species to a specific cluster. The exclusive use of statistical measures of fidelity to identify diagnostic species for a local-scale classification should however be considered attentively due to lower accuracy of these measures at a finer scale (Chytrý *et al.*, 2002).

Table 7-3. Quantitative comparison between fidelity diagnostics and diagnostics published in Siebert *et al.* (2010), which were based on a more subjective identification of diagnostic species.

	Number of diagnostics					
Community name in Siebert *et al.* (2010)	**In Siebert *et al.* (2010)**	**Fidelity**	**Matching diagnostics**	**% Match**	**No of fidelity diagnostics outside published group**	**No of diagnostics that lost diagnostic value after fidelity measures**
1.1 *Xerophyta humilis – Oldenlandia herbacea* seepage	3	0	0	0	0	3
1.2 *Sclerocarya birrea – Bothriochloa radicans* ridge bushveld	3	5	2	67	3	1
1.2.1 *Senna italica* variant	No diagnostic spp group	0	-	-	-	-
1.2.2 Typical variant	5	0	0	0	0	5
2.1 *Melhania rehmannii – Enneapogon scoparius* mixed bushveld	7	0	0	0	0	7
2.1.1 *Lannea schweinfurthii* variant	6	6	2	33	4	4
2.1.2 *Aristida canescens* variant	4	4	3	67	1	1
2.2 *Maerua parvifolia – Agathisanthemum bojeri* mopane bushveld	10	7	5	50	2	5
3.1 *Eragrostis trichophora – Sporobolus stapfianus* mud pans	9	6	6	67	0	3
3.2 *Barleria elegans – Acacia karroo* streambank woodland	8	2	2	25	0	6
4.1 *Philenoptera violacea – Jasminum fluminense* riverbank woodland	6	2	0	0	2	6
4.1.1 *Hyphaene coriacea* variant	9	5	3	60	2	6
4.1.2 *Nuxia oppositifolia* variant	11	6	5	45	1	6
4.2 *Combretum imberbe – Enneapogon cenchroides* open woodland	5	2	2	40	0	3
Overall	**86**	**45**	**30**	**35**	**15**	**56**

7.6 References

BROWN, L.R., MARAIS, H., HENZI, S.P. & BARRET, L. Vegetation classification as the basis for baboon management in the Bourke‘s Luck Section of the Blyde Canyon Nature Reserve, Mpumalanga. *Koedoe*, 48(2):71–92.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13:79–90.

CLEAVER, G., BROWN, L.R. & BREDENKAMP, G.J. 2005. The phytosociology of the Vermaaks, Marnevicks and Buffelsklip valleys of the Kammanassie Nature Reserve, Western Cape. *Koedoe*, 48(1):1–16.

COWLING, R.M., GIBBS-RUSSELL, G.E., HOFFMAN, M.T. & HILTON-TAYLOR, C. 1989. Patterns of plant species diversity in southern Africa. (*In* Huntley, B.J. *ed*., Biotic diversity in southern Africa: Concepts and conservation. Oxford University Press: Cape Town. p. 19–50).

DAEMANE, M.E., CILLIERS, S.S & BEZUIDENHOUT, H. 2012. Classification and description of the vegetation in the Spitskop area in the proposed Highveld National Park, North West Province, South Africa. *Koedoe*, 54(1): Art. #1020, 7 pages. http://dx.doi.org/10.4102/koedoe. Date of access: February 2012.

ECKHARDT, H.C., VAN ROOYEN, N. & BREDENKAMP, G. 1997. Plant communities of the forests, woodlands and thickets in northern KwaZulu-Natal. *Koedoe*, 40:91–112.

GÖTZE, A.R., CILLIERS, S.S. & KELLNER, K. 2003. Analysis of the riparian vegetation (Ia land type) of the proposed Vhembe-Dongola National Park, Limpopo Province, South Africa. *Koedoe*, 46(2):45–64.

HENNEKENS, S.M. 1996. MEGATAB: A visual editor for phytosociological tables. User's guide version October 1996. IBN-DLO: Wageningen, Lancaster University, Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HILL, M.O. 1979. TWINSPAN – a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology & Systematics, Cornell University: Ithaca, NY.

KENT, M. 2012. Phytosociology and the Zurich-Montpellier (Braun-Blanquet) school of subjective classification. (*In* Kent, M., *ed*. Vegetation description and analysis: a practical approach, 2nd edn, John Wiley & Sons: England. p 245–275).

MORGENTHAL, T.L. & CILLIERS, S.S. 1999. Vegetation analysis of Pedlar‘s Bush, Mpumalanga, and its conservation. *South African Journal of Botany*, 65:270–280.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

O‘KEEFE, T. & ALARD, G. 2002. Effects of herbivores and fire on riparian and upland savanna ecosystems. Field Operations Manual for Herbivore & Fire Exclosures on the Sabie and Letaba Rivers in the Kruger National Park. Unpublished report, SANParks.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

RUTHERFORD, M.C., MUCINA, M.C. & POWRIE, L.W. 2012. The South African National Vegetation Database: History, development, applications, problems and future. South African Journal of Science, 108(1/2) Art.#629, 8 pages, DOI.org/10.4102/sajs.v108i1/2.629. Date of access: February 2012.

SIEBERT, F. ECKHARDT, H.C. AND SIEBERT, S.J. 2010. The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa. *Koedoe*, 52(1): Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777. Date of access: November 2010.

TICHÝ, L. & HOLT, J. 2006. JUICE. Program for management, analysis and classification of ecological data. Program manual. Vegetation Science Group, Masaryk University, Brno.

CHAPTER 8

A SYNTHESIS OF RIPARIAN ZONE VEGETATION IN THE MOPANE BIOREGION OF SOUTH AFRICA

8.1 Introduction and background

Riparian vegetation plays a critical role in the health of riparian ecosystems due to its importance to maintain good water quality and provide habitat for many species. Riparian systems are transition zones between land and water ecosystems and, although linked in organized networks across landscapes, they are often described as a mosaic of landforms, communities and environments within the larger landscape (Naiman & Décamps, 1997; Nilsson & Svedmark, 2002). They provide important ecosystem services (Kauffman *et al.*, 1997; Tickner *et al.*, 2001; Meek *et al.*, 2010) and therefore serve as a framework for understanding diversity and dynamics of communities associated with these complex habitats. The ecological health of riparian ecosystems is often linked to plant diversity and evenness (Bowers & Boutin, 2008).

Delineation of riparian zones is challenging, especially in heterogeneous landscapes, such as the South African savannas (Kröger *et al.*, 2009). Riparian zones are however, not limited to the densely vegetated fringes along macro-channels, since the prominent lateral-vertical gradients of riparian systems (Van Coller *et al.*, 1997) are responsible for changes and rapid turnover of vegetation composition and hence, diversity.

Riparian plant communities are typically assembled by plant species that are well adapted to disturbances in combination of less-specialized and less frequently disturbed plant species (Naiman *et al.*, 1998). Riparian corridors therefore have complex plant distributions, which influence plant species diversity patterns at both local and regional scales and further reflect both anthropogenic and natural disturbances (Ward, 1998). Vegetation classification of riparian zones is often a secondary output for terrestrial phytosociological studies. These descriptions are however valuable to end-users and are often referred to in riparian monitoring and catchment management projects (e.g. Everson *et al.*, 2000; State of the Rivers report, 2001; O‘Keefe & Rogers, 2003).

Azonal vegetation, including vegetation along riparian zones, has long been an orphan of vegetation research and mapping in South Africa due to its complexity and its limited extent (Mucina & Rutherford, 2006). The critical assessment of classical approaches of vegetation classification against more recent approaches at various spatial scales revealed that the Modified TWINSPAN along with statistical measures of species fidelity present a more rigorous vegetation synthesis at an intermediate scale (Chapter 6). The riparian zone in the Mopane Bioregion of South Africa (Mucina & Rutherford, 2006) stretches across large, hydrological delineated areas within the Mopaneveld of South Africa, covering approximately 10 % of the Mopaneveld in South Africa. A meta-analysis of the riparian zone vegetation in the Mopane Bioregion is therefore suggested to present a vegetation synthesis at an intermediate-scale.

The Mopaneveld in southern Africa is drained by several large rivers, such as the Limpopo (Botswana, South Africa, Zimbabwe & Mozambique), Zambezi (Botswana, Zimbabwe, Zambia & Mozambique), Save (Zimbabwe), Chobe (Botswana), Okavango (Botswana), Cunene (Namibia & Angola), Shire (Malawi) and Luangwa (Zambia & Malawi) (Werger & Coetzee, 1978; Cole 1986; Mapaure 1994). In South Africa, vegetation dominated by *Colophospermum mopane* is associated with heavier-textured soil on the wide, flat valley bottoms of the Limpopo River valley. Other rivers of smaller magnitude that drain the area (from North to South), include the Levhuvhu (synonyms: Levubu, Levuvhu), Letaba and the Olifants. These perennial rivers are furthermore supported by non-perennial rivers and streams of which the Shingwedzi, Tsendze, Manyeleti and Timbavati is better-known in the South African Lowveld, especially to regular tourists (Figure 8-1).

Vegetation classification studies on riparian zones of rivers draining the Mopane Bioregion include, amongst those listed in Table 8-1, the series of unpublished reports by Bredenkamp and Van Rooyen as part of the Kruger National Park Rivers Research Program (i.e. reports on the Letaba, Bredenkamp & Van Rooyen, 1993a; Levhuvhu, Bredenkamp & Van Rooyen, 1993b; Olifants, Bredenkamp & Van Rooyen, 1993c).

In the phytosociological synthesis of Mopaneveld, Du Plessis (2001) delineated terrestrial Mopaneveld by continuously applying the classical TWINSPAN algorithm (Hill, 1979) at a single level of division to the complete Mopaneveld relevé dataset. The azonal relevés were separated from the terrestrial relevés through this procedure and stored for further analysis (Du Plessis 2001). Even after this procedure, analyses of the entire Mopaneveld dataset revealed a riparian zone vegetation type, namely the *Croton megalobotrys* – *Colophospermum mopane* (Siebert *et al.*, 2003). This chapter will present an analysis of some of the originally 264 omitted azonal relevés in combination with the relevés from the *Croton megalobotrys* – *Colophospermum mopane* vegetation type and other data sets that were not included in the synthesis by Du Plessis (2001) (See Table 8-1). It will present the first synthesis of riparian vegetation in the Mopane Bioregion of South Africa. This synthesis is aimed at providing insight into the broad vegetation types of riparian zones along the Limpopo, Luvuvhu, Letaba and Olifants rivers and their tributaries.

Since rivers serve as ecological corridors in heterogeneous landscapes (Naiman & Décamps, 1997), it is expected that riparian plant communities along rivers flowing through Mopaneveld are similar to those further south, outside the distribution range of *Colophospermum mopane* or Mopaneveld. The descriptions of the riparian zone vegetation in the Mopane Bioregion will therefore be placed in context to described plant communities outside the distribution range of Mopaneveld, but within the Lowveld Savanna of South Africa.

Please note that this chapter is presented in more detail than the previous chapters in terms of the methodological approach and descriptions of plant communities since the research presented here is original and is not concerned with comparisons of previously identified vegetation units, as in Chapters 5–7.

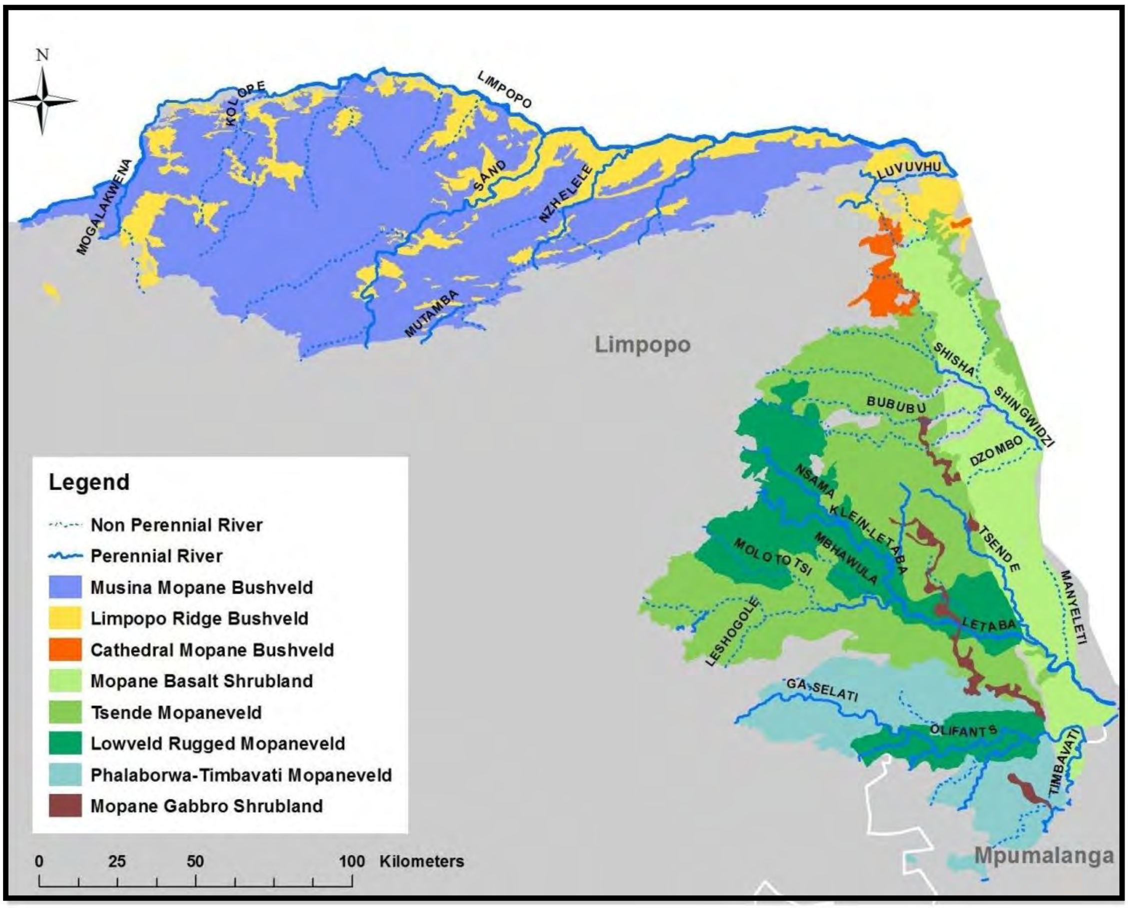


Figure 8-1 Major rivers and smaller tributaries draining the Mopane Bioregion (Mucina & Rutherford, 2006) vegetation types in South Africa.

Table 8-1 A summary of studies undertaken along the major rivers draining Mopaneveld in South Africa. (KNPRRP = Kruger National Park Rivers Research Program)

River	Authors	Year	Journal	Title	Major findings
Limpopo	Straub, AF**Ø	2002	Unpublished MSc dissertation, University of Pretoria	The vegetation of Breslau Game Farm, Northern Province, South Africa Available from: http://upetd.up.ac.za/thesis/available/etd-10102007-154857/	Two distinct plant communities identified and described, of which one presents the alluvial floodplains of the Limpopo River, the *Salvadora australis – Acacia tortilis* Woodland community.
Limpopo	Gotze, AR, Cilliers, SS, Bezuidenhout, H & Kellner K**Ø	2003	*Koedoe* **46**(2)	Analysis of the riparian vegetation (Ia land type) of the proposed Vhembe-Dongola National Park, Limpopo Province, South Africa	Four plant communities identified and described of which all represent riparian vegetation.
Limpopo	O'Connor	2010	*Austral Ecology* (2010) **35**, 778–786	Transformation of riparian forest to woodland in Mapungubwe National Park, South Africa, between 1990 and 2007	Riparian forest along the Limpopo River was degraded to Woodland as a result of (1) drought stress, (2) drought in combination of creeper infestation, and (3) flooding
Limpopo	Els	2010	Unpublished MSc dissertation, North-West University	The implementation of selected technologies to enhance the restoration of indigenous tree species in the deforested riparian areas in the Mapungubwe National Park, South Africa Availablle from: http://dspace.nwu.ac.za/handle/10394/4571	Extensive forest degradation along the Limpopo and Shashe Rivers prompted the revegetation of indigenous trees in these areas of the Mapungubwe National Park. The successful establishment of tree seedlings is presented with a wide range of constraints and limiting conditions.
Limpopo	Stalmans, M, Gertenbach, WPD & Carvalho-Serfontein, F	2004	*Koedoe* **47**(2)	Plant communities and landscapes of the Parque Nacional do Limpopo, Moçambique	Fifteen distinct plant communities identified and described, of which the *Acacia tortilis – Salvadora persica* Short Woodland, the *Acacia xanthophloea – Phragmites* spp Woodland, and the *Acacia xanthophloea – Faidherbia albida* Tall Forest have relevance to this study.
Limpopo tributaries	Dekker, B & Van Rooyen, N**	1995	*S. Afr. J. Bot.* **61**(3): 158–167	The physical environment and plant communities of the Messina Experimental Farm	Eight plant communities, one divided into three variations, are discussed. The *Hyphaene coriacea – Eragrostis rotifer* short sparse woodland and the *Monechma divaricatum – Colophospermum mopane* low forest present the riparian zone vegetation.
Limpopo & tributaries	Gertenbach, WPD**	1983	*Koedoe* **26**: 9–121	Landscapes of the Kruger National Park	Thirty-five landscapes are described, of which *Colophospermum mopane* is abundant in fifteen landscapes and one is not dominated by *C. mopane*, but forms a riparian zone within Mopaneveld. The vegetation data of the bottomlands and riparian zones of all these landscapes are included in this synthesis.

Levuvhu & tributaries	Van Rooyen, N, Theron, G.K. & Grobbelaar, N.**	1981	*Jl S. Afr. Bot*. 7(2): 213–246	A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 1. The Higrophilous communities.	The plant communities of the riparian zones as well as seasonal streams and pans are described.
Levuvhu	Bredenkamp, GJ and Van Rooyen, N**$^{\O}$	1993	Unpublished report to the KNPRRP	A survey of the vegetation of the Levuvhu River in the Kruger National Park	Twelve distinct plant communities were identified and described under three major types. All of which are regarded as vegetation of the riparian zone.
Letaba & tributaries	Gertenbach, WPD**	1983	*Koedoe* **26**: 9–121	Landscapes of the Kruger National Park	Thirty-five landscapes are described, of which *Colophospermum mopane* is abundant in fifteen landscapes and one is not dominated by *C. mopane*, but forms a riparian zone within Mopaneveld. The vegetation data of the bottomlands and riparian zones of all these landscapes are included in this synthesis.
Letaba	Bredenkamp, GJ and Van Rooyen, N**$^{\O}$	1993	Unpublished report to the KNPRRP	A survey of the vegetation of the Letaba River in the Kruger National Park	Thirteen distinct plant communities were identified and described under four major types. All of which are regarded as vegetation of the riparian zone.
Olifants	Bredenkamp and Van Rooyen***$^{\O}$	1993	Unpublished report to the KNPRRP	A survey of the vegetation of the Olifants River in the Kruger National Park	Eight distinct plant communities were identified and described under five major communities. All of which are regarded as vegetation of the riparian zone.
Olifants	Myburgh, WJ	1999	Unpublished report to WRC	Oewerplantegroei van die Olifantsriviersisteem – ‗n ekologiese perspektief	Nine major plant communities identified and described of which only the *Ficus sycomorus – Abutilon angulatum* var. *angulatum* Treeveld has relevance to this study.
Olifants & tributaries	Gertenbach, WPD**	1983	*Koedoe* **26**: 9–121	Landscapes of the Kruger National Park	Thirty-five landscapes are described, of which *Colophospermum mopane* is abundant in fifteen landscapes and one is not dominated by *C. mopane*, but forms a riparian zone within Mopaneveld. The vegetation data of the bottomlands and riparian zones of all these landscapes are included in this synthesis.

**Floristic data were obtained from this data set to compile a synthesis of the Mopaneveld riparian vegetation as presented in this chapter.

**$^{\O}$ Floristic data sets that were not included in the Du Plessis (2001) synthesis.

8.2 Objectives

The objectives of this chapter are consistent with the secondary objective of this thesis, i.e. to present a phytosociological synthesis of riparian vegetation in the Mopane Bioregion (Mucina & Rutherford, 2006) of South Africa.

More specific objectives that are being targated in this chapter are to present a phytosociological synthesis of the vegetation along major rivers and tributaries draining the Mopaneveld in South Africa following the modern approach in combination with further options in JUICE (Tichý & Holt, 2006) to strengthen the classification results.

8.3 Methods

8.3.1 Delineation of riparian relevés

For the purpose of this study, data exclusively from the South African Mopaneveld (i.e. the Mopane Bioregion, Mucina & Rutherford, 2006) was used to compile a synthesis. Data used in this synthesis is indicated in the summary table (Table 8-1). A total of 1191 relevés, of which 835 relevés were not included in the synthesis by Siebert *et al.* (2003) were exported from the floristic database program TURBOVEG (Hennekens & Schaminée, 2001) to JUICE 7.0 (Tichý & Holt, 2006) in which analyses of the vegetation were undertaken. The first step in the classification procedure was to identify relevés that represent riparian zones for consideration in analyses. For this purpose, the data were applied to the classic TWINSPAN algorithm (Hill, 1979) at 2 levels of division, which separated the data into four clusters presenting the following habitat zones:

1. Riverbed (93 relevés)
2. Riverbank (256 relevés)
3. Terrestrial uplands savanna (633 relevés)
4. Floodplains (209 relevés)

Clusters 1, 2 and 4 were considered to present riparian vegetation. Cluster 3, i.e. the terrestrial uplands savanna cluster contains the largest number of relevés (633 relevés), which could possibly include non-riparian savanna relevés. These were identified and omitted from the data set. The criteria used to identify ‗riparian‘ relevés from these 633 relevés were based on the presence of diagnostic riparian species. The list of diagnostic species (Table 8-2) was compiled using relevant literature on the descriptions of riparian vegetation (e.g. Gertenbach, 1983; Bredenkamp & Van Rooyen, 1993a,b,c; Straub, 2002; Götze *et al.*, 2003; Siebert *et al.*, 2010). At least two of these species need to be present in a relevé to be considered as a relevé representing a riparian zone. Since riparian zones are disturbance-mediated ecosystems (Naiman & Décamps, 1997; Meek *et* *al.*, 2010), it is expected that disturbance-associated species would commonly be presented as diagnostics for riparian zones. Such species are pointed out in Table 8-2. To prevent the selection of relevés according to species that are only present in a certain area due to disturbance, the following parameters for selection of relevés were set: only relevés which included more than one of the non-disturbance diagnostic species listed in Table 8-2, in an abundance of 1– 5% of the sampling plot (Braun-Blanquet abundance score of 1 or more), were considered as ‗riparian' relevés. Relevés containing only disturbance-species were considered only when the sampling origin of the relevé could be confirmed as riparian. Relevés failing to the above criteria were omitted from the data set prior to further analyses.

Table 8-2 Species that are considered diagnostic of riparian zones according to the descriptions by Gertenbach, 1983; Bredenkamp & Van Rooyen, 1993a,b,c; Straub, 2002; Götze *et al.*, 2003; Siebert *et al.*, 2010. Species marked with an asterisk (*) present disturbance-associated species.

Trees and shrubs	**Graminoids**	**Forbs**
Acacia schweinfurthii	*Cynodon dactylon**	*Centella coriacea*
Berchemia discolor	*Dactyloctenium aegyptium**	*Cissampelos mucronata*
Breonadia salicina	*Echinochloa colona*	*Cyperus esculentus**
Capparis tomentosa	*Phragmites mauritianus*	*Cyperus sexangularis**
Croton megalobotrys	*Phragmites australis*	*Jasminum fluminense*
Ficus capreifolia	*Sporobolus africanus**	All *Ludwigia* spp.
Ficus sycomorus		All *Persicaria* spp.
Flueggea virosa		
Kraussia floribunda		
Nuxia oppositifolia		
Phoenix reclinata		
Phyllanthus reticulatus		
Xanthocercis zambesiaca		

8.3.2 Classification of major vegetation groups

A final total of 735 relevés were imported in JUICE (Tichý & Holt, 2006) for analysis through classical phytosociological procedures. For the purpose of identifying the major types of riparian vegetation in the Mopaneveld, the Modified TWINSPAN (Roleček *et al.*, 2009) function in JUICE 7.0 (Tichý & Holt, 2006) was applied to the dataset at the following classification parameters:

Pseudospecies cutlevels: 3 (0-5-25)
Minimum group size: 2
No of clusters: 4
Similarity index: Jaccard

8.3.3 Classification of all riparian plant communities

For the purpose of presenting a clean, hierarchical classification of all riparian plant communities, the Modified Twinspan (Roleček *et al.*, 2009) algorithm in JUICE 7.0 (Tichý & Holt, 2006) was performed to deliver 6 clusters for a finer differentiation of the plant communities along major rivers in the Mopane Bioregion. Due to the distinctly different character of the Azonal vegetation and the Savanna-riparian interface groups (Figure 8-2), the naming of the plant communities and identification of diagnostic species are handled in two separate two-way tables (Appendices 8-1 & 8-2). To determine the hierarchical level of each cluster, similarity indices were calculated between each cluster in JUICE 7.0 (Tichý & Holt, 2006). Jaccard and Sørensen similarity indices were calculated using square root data transformation in combination with the application of all available distances between each vegetation cluster. Similarity index values are presented with the hierarchical dendrogram in Figure 8-2.

To identify diagnostic species for each of the plant communities in the azonal vegetation group, and in the savanna-riparian interface respectively, statistical measures of fidelity were applied to the data and are presented in two separate two-way synoptic percentage fidelity tables (Appendices 8-1 & 8-2). Fischer‘s exact test was applied along with the Phi-coefficient fidelity measure to calculate the true probability of obtaining the observed number of occurrences of the species in the vegetation unit under the null hypothesis of independence (Tichý & Holt, 2006). For the purpose of applying Fischer‘s exact test in combination with the Phi-coefficient fidelity measure, p was selected at <0.001 to be able to identify ‗true diagnostics‘. Only species with a fidelity measure greater than 30 (p = <0.001) are considered true diagnostics. Through the application of fidelity in combination of Fischer‘s exact test, diagnostic species have negative correlations with clusters in which they are not diagnostic, which limits subjectivity in the identification of diagnostic species.

Classical table arrangement procedures (e.g. in Van Rooyen *et al.*, 1981; Bredenkamp & Van Rooyen, 1991; Götze *et al.*, 2003; Siebert *et al.*, 2010) were followed to present the results of the classification in an orderly system. These two-way fidelity tables (Appendices 8-1 & 8-2) are used to assist with the naming and description of plant communities. To limit the presentation of all these tables in the text, a summary table is presented at the description of each plant community (Tables 8-5 to 8-10).

8.3.4 Naming of plant communities

Identification of plant communities at different hierarchical levels remains a subjective classification system. In South Africa, no formal guidelines exist for the naming of plant communities, although the general consensus is that communities, sub-communities and variants should be classified according to species that are confined to each hierarchical level. The Modified TWINSPAN algorithm proposed by Roleček *et al.* (2009), attempts to address the problem of subjective hierarchy in plant community classification. For the purpose of classifying a vegetation cluster as a plant community, sub-community, or variant, a more objective approach was tested in which the Modified TWINSPAN algorithm was applied in combination with dissimilarity indices to assign each ‗cluster‘ to a certain hierarchical level. Jaccard and Sørensen dissimilarity indices were applied to the data set in JUICE 7.0 (Tichý & Holt, 2006). Clusters with highest dissimilarity values are considered as plant communities, followed by lower values for sub-communities, and lowest dissimilarity between variants. Results obtained from the indices are presented in boxes between different vegetation clusters in Figure 8-2.

To conform to the International Code of Phytosociological Nomenclature (Weber *et al.*, 2000), the use of species that are not truly characteristic to a vegetation cluster, were avoided. Diagnostic, constant and dominant species were identified through various statistical measures, which were applied in JUICE 7.0. The lower threshold values for diagnostic, constant and dominant species were set to 30, 40 and 50 respectively under the function *‗Analysis of Columns of Synoptic Tables’* in JUICE 7.0 (Tichý & Holt, 2006). Subsequently, plant communities were named by consistently using a dominant species (if any), followed by a diagnostic species and a constant species. Definitions of diagnostic, constant and dominant species, as being used in this chapter, follow below.

Diagnostic species:

The identification of diagnostic species is based on the presence or absence of species within a cluster relative to the other clusters. The Phi-coefficient value is a measure of the uniqueness of a species to a cluster, i.e. the strength of its fidelity. Therefore, the higher the fidelity value the more unique the species is to that cluster. For the purpose of this synthesis, a fidelity value higher than 30 presents a diagnostic species.

Constant species:

Similar to diagnostic species, constant species are also based on the presence and absence of species, but only within the relevant cluster. The value assigned to a constant species therefore indicates the percentage relevés in which the species of a particular cluster is present, i.e. its frequency. The higher the frequency value the more common the species is to that cluster.

Dominant species:

Dominant species identification is based on the cover-abundance value of species within a specific cluster. The value of a dominant species indicate a ranking cover according to the percentage of the relevés that make up the cluster in which the species exceeds the minimum cover value, in this case selected as having a cover abundance of ≥50%.

8.3.5 Plant species diversity assessments

Plant species diversity was calculated directly in JUICE 7.0 (Tichý & Holt, 2006) via the option of *Short Header Data Analyses*. For each plant community (i.e. JUICE vegetation cluster), the Shannon Wiener and Simpson diversity indices, and Pielou‘s and Smith-Wilson evenness indices were selected to calculate mean values of plant species diversity and evenness. These index values are presented in Table 8-4. The overall comparison of species diversity and evenness across the different plant communities is presented in Figure 8-3 and discussed under section 8-5.

8.3.6 Discussion of plant communities

Discussions and descriptions of the vegetation are supported by Tables 8-3 and 8-4 in combination with each table that accompanies the discussion of a plant community (i.e. Tables 8-5 to 8-10). These tables contain the most important distinguishable features of the community or sub-community. Diagnostic species with their fidelity values, constant species with their percentage frequency values, and dominant species with their rankings supplied directly by JUICE 7.0 are presented in these summary tables. The purpose of the summary tables is to limit the presentation of extensive two-way tables in the text. The values in the summary tables were however obtained directly from a JUICE 7.0 output file after applying the *Analysis of Columns of Synoptic Tables*.

8.4 Results

8.4.1 Classification results

Results of the Modified TWINSPAN algorithm along with dissimilarity analyses revealed the identification of six distinctly different plant communities in the riparian zone of the Mopane Bioregion (Figure 8-2) and will be discussed under section 8.5 of this chapter.

8.4.2 Dissimilarity indices and the discussion of the resulting patterns

Based on the assumption that higher dissimilarity values denote higher rankings in the classification hierarchy, the riparian vegetation within Mopaneveld is represented by (1) Azonal riparian vegetation (J=31.93), and savanna-riparian interface vegetation (J=60.86), which present two communities, i.e. the upper riparian terrace community and the floodplains community (Figure 8-2). Due to its low dissimilarity value (J=31.93), the Azonal riparian vegetation cluster would be considered a vegetation unit of low rank, possibly at plant community level, whereas the savanna-riparian interface vegetation (J=60.86) would present vegetation at a higher hierarchical level comprising several plant communities. According to dissimilarity values, the *Phragmites* *mauritianus* – *Cynodon dactylon* – *Nuxia oppositifolia* reedbeds and the riparian terrace vegetation should fall within a single plant community. Literature on savanna riparian ecosystems does not support this classification hierarchy, since the riparian reedbeds are often classified at even higher hierarchical levels (e.g. Bredenkamp & Van Rooyen, 1991, 1993a,b,c). Even the riparian terrace communities (dissimilarity value of 35.27) could hardly be ecologically explained as clusters of lower hierarchy. These clusters are similar to plant communities of higher hierarchy in the literature (e.g. Bredenkamp & Van Rooyen 1991, 1993a,b,c).

Results obtained from statistical values therefore present a most objective classification system, although subjective field knowledge and interpretation should not be neglected in hierarchical vegetation cluster classification. Ecologically, it would not make sense to present the vegetation of the macro-channel floor (i.e. typically the reedbed community) and the macro-channel bank (i.e. typically the river terrace community) below the plant community hierarchical level.

The following plant communities along riparian zones in the Mopane Bioregion of South Africa (Mucina & Rutherford 2006) are therefore proposed (Figure 8-2):

1. The *Phragmites mauritianus* – *Cynodon dactylon* – *Nuxia oppositifolia* reedbed community
2. The *Croton megalobotrys* – *Xanthocercis zambesiaca* – *Philenoptera violacea* riparian forest community
3. The *Setaria sphacelata* – *Combretum hereroense* – *Philenoptera violacea* dry riparian woodland community
4. The *Panicum maximum* – *Diospyros mespiliformis* – *Philenoptera violacea* dry riverbank community
5. The *Combretum apiculatum* – *Colophospermum mopane* dry riparian uplands community
6. The *Acacia tortilis* – *Salvadora australis* – *Urochloa mosambicensis* sodic floodplains community

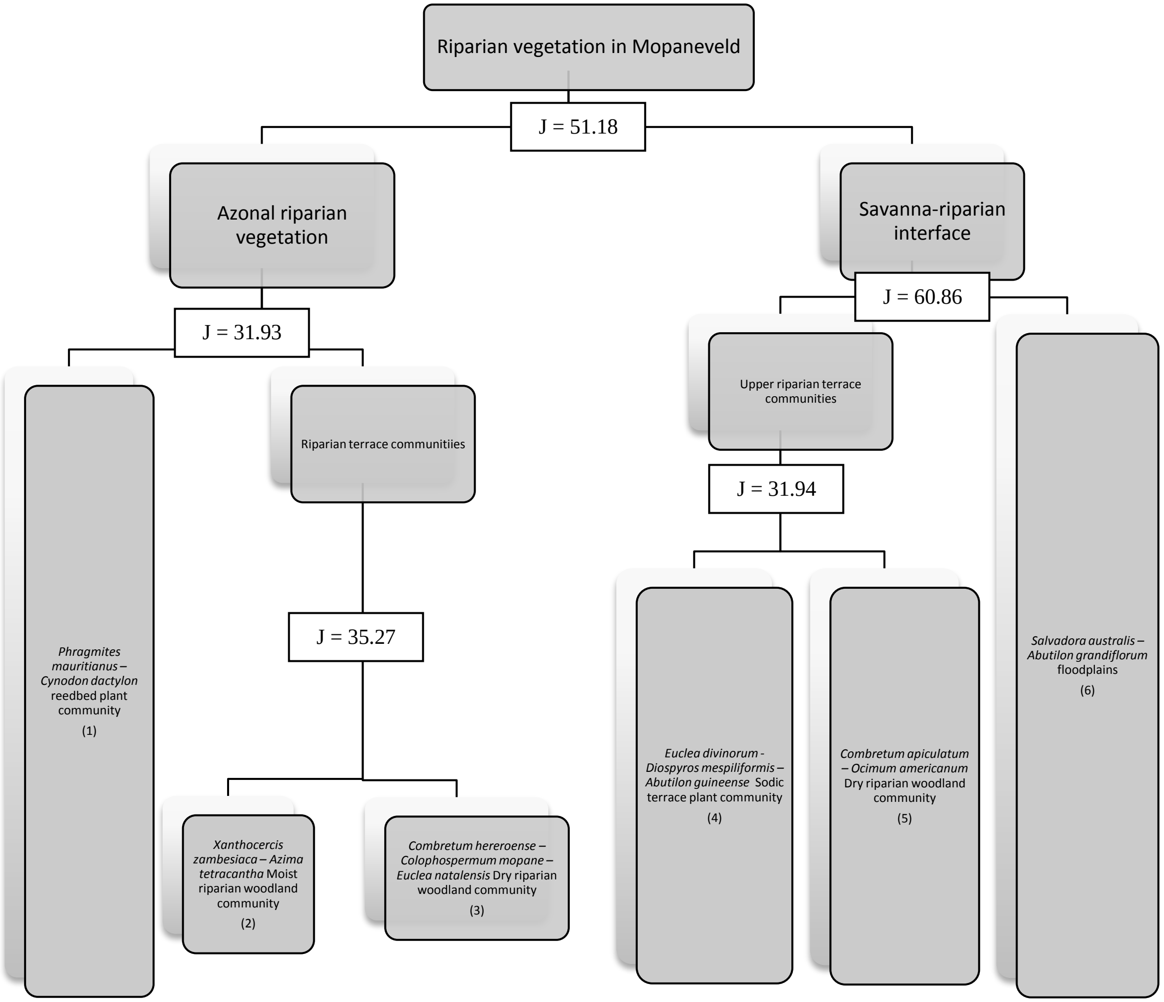


Figure 8-2 The hierarchical classification of riparian vegetation associated with the Mopane Bioregion. Jaccard (J) dissimilarity values (%) are presented at all hierarchical levels to assist in the statistical discrimination between plant communities at lower hierarchy.

8.5 Discussion of riparian plant communities

Each of the riparian plant communities are described in accordance to Table 8-3 and Table 8-4, along with a summary table presenting diagnostic, constant and dominant species for each plant community respectively (Tables 8-5 – 8-10).

Table 8-3. The percentage contribution of relevés within each plant community respectively to each of the major rivers and smaller tributaries in the Mopane Bioregion.

Plant community name	**Contribution of relevés (%)**				
	Letaba	**Olifants**	**Limpopo**	**Levhuvhu**	**Smaller tributaries**
1. *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed	57	26	0	15	2
2. *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest	2	0	22	70	6
3. *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland	43	46	0	1	10
4. *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank	14	35	0	19	32
5. *Combretum apiculatum – Colophospermum mopane* dry riparian uplands	41	15	33	0	11
6. *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains	0	0	97	0	3

Table 8-4. Plant diversity and evenness index values for each riparian plant community of the Mopane Bioregion (Mucina & Rutherford, 2006).

Plant community name	**Diversity and evenness index values**			
	Shannon diversity	**Simpson diversity**	**Pielou evenness**	**Smith-Wilson evenness**
1. *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed	2.357	0.831	0.863	0.812
2. *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest	2.255	0.818	0.820	0.667
3. *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland	2.631	0.885	0.913	0.857
4. *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank	2.850	0.998	0.841	0.738
5. *Combretum apiculatum – Colophospermum mopane* dry riparian uplands	3.121	1.092	0.908	0.853
6. *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains	2.412	0.844	0.745	0.575

1. The *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed plant community

This community represents the vegetation of the lower riparian zone, stretching mostly across the macro-channel floor of larger rivers running through the Mopaneveld, more specifically the Letaba and Olifants Rivers, and to a lesser extent, the Levuvhu River (Table 8-3). The cosmopolitan reed species, *Phragmites mauritianus* is most conspicuous in this community. It is statistically also the only dominant species in this community (Table 8-5). This reedbed plant community is characterized by diagnostic species listed in Table 8-5 of which the reed, *Phragmites mauritianus* and the grass *Cynodon dactylon* represents the diagnostic species with highest frequency values, also referred to as constant species. Other species that are both diagnostic and constant include shrubs such as *Flueggea virosa* and *Pluchea dioscoridis* (Table 8-5). Trees are less common, but include typical macro-channel floor species, such as *Breonadia salicina* and *Nuxia oppositifolia* (Table 8-5). *Breonadia salicina* is typically associated with bedrock and/or rocky substrates in the riverbed, whereas *Nuxia oppositifolia* are distributed along alluvial substrates at lower elevations on the macro-channel floor (Parsons *et al.*, 2006). The exotic forbs *Xanthium strumarium* and *Senna occidentalis* are also diagnostic to this community (Table 8-5). Alien invasive species respond differently to disturbances in riparian zones, although most colonization by alien invasion after the large, infrequent flood in 2000 occurred on bedrock distributary and braid bar geomorphic units (Foxcroft *et al.*, 2008).

Table 8-5. Diagnostic, constant and dominant species of the *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed plant community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Phragmites mauritianus (80.3)	R	*Phragmites mauritianus* (95)	R	*Phragmites mauritianus* (2)	R
Cynodon dactylon (61.1)	G	*Cynodon dactylon* (76)	G	-	
Pluchea dioscoridis (52)	S	*Nuxia oppositifolia* (68)	T	-	
*Xanthium strumarium** (50.1)	F	*Flueggea virosa* (66)	S	-	
Sporobolus africanus (48.8)	G	*Croton megalobotrys* (65)	T	-	
Kanahia laniflora (47)	F	*Gymnosporia senegalensis* (59)	S	-	
Breonadia salicina (45.5)	T	*Xanthium strumarium* * (58)	F	-	
Nuxia oppositifolia (44.3)	T	*Breonadia salicina* (56)	T	-	
Dichanthium annulatum (40.2)	G	*Pluchea dioscoridis* (41)	S	-	
Ludwigia stolonifera (39.7)	F			-	
Flueggea virosa (33.6)	S			-	
*Senna occidentalis** (32.3)	S			-	
Aeschynomene indica (31.4)	S			-	
Eriochloa meyeriana (30.8)	G			-	
*Argemone ochroleuca** (30.5)	F			-	

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

This community is assembled from the *Phragmites mauritianus* Reed Community of the Olifants River (Bredenkamp & Van Rooyen, 1993c), the *Phragmites mauritianus – Nuxia oppositifolia* Riverbed Community of the Levubu (Levuvhu) River (Bredenkamp & Van Rooyen 1993b), and the *Phragmites mauritianus – Cynodon dactylon* reed communities of the Letaba River (Bredenkamp & Van Rooyen 1993a). The *Ficus sycomorus – Abutilon angulatum* var. *angulatum* treeveld along the Olifants River (Myburgh, 1999) is the only community that shares a significant number of species with the *Phargmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed plant community. This community is not represented along the Limpopo River in the northern distribution range of Mopaneveld in South Africa (Table 8-3).

Although outside its distribution range, this community is floristically related to the *Phragmites mauritianus–Vernonia glabra* River Reedbed (Siebert & Eckhardt, 2008) and the *Phragmites mauritianus* vegetation types (Van Coller *et al.*, 1997), of the Sabie River further South. The *Phragmites mauritianus* reed communities and riparian forests described by Bredenkamp and Van

Rooyen (1991) for the Sabie and Crocodile Rivers respectively, also shares many common and diagnostic species with this community. Although these communities were identified through local-scale studies, they have many diagnostic species in common, which emphasizes that riparian communities, especially on the macro-channel floor, are a continuum of assemblages along the riparian corridor and is not commonly associated with geographic regions.

Phragmites mauritianus, the dominant species of this community (Table 8-5), usually forms a broad, continuous band in the active channel bed bordering the water edge. According to Van Coller *et al.*, (1997), *Phragmites mauritianus* vegetation types are mostly confined to pool rapid channel types and associated morphological units of lateral and braid bars on the macro-channel floor. Large increases in reed cover are, however considered undesirable as they can lead to increased sediment accumulation and loss of habitat diversity (Kotchy *et al.*, 2000).

According to the diversity index values calculated for the *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* community, diversity is low (Shannon-Diversity Index value = 2.357) (Table 8-4).

2. The *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest community

This community is typically associated with floodplains containing deep, alluvial soil on the lower macro-channel banks of the Limpopo and Levuvhu Rivers. The diagnostic tree, *Xanthocercis zambesiaca*, reaches heights of 30 m at more pristine areas along the Limpopo River (Straub, 2002). The woody layer of this community is well-developed and often forms a dense sward of trees, such as *Xanthocercis zambesiaca*, *Faidherbia albida*, *Acacia xanthophloea*, *A. robusta* and *Croton megalobotrys*, strangling shrubs, such as *Acacia scweinfurthii* and *Azima tetracantha*, and woody climbers, such as *Capparis tomentosa*. Diagnostic species are listed in Table 8-6, of which the tree *Xanthocercis zambesiaca* has the highest diagnostic value, although statistically not considered a constant species (Table 8-6). *Croton megalobotrys* is not considered a diagnostic species, although it is the most dominant tree species in this community (Table 8-6). The grass layer is sparse, with the most common grasses being *Setaria verticillata* and *Panicum schinzii* (Table 8-6).

This community includes the *Cenchrus ciliaris – Faidherbia albida* sub-community along the Limpopo River (Götze *et al.*, 2003), the *Acacia xanthophloea – Azima tetracantha* floodplain forests

Table 8-6. Diagnostic, constant and dominant species of the *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Xanthocercis zambesiaca (65.9)	T	*Croton megalobotrys* (76)	T	*Croton megalobotrys* (5)	T
Acacia schweinfurthii (55.8)	S	*Philenoptera violacea* (64)	T	*Acacia xanthophloea* (4)	T
Azima tetracantha (58.4)	S	*Xanthocercis zambesiaca* (57)	T		
Faidherbia albida (54.7)	T	*Acacia tortilis* (53)	S		
Capparis tomentosa (46.2)	L	*Acacia robusta* (51)	S		
Acacia xanthophloea (41.6)	T	*Faidherbia albida* (50)	T		
Acacia tortilis (40.3)	T	*Acacia schweinfurthii* (50)	S		
Setaria verticillata (38.5)	G	*Capparis tomentosa* (50)	L		
Acacia robusta (30.6)	T	*Combretum microphyllum* (46)	L		
Panicum schinzii (30.5)	G	*Gymnosporia senegalensis* (43)	S		
Thilachium africanum (30.2)	S	*Acacia xanthophloea* (43)	T		

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

of the Levuvhu River (Bredenkamp & Van Rooyen 1993b) and to a lesser extent, the *Xanthocercis zambesiaca – Acacia tortilis* closed woodland community on high banks of the Limpopo River (Straub, 2002). It is also strongly related to the *Acacia/Faidherbia* forest to woodland on alluvium along the Shashe, Limpopo and Umzingwane rivers, southwest Zimbabwe (Timberlake & Mapaure, 1999).

Riparian forest communities, in particular along the Limpopo River, face transformation from forest to dry riparian woodland in response to various disturbances along riparian ecosystems. Catchment dams in the Limpopo River have caused deaths of diagnostic species within this community as reported by O'Connor (2001). Mortality of the diagnostic species, *Faidherbia albida* caused great concern to conservationists. In a more recent study, O'Connor (2010) revealed evidence of a riparian forest along the Limpopo River being transformed from moist riparian forest to dry riparian woodland in less than 15 years. Mortality of forest species was attributed mainly to drought stress as a response to water abstraction. In protected areas, the effects of water abstraction upstream are exacerbated by increasing numbers of elephants along the riparian zones. Elephants have contributed to the replacement of diagnostic riparian forest tree species by species not preferred by elephants, such as *Philenoptera violacea* , *Xanthocercis zambesiaca* and *Schotia brachypetala* (O'Connor, 2010). Poor regeneration of riparian woodland species, in particular *Xanthocercis zambesiaca* along the Shashe, Limpopo and Umzingwane rivers was already mentioned in 1999 by Timberlake and Mapaure. Sites in which species such as *Faidherbia albida*, *Acacia galpinii*, *Xanthocercis zambesiaca* and *Schotia brachypetala* were prominent, were identified as sites of botanical interest.

A large area of this community occurs in the Kruger National Park along the Levuvhu River (70% of the relevés in this community were sampled along the Levuvhu River, Table 8-3) where it is relatively well protected against human interference. The increasing elephant population along large rivers in the Kruger National Park (Smit & Ferreira, 2010), however poses a possible threat to this sensitive and scarce riparian community.

Although alien invasive species do occur in this community, their numbers are non-significant, probably due to successful eradication by the Working for Water Programme (Foxcroft *et al.*, 2008). Alien species that are commonly found in this community, although in low numbers include annual forbs such as *Flaveria bidentis*, *Achyranthes aspera*, *Boerhavia diffusa* and various non-woody shrub species of the *Datura* genus.

Diversity and evenness is lowest in the *Croton megalobotrys* – *Xanthocercis zambesiaca* – *Philenoptera violacea* riparian forest community (Table 8-4).

3. The *Setaria sphacelata* – *Combretum hereroense* – *Philenoptera violacea* dry riparian woodland community

This community is presented mainly by the drier macro-channel banks of the Olifants and Letaba Rivers (Table 8-3). Although only presented by 14 relevés, this community is also found along the Levuvhu River in the north. It is less frequently flooded than the *Croton megalobotrys* – *Xanthocercis zambesiaca* – *Philenoptera violacea* riparian forest community (community 2) and the *Phragmites mauritianus* – *Cynodon dactylon* – *Nuxia oppositifolia* reedbeds (community 1). It is characterized by a mixture of moderately open grassy shrubveld to closed woodland, which includes tall trees, climbers, a dense undergrowth of multi-stemmed shrubs, and various forbs and grasses. Only six diagnostic species characterize this riparian woodland community (Table 8-7), although these species include trees with wide ecological amplitudes since they are able to tolerate dynamic conditions on ecotones, i.e. between terrestrial uplands on drier soil, and riparian forests on deep, alluvial soil. Various *Combretum* species are associated with this community, of which *Combretum hereroense* (46.6) and *C. imberbe* (31.9) are the most diagnostic. Other *Combretum* species that are commonly associated with riparian landscapes include *C. mossambicense* and *C. microphyllum*, which are not included in Table 8-7. According to statistical measures this community contains no dominant trees, although *Croton megalobotrys* and *Gymnosporia senegalensis* are constant species in this community. Other important constant species include woody species such as *Diospyros* *mespiliformis* and *Flueggea virosa* and the grass *Urochloa mosambicensis* (Table 8-7). *Colophospermum mopane* is considered a diagnostic species for this community. *Colophospermum mopane* is known for its ability to dominate landscapes across extreme environmental conditions (Timberlake, 1995), explaining its dominance along this drier riparian zone.

Table 8-7. Diagnostic, constant and dominant species of the *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Combretum hereroense (46.6)	T	*Philenoptera violacea* (82)	T	*Setaria sphacelata* (1)	G
Colophospermum mopane (40.2)	T	*Croton megalobotrys* (80)	T	*Panicum maximum* (1)	G
Cassia abbreviata (36.3)	T	*Gymnosporia senegalensis* (60)	S		
Philenoptera violacea (35.1)	T	*Combretum imberbe* (48)	T		
Euclea natalensis (33.6)	T	*Diospyros mespiliformis* (44)	T		
Combretum imberbe (31.9)	T	*Flueggea virosa* (43)	S		
		Urochloa mosambicensis (42)	G		

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

Species noticeable in this community, but without diagnostic value, include grasses such as *Cynodon dactylon*, *Urochloa mosambicensis* and *Panicum maximum* and woody species such as *Nuxia oppositifolia*, *Flueggea virrosa*, *Spirostachys africana*, *Diospyros mespiliformis*, *Ficus sycomorus* and *Gymnosporia senegalensis*.

This community is assembled from different communities identified along the Olifants Rivers (Bredenkamp and Van Rooyen, 1993c). It represents the *Maytenus senegalensis* (syn. *Gymnosporia senegalensis*) – *Eragrostis rotifer* Riverbed Open Scrub, the *Sporobolus ioclados – Croton megalobotrys* River Terrace Woodland and the *Ficus sycomorus – Xanthium strumarium* River Terrace Woodland subcommunities of the *Breonadia salicina – Nuxia oppositifolia* Riverbed and Terrace Communities (Bredenkamp & Van Rooyen, 1993c). This community is also well presented along the Letaba River, and was described by Bredenkamp and Van Rooyen (1993a) as the *Lonchocarpus capassa* (syn. *Philenoptera violacea) - Croton megalobotrys - Colophospermum mopane* dry riparian woodland. Apart from this strong affinity to the above community, it also contains elements of the *Croton megalobotrys – Combretum erythrophyllum* moist terrace woodland and the *Croton megalobotrys – Maytenus senegalensis* (syn. *Gymnosporia senegalensis*) riparian forest. It furthermore includes the vegetation of the *Croton megalobotrys – Panicum deustum* riverine woodland (Siebert *et al.*, 2010) with special reference to the *Philenoptera violacea – Jasminum fluminense* riverbank woodland.

Although only a limited number of relevés represent the riparian forests along the Levuvhu River (Table 8-3) this community is related to the *Afzelia quanzensis* – *Combretum microphyllum*, and the *Garcinia livingstonei* – *Phragmites mauritianus* riparian forests (Bredenkamp & Van Rooyen 1993b). The *Spirostachys africana* – *Setaria sagittifolia* Riparian Forest community (Bredenkamp & Van Rooyen, 1993c) of the Olifants River is also well presented in this community.

This community is furthermore floristically related to the Thickets of the Sabie and Crocodile rivers (Landscape 4, Gertenbach, 1983), and strongly associated with the *Lippia javanica* – *Gymnosporia senegalensis* riverbank scrub sub-community along the Sabie River (Siebert & Eckhardt, 2008), except for the strong abundance of *Colophospemum mopane* and *Croton megalobotrys* in this community, which is not present further south.

No alien species are significantly abundant in this community.

Diversity is considered intermediate, although highest evenness is calculated for this community (Table 8-4).

4. The *Panicum maximum* – *Diospyros mespiliformis* – *Philenoptera violacea* dry riverbank community

This community is well presented on higher riverbank terraces of the Olifants River and smaller tributaries (Table 8-3) where it forms a transition between the lush riparian vegetation and the terrestrial uplands. It represents the *Colophospermum mopane* – *Schmidtia pappophoroides* Dry Riparian Bushveld and partially the *Terminalia prunioides* – *Geigeria burkei* Open Savanna (Bredenkamp & Van Rooyen, 1993c). It is also assembled by seasonally wet Mopaneveld savannas, i.e. areas adjacent to ephemeral streams and pans (Siebert *et al.*, 2010). Geology that underlies this community is mainly granite and gneiss with a clayey soil texture on the bottomlands which vary from Valsrivier, Sterkspruit and Glenrosa soil forms. Sodic patches, i.e. soil with a high sodium content, also form part of this community, although they are less distinct than the *Acacia tortilis* – *Salvadora australis* – *Urochloa mosambicensis* sodic floodplains community (community 6). This community occurs higher up along the riparian catena and is therefore only flooded during extreme flooding events, hence the low abundance of species true to moist riparian zones.

The vegetation is characterized by a moderately open tree or shrubveld with a sparse grass cover in areas exposed to herbivory, due to the palatability of the vegetation associated with these patches. The diagnostic shrub, *Euclea divinorum* is most commonly associated with the sodic paches within this community, whereas *Diospyros mespiliformis*, *Combretum hereroense* and *Gymnosporia* *senegalensis* are prominent diagnostic woody species (Table 8-8) along the entire range of this community. *Colophospermum mopane*, *Combretum hereroense*, *C. imberbe*, *Philenoptera violacea*, *Grewia bicolor* and *Dichrostachys cinerea* represent the constant woody species in this community. The tree *Philenoptera violacea* is also a common diagnostic species for dry riparian woodland communities according to previous studies (Bredenkamp & Van Rooyen 1993a). The grass layer is usually sparse due to the concentration of herbivores in this community, although dominant species are mostly perennial grasses, e.g. *Urochloa mosambicensis*, *Panicum maximum*, *Digitaria eriantha* and *Cenchrus ciliaris* along with *Acacia xanthophloea* and *Philenoptera violacea* (Table 8-8). Other species that differentiate this community, which are listed as diagnostics in Table 8-8 include trees such as *Combretum imberbe*, *Spirostachys africana*, *Euclea natalensis* and *Peltophorum africanum*.

Table 8-8. Diagnostic, constant and dominant species of the *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Diospyros mespiliformis (47.2)	T	*Panicum maximum* (76)	G	*Panicum maximum* (16)	G
Euclea divinorum (46.6)	S	*Philenoptera violacea* (60)	T	*Urochloa mossambicensis* (1)	G
Combretum hereroense (46.1)	T	*Urochloa mossambicensis* (60)	G	*Philenoptera violacea* (1)	T
Gymnosporia senegalensis (45.3)	S	*Combretum hereroense* (46)	T	*Digitaria eriantha* (1)	G
Philenoptera violacea (42.8)	T	*Dichrostachys cinerea* (46)	S	*Cenchrus ciliaris* (1)	G
Combretum imberbe (41.4)	T	*Colophospermum mopane* (45)	T	*Acacia xanthophloea* (1)	T
Spirostachys africana (41.2)	T	*Grewia bicolor* (44)	S		
Abutilon guineense (38.4)	F	*Combretum imberbe* (44)	T		
Euclea natalensis (36.9)	T				
Peltophorum africanum (35)	T				
Phyllanthus asperulatus (34.7)	F				
Melhania forbesii (31.7)	F				
Cucumis africanus (31.3)	F				

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

There is much resemblance in species and structure between the *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community and the *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland community (community 3). The *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community is, however, less of a continuum in the landscape since it occurs on higher elevations of larger rivers and is also to some extent associated with streambanks and pans. The main difference between the *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community and the *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland community (community 3), is the abundance of *Croton megalobotrys* in community 3, which is absent from this community, as well as the dominance of *Acacia xanthophoea* in this community, which is absent from community 3.

This community is assembled by the *Lonchocarpus capassa* (syn. *Philenoptera violacea*) – *Acacia nigrescens* dry riparian woodland (Bredenkamp & Van Rooyen, 1993a), the *Sporobolus fimbriatus – Grewia bicolor* seasonally wet savanna (Siebert *et al.*, 2010) and bottomland zones of the *Combretum spp./Colophospermum mopane* woodland of the Timbavati-area (Landscape 6 of Gertenbach, 1983), the Phalaborwa Sandveld (Landscape 8), Letaba River Rugged Veld (Landscape 10) and Tsende Sandveld (Landscape 11).

According to comparisons of diagnostic and constant species, the *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community described here, is strongly related to the *Euclea divinorum – Spirostachys africana* dry riparian woodland communities along the Sabie River further south (Bredenkamp & Van Rooyen, 1991), except for Mopaneveld diagnostics that are common to this community, such as *Colophospermum mopane* and *Grewia bicolor*.

No alien invasive species are significantly abundant in this community.

Diversity of this community is high, although evenness is intermediate when compared to the other riparian communities (Table 8-4).

5. The *Combretum apiculatum – Colophospermum mopane* dry riparian uplands community

This extensive dry riparian uplands community is mostly situated on elevated, dry river banks or terraces, and on floodplains higher up the river bank. From the data used for the synthesis of riparian vegetation, it is best represented along the Letaba River, although it is also well presented along the Limpopo River (Table 8-3). The *Combretum apiculatum – Colophospermum mopane* dry riparian uplands community covers most of the geological substrates typical to the Lowveld Mopaneveld, i.e. granite and gneiss, basalt, and sandstone. Soil form varies from shallow Mispah and Glenrosa to deeper Hutton closer to the larger rivers.

The structure of this plant community varies from open shrubland to closed savanna woodland. Although the data that constitutes this community was classified as part of the riparian zone, this community is floristically strongly related to the surrounding Mopaneveld Lowveld savanna, i.e. the

Cissus cornifolia – Colophospermum mopane major vegetation type (Du Plessis, 2001), although the community described here is more commonly distributed along Mopaneveld bottomlands and riparian zones.

Table 8-9. Diagnostic, constant and dominant species of the *Combretum apiculatum – Colophospermum mopane* dry riparian uplands community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Combretum apiculatum (64.8)	T	*Combretum apiculatum* (76)	T	NONE	
Terminalia prunioides (52.7)	T	*Colophospermum mopane* (75)	T		
Tephrosia purpurea (52.6)	F	*Terminalia prunioides* (61)	T		
Ocimum americanum (48.6)	F	*Panicum maximum* (55)	G		
Melinis repens (48.1)	G	*Enneapogon cenchroides* (51)	G		
Grewia flava (43)	S	*Tephrosia purpurea* (48)	F		
Colophospermum mopane (38.9)	T	*Hibiscus micranthus* (46)	F		
Panicum coloratum (37.7)	G	*Evolvulus alsiniodes* (42)	F		
Acalypha vilicaulis (36.6)	F	*Grewia bicolor* (42)	S		
Commiphora mollis (36.1)	T				
Crabbea velutina (35.4)	F				
Melhania rehmannii (34.7)	F				
Cissus cornifolia (34.5)	S				
Oropetium capense (33.8)	G				
Phyllanthus maderaspatensis (33)	F				
Kirkia acuminata (32.7)	T				
Aristida congesta (32.4)	G				
Commiphora tenuipetiolata (32)	T				
Clerodendrum ternatum (31.4)	F				
Indigofera hermannioides (30.9)	F				
Sclerocarya birrea (30.8)	T				
Enneapogon scoparius (30.5)	G				

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

According to fidelity measures criteria, a total of 22 species are diagnostic to this community and include seven tree species of which *Combretum apiculatum* (64.8) and *Terminalia prunioides* (52.7) have the highest fidelity to this community (Table 8-9). Most of the diagnostic species listed in Table 8-9 are not typical riparian species and also form part of upland terrestrial communities, which are distributed far from rivers and streams. Considering the constant species listed in the summary table, this community could be described as a *Colophospermum mopane – Combretum apiculatum* community on bottomlands.

This community is assembled from various data sets on bottomland Mopaneveld, which include the *Lonchocarpus capassa* (=*Philenoptera violacea*) – *Acacia nigrescens* community from the *Lonchocarpus capassa* (=*Philenoptera violacea*) – *Croton megalobotrys* – *Colophospermum mopane* dry Riparian woodland (Bredenkamp & Van Rooyen, 1993a), the T*erminalia prunioides* – *Grewia villosa* Open Savanna (Bredenkamp & Van Rooyen, 1993c), the *Schmidtia pappophoroides* – *Colophospermum mopane* lowland savanna (Siebert *et al.*, 2010) as well as most bottomlands of landscapes dominated by *Colophosperum mopane* (Landscapes 6–12, 15, 16, 22–27, Gertenbach, 1983).

When this community is floristically compared to riparian vegetation to the south, i.e. the Sabie and Crocodile Rivers, there is a great deal of resemblance in diagnostic species (e.g. in Bredenkamp & Van Rooyen, 1991; Siebert & Eckhardt, 2008), except for the dominance by *Colophospermum mopane*, the constancy of *Grewia bicolor* and the diagnostic character of *Kirkia acuminata*, which are all absent or very low in abundance further south.

This community has the highest diversity and evenness scores for the study area (Table 8-4), which can be explained by its transition between true riparian and terrestrial upland communities.

6. The *Acacia tortilis* – *Salvadora australis* – *Urochloa mosambicensis* sodic floodplains community

The *Acacia tortilis* – *Salvadora australis* – *Urochloa mosambicensis* floodplains of the Limpopo River are distinctly different from the other savanna-riparian interface communities (Jaccard dissimilarity value = 60.86), and presents the highest dissimilarity value between communities (Figure 8-2). It is associated with sodic soil along the lower footslopes and ancient floodplains, toward the outskirts of lush riparian woodlands and forests of the Limpopo River (Table 8-3) (Götze *et al.*, 2003; Straub, 2002). Sodic patches are typically found in semi-arid savannas and are commonly referred to as areas containing fine particles at the soil surface with high levels of exchangeable sodium and other minerals (Dye & Walker, 1980; Pickett *et al.*, 2003). Sodic soil are generally regarded as stressful environments for vegetation, although they are more palatable than crest vegetation to large herbivores, especially grazers and mixed feeders (Tarasoff *et al.*, 2007; Levick & Rogers, 2008). Due to herbivore preference, this community is mostly over-utilized and in some areas the soil is compacted.

Table 8-10. Diagnostic, constant and dominant species of the *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains community. Values as obtained by statistical measures in JUICE are presented in brackets.

Diagnostic species **(Phi-coefficient fidelity value; p = <0.001)**		**Constant species** **(Percentage frequency)**		**Dominant species** **(Average cover abundance presented as a ranking score in JUICE)**	
Salvadora australis (70.1)	S	*Acacia tortilis* (88)	T	*Acacia tortilis* (12)	T
Abutilon grandiflorum (70.6)	F	*Urochloa mosambicensis* (82)	G	*Urochloa mosambicensis* (9)	G
Acacia tortilis (69.1)	T	*Abutilon grandiflorum* (64)	F	*Colophospermum mopane* (6)	T
Lycium cinereum (64.2)	S	*Salvadora australis* (61)	S	*Eragrostis lehmanniana* (3)	G
Setaria verticillata (61.3)	G	*Enneapogon cenchroides* (60)	G	*Aristida congesta* (3)	G
Cucumis zeyheri (50.8)	F	*Setaria verticillata* (55)	G	*Hyphaene petersiana* (2)	T
Tribulus zeyheri (48)	F	*Lycium cinereum* (51)	S	*Panicum maximum* (1)	G
Sida cordifolia (46.1)	F	*Chloris virgata* (47)	G	*Litogyne gariepina* (1)	F
Pseudognaphalium luteo-album (44.6)	F	*Sida cordifolia* (44)	F	*Heliotropium supinum*(1)	F
Urochloa mosambicensis (42.8)	G	*Panicum maximum* (41)	G	*Eriochloa fatmensis* (1)	G
Chloris virgata (41.5)	G			*Enneapogon cenchroides* (1)	G
Hydnora africana (39.5)	F			*Boerhavia diffusa* (1)	F
Hypertelis salsoloides (38)	G			*Acacia xanthophloea* (1)	T
Boscia foetida (37)	T			*Acacia nilotica* (1)	T
Cucumis metuliferus (36.6)	F				
*Chenopodium album** (36.5)	F				
Geigeria burkei (36.5)	F				
Cyathula orthacantha (36)	F				
Echinochloa colona (35.4)	G				
Grewia subspathulata (35.2)	S				
*Boerhavia diffusa** (35.1)	F				
Abutilon pycnodon (34)	F				
Leucas sexdentata (32.2)	F				
Trianthema triquetra (32.2)	F				
Hermannia modesta (32.1)	F				
Litogyne gariepina (31.2)	F				
Ammania baccifera (31)	F				
Trianthema salsoloides (30.1)	F				

*Exotic species; G = grass; F = forb; R = reed; S = shrub; T = tree

This community is characterized by a high tree savanna with a well developed shrub layer. Due to extensive herbivory, the field layer is very sparse and in some parts completely absent. The woody layer in this community is dominated by *Colophospermum mopane* and *Acacia tortilis* (Table 8-10). Although sparsely distributed, species in the field layer is of high characteristic value and include the forbs *Abutilon grandiflorum*, *Lycium cinereum*, *Cucumis zeyheri*, *Tribulus zeyheri*, *Pseudognaphalium luteo-album*, and grasses such as *Setaria verticillata*, *Chloris virgata*, *Urochloa mosambicensis, Hypertelis salsoloides* and *Echinochloa colona* (Table 8-10). Species that are typically characteristic of sodic substrates include *Trianthema triquetra* and *T. salsoloides*, which are diagnostic forbs in this community. The field layer is characterized by high abundances of various annual species due to the dynamic ecology of this community.

The *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* floodplains is floristically related to the *Salvadora australis – Cucumis zeyheri* community along the Limpopo at Mapungubwe National Park (Götze *et al.*, 2003), and the *Chloris virgata – Salvadora australis* community (Straub, 2002). Gertenbach (1983) also identified a *Salvadora* floodplains landscape (landscape 35), although it is more commonly found along the Shingwedzi, Bububu, Mphongolo and Phugwane rivers in the Kruger National Park. The plant assemblages of this landscape are similar, although many diagnostic species of the *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* floodplains are not typically found in the *Salvadora angustifolia* floodplains (Gertenbach, 1983).

Most of the diagnostic species of the *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains community are also characteristic of sodic patches found outside the distribution range of Mopaneveld, more typically found along the larger rivers of the Lowveld Savanna, e.g. the Sabie and Crocodile rivers. In a recent classification of the riparian vegetation along a section of the Sabie River, sodic patches on periodically flooded soils were classified as the *Sporobolus nitens– Euclea divinorum* dry sodic savanna (Siebert & Eckhardt, 2008). Although there is little resemblance in the woody layer, the field layer is also characterized by annual forbs and grasses, including *Portulaca kermesina*, *Trianthema triquetra*, *T. salsoloides*, *Tribulus terrestris*, *Tragus berteronianus*, *Chloris virgata* and *Hypertelis salsoloides* (Siebert & Eckhardt, 2008).

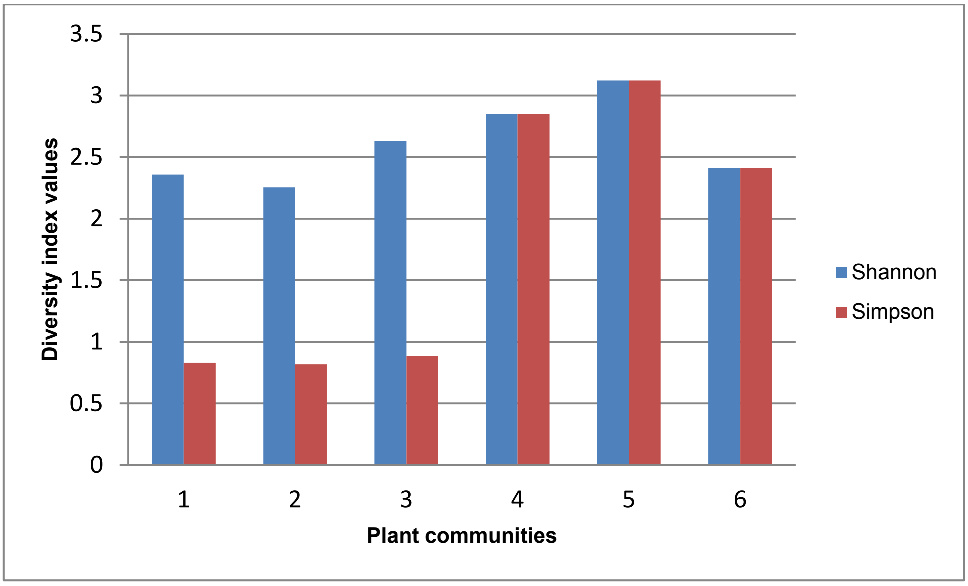
A few alien species are abundant in this community, although they are all annual forbs which cover areas exposed to disturbance, usually extensive grazing and trampling. None of the alien species that occur in high abundance in this community are regarded as invasion threats.

Diversity of this community is intermediate, although the lowest evenness values are calculated in this community (Table 8-4), possibly due to the dominance of many different species (Table 8-10).

8.6 Plant species diversity and evenness

Each plant community along the riparian zone in the Mopane Bioregion has its own unique plant species diversity (Table 8-4). Due to the dynamic, trans-ecological boundary character of riparian zone communities, the diversity is expected to reveal higher index values than the terrestrial plant communities. Evenness, rather than diversity, has however been reported as being a better measure of ecosystem health (Crowder *et al.*, 2010).

a)



b)

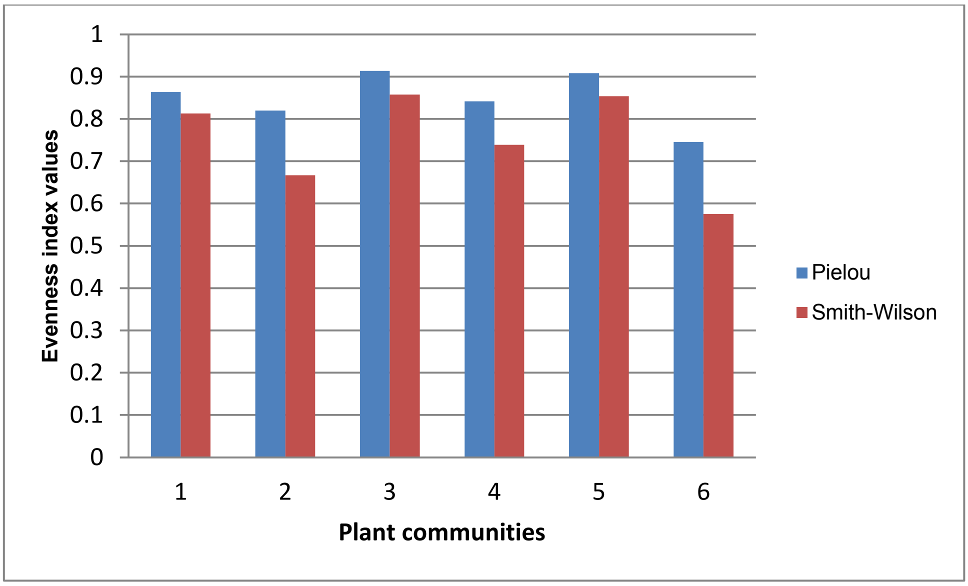


Figure 8-3 Species diversity (a) and evenness (b) index values among the six plant communities along the riparian zones within the Mopane Bioregion. (Numbers of plant communities are as follow: 1. *Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed community; 2. *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest community; 3. *Setaria sphacelata – Combretum hereroense – Philenoptera violacea* dry riparian woodland community; 4. *Panicum maximum – Diospyros mespiliformis – Philenoptera violacea* dry riverbank community; 5. *Combretum apiculatum – Colophospermum mopane* dry riparian uplands community; 6. *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains community).

Shannon-Wiener as well as Simpson diversity index values reveal lowest species diversity for the *Croton megalobotrys – Xanthocercis zambesiaca – Philenoptera violacea* riparian forest community (community 2) and highest species diversity in the *Combretum apiculatum – Colophospermum mopane* dry riparian uplands community (community 5) (Figure 8-3a).

Evenness index values among the different plant communities, revealed similar patterns (Figure 8-3b), although lowest evenness is calculated for the *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains community (community 6) (Pielou = 0.734; Smith-Wilson = 0.575) due to the dominance of several species (Table 8-10). Overall, the evenness is higher than expected for communities in which there is an obvious dominance by a single species, such as *Phragmites mauritianus* in the reedbeds (*Phragmites mauritianus – Cynodon dactylon – Nuxia oppositifolia* reedbed community, community 1) and *Colophospermum mopane* in the dry riparian uplands community (community 5). Results of diversity and evenness calculations, however, revealed the opposite. The community in which *Colophospermum mopane* dominates (i.e. community 5), has the highest diversity index values combined with high evenness (Figure 8-3). These results are contrasting to literature in which it is claimed that the dominance of *Colophospermum mopane* suppresses diversity in savanna ecosystems (e.g. O'Connor, 1992; Mlambo *et al.*, 2005). These results are, however not yet convincing and should be researched in context of other savanna types and riparian zone communities. Mopaneveld floristic diversity comparisons should be done at a regional scale to quantify these premature findings.

8.7 Conclusions

Plant communities in the riparian landscape can be classified at different hierarchical levels due to their discontinuous distribution in small, isolated patches, which depend largely on the geomorphology of the particular section of the riparian zone (Van Coller *et al.*, 1997). The high similarity (i.e. low dissimilarity) between the reedbeds and the riparian terrace vegetation could be ascribed to the phenomenon of isolated, elevated islands within the riverbed, (i.e. the macro-channel floor) which is suitable for the colonization by many riparian terrace plants. Due to their fragmented distribution within the riverbed, these islands typically host *Phragmites mauritianus* and other related herbaceous species. In addition to the diagnostic species of reedbed communities, these islands are colonized by species common to the macro-channel bank, since they are elevated and therefore flooded only periodically. Similarly are the floristic links of the clusters within the ‗Upper riparian terrace' vegetation cluster.

Colophospermum mopane is often dominant in the woody layer up to the riparian fringe. However, the azonal riparian vegetation is characterized by vegetation distinctly different from the terrestrial uplands. Mopaneveld vegetation along the riparian zones is therefore only distinctly different from the surrounding terrestrial Mopaneveld on the uplands. The riparian vegetation within the Mopane Bioregion is floristically linked to described plant communities and landscapes towards the southern parts of the Kruger National Park and surrounding conservancies. It is only the *Acacia tortilis – Salvadora australis – Urochloa mosambicensis* sodic floodplains along the Limpopo River in the north that is distinctly different from other riparian communities. Riparian plant communities can therefore not strictly be linked to geographic regions. It is suggested to be linked to elevation and distance from water, although no quantitative data have been available to test it here.

Multivariate statistical methods have been tested to best present the riparian vegetation within the Mopane Bioregion. Although modern classification techniques have been developed to eliminate subjectivity to vegetation science, observations from field ecologists should be recognized in the descriptions of plant communities. The application of the Modified TWINSPAN application in JUICE 7.0 in combination with Phi-coefficient values elucidated by the Fischer‘s exact test was found to be suitable to identify diagnostic, constant and dominant species within communities, although the selection of the below threshold values (in this study subjectively selected as 30, 40 and 50 for diagnostic, constant and dominant species respectively) remains a biased approach.

To obtain total objectivity in classification hierarchy and community descriptions is challenging for the field ecologist. Even with the application of novel classification algorithms, such as Modified TWINSPAN (Roleček *et al.*, 2009), classification hierarchy should be sensitive to field knowledge and interpretations.

Riparian zones are disturbance-mediated ecosystems that are often been associated with invasion by alien species (Foxcroft *et al.*, 2008; Meek *et al.*, 2010). This floristic analysis, however, revealed insignificant abundances of alien invasive species along the studied riparian zones. Low alien species numbers could possibly be ascribed to the data source, which were all collected in conservation areas. Native species are usually much more abundant than aliens in conservation areas. Alien invasion is very dynamic, and the low numbers of alien species is probably not a true reflection of the current state of the riparian vegetation in terms of invasion, since the data were not all collected recently. The successful alien eradication programme of the South African government, Working for Water Programme (Zimmerman *et al.*, 2004), could also have contributed to low numbers of alien invasion along the studied rivers. The existence of these species, however, indicates that riparian areas are being invaded by alien plant species, although their numbers are being controlled.

Plant species diversity and evenness revealed contrasting results since the diversity of the riparian forest community was calculated the lowest, in combination with low evenness, whereas highest diversity and evenness values were calculated for the riparian uplands community in which *Colophospermum mopane* dominates. The high diversity of the riparian uplands community can possibly be ascribed to its location along the riparian-terrestrial boundary. In most terrestrial vegetation studies, these areas are commonly avoided during sampling due to its heterogeneity. Since most of the data which contributed to this study were sampled with the intention to describe communities along large rivers, these areas have not been neglected, which resulted in the identification of a boundary-type community with highest diversity patterns. Diversity and evenness comparisons across various terrestrial and azonal savanna communities should however, be assessed in more detail to clarify patterns of diversity in the Mopane Bioregion.

This study aimed to provide an overview of the most representative riparian vegetation within the Mopane Bioregion. All of the identified plant communities described in this study present vegetation at a high hierarchical level and could be sub-divided into smaller patches nested within, similar to what was described in the local-scale studies used in this synthesis. Due to the ecology of riparian ecosystems, these sub-groups, however, present vegetation patches associated with specific hydrological and geomorphological patterns. Interactions between hydrology and fluvial geomorphology are critical determinants of vegetation heterogeneity in all river systems (Rogers and O'Keefe, 2003). It should therefore be considered to link all plant communities to hydrology and geomorphology, although it is beyond the scope of this study.

8.8 References

BOWERS, K. & BOUTIN, C. 2008. Evaluating the relationship between floristic quality and measures of plant biodiversity along stream bank habitats. *Ecological indicators*, 8:466–475.

BREDENKAMP, G.J. & VAN ROOYEN, N. 1991. A survey of the riparian vegetation of the Sabie River in the Kruger National Park. Unpublished report, Ekotrust.

BREDENKAMP, G.J. & VAN ROOYEN, N. 1993a. A survey of the riparian vegetation of the Letaba River in the Kruger National Park. Unpublished report, Ekotrust.

BREDENKAMP, G.J. & VAN ROOYEN, N. 1993b. A survey of the riparian vegetation of the Levhuvhu River in the Kruger National Park. Unpublished report, Ekotrust.

BREDENKAMP, G.J. & VAN ROOYEN, N. 1993c. A survey of the riparian vegetation of the Olifants River in the Kruger National Park. Unpublished report, Ekotrust.

COLE, M.M. 1986. The Savannas: biogeography and geobotany. Academic Press: London. 438 p.

CROWDER, D.W., NORTHFIELD, T.D., STRAND, M.R. & SNYDER, W.E. 2010. Organic agriculture promotes evenness and natural pest control. *Nature*, 466: DOI:10.1038/nature09183. Date of access: November 2010.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

DYE, P.J. & WALKER, B.H. 1980 Vegetation-environment relations on sodic soils of Zimbabwe Rhodesia. *Journal of Ecology*, 68:589–606.

EVERSON, C.S., BURGER, C., OLBRICH, B.W. & GUSH, M.B. 2000. Verification of estimates of water use from riverine vegetation on the Sabie River in the Kruger National Park. WRC Report No 877/1/01.

FOXCROFT, L.C., PARSONS, M. & MCLOUGHLIN, C.A. 2008. Patterns of alien plant distribution in a river landscape following an extreme flood. *South African Journal of Botany*, 74:463–475.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*, 26:9–121.

GÖTZE, A.R., CILLIERS, S.S., BEZUIDENHOUT, H. & KELLNER, K. 2003. Analysis of the riparian vegetation (Ia land type) of the proposed Vhembe-Dongola National Park, Limpopo Province, South Africa. *Koedoe*, 46(2):45–64.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG: A comprehensive database management system for vegetation data. *Journal of Vegetation Science,* 12:589–591.

HILL, M.O. 1979. TWINSPAN – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University Ithaca, N.Y.

KAUFFMAN, J.B., BESCHTA, R.L., OTTING, N. & LYTJEN, D. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries*, 22:12–24.

KOTSCHY, K., ROGERS, K.H. & CARTER, A. 2000. Patterns of change in reed cover and distribution in a seasonal riverine wetland in South Africa. *Folia Geobotanica*, 35:363–373.

KRÖGER, R., KHOMO, L.M., LEVICK, S. & ROGERS, K.H. 2009. Moving window analysis and riparian boundary delineation on the Northern Plains of Kruger National Park, South Africa. *Acta Oecologica*, 35:573–580.

LEVICK, S. & ROGERS, K. H. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*, 141:489–98.

MAPAURE, I. 1994. The distribution of *Colophospermum mopane* (Leguminosae – Caesalpinioideae) in Africa. *Kirkia,* 15(1):1–5.

MEEK, C.S., RICHARDSON, D.M. & MUCINA, L. 2010. A river runs through it: Land-use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa. *Biological Conservation*, 143:156–164.

MLAMBO, D., NYATHI, P. & MAPAURE, I. 2005. Influence of *Colophospermum mopane* on surface soil properties and understorey vegetation in a southern African savanna. *Forest Ecology and Management*, 212:394–404.

MUCINA, L. & RUTHERFORD, M.C (*eds*). 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. 807p.

MYBURGH, W.J.1999. Oewerplantegroei van die Olifantsriviersisteem: n ekologiese perspektief. WRC report 663/1/99.

NAIMAN, R.J. & DÉCAMPS, H. 1997. The ecology of interfaces: riparian zones. *Annual Reviews of Ecology and Systematics*, 28:621–658.

NAIMAN, R.J., FETHERSTON, K.L., MCKAY, S. & CHEM, J. 1998. Riparian forests. (*In* Naiman, R.J. & Bilby, R.E. *eds*, River Ecology and Management: Lessons from the Pacific Coastal Region. Springer-Verlag: New York, p.289–323).

NILSSON C. & SVEDMARK, M. 2002. Basic Principles and Ecological Consequences of Changing Water Regimes: Riparian Plant Communities. *Environmental Management*, 30(4):468–480.

O'CONNOR, T.G. 1992. Woody vegetation-environment relations in a semi-arid savanna in the northern Transvaal. *South African Journal of Botany*, 58(4):268–274.

O'CONNOR, T.G. 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in semi-arid African savanna. *Journal of Applied Ecology*, 38:1314–1325.

O'CONNOR, T.G. 2010. Transformation of riparian forest to woodland in Mapungubwe National Park, South Africa, between 1990 and 2007. *Austral Ecology*, 35:778–786.

O'KEEFE, J. & ROGERS, K.H. 2003. Heterogeneity and management of the Lowveld rivers. (*In* Du Toit, J.T., Rogers, K.H. & Biggs, H.C., *eds*., The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press: Washington. p. 447–468).

PARSONS, M., McLOUGHLIN, C.A., ROUNTREE, M.W. & ROGERS, K.H. 2006. The biotic and abiotic legacy of a large infrequent flood disturbance in the Sabie River, South Africa. *Rivers Research Applications*, 22:187–201.

PICKETT, S.T.A., CADENASSO, M.L. & MENNING, T.L. 2003. Biotic and Abiotic Variability as Key Determinants of Savanna Heterogeneity at Multiples Spatiotemporal Scales. (*In* Du Toit, J.T., Rogers, K.H. & Biggs, H.C., *eds*., The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press: Washington. p. 22–40).

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

ROGERS, K.H. & O'KEEFE, J. 2003. River heterogeneity: Ecosystem structure, function and management (*In* Du Toit, J.T., Rogers, K.H. & Biggs, H.C., *eds*. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington. pp 189–218).

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

SIEBERT, F. AND ECKHARDT, H.C., 2008. The vegetation and floristics of the Nkhuhlu exclosures, Kruger National Park. *Koedoe,* 50(1):126–144.

SIEBERT, F. ECKHARDT, H.C. AND SIEBERT, S.J. 2010. The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa. *Koedoe*, 52(1): Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777. Date of access: November 2010.

SMIT, I.P.J. & FERREIRA, S.M. 2010. Management intervention affects river-bound spatial dynamics of elephants. *Biological Conservation*, 143:2172–2181.

STATE OF THE RIVERS REPORT. 2001. Crocodile, Sabie-Sand and Olifants River systems. A report of the River Health Programme http://www.csir.co.za/rhp/. WRC Report No, IT 147/01.

STRAUB, A. 2002. The vegetation of Breslau Game Farm, Northern Province, Souh Africa. Pretoria: UP (Dissertation, MSc) 150p.

TARASOFF, C.S., MALLORY-SMITH, C.A. & BALL, D.A. 2007. Comparative plant responses of *Puccinellia distans* and *Puccinellia nuttalliana* to sodic versus normal soil types. *Journal of Arid* Environments, 70:403–17.

TICHÝ, L. & HOLT, J. 2006. JUICE v.7.0. Program for management, analysis and classification of ecological data. Program manual. Vegetation Science Group: Masaryk University, Brno.

TICKNER, D.P., ANGOLD, P.G., GURNELL, A.M. & MOUNTFORD, J.O. 2001. Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Progress in Physical Geography*, 25:22–52.

TIMBERLAKE, J.R. 1995. *Colophospermum mopane*: annotated bibliography and review. *The Zimbabwe Bulletin of Forestry Reseach*, 11:1–49.

TIMBERLAKE, J.R. & MAPAURE, I. 1999. Vegetation survey of Maramani/Tuli area, Southwest Zimbabwe. Unpublished report on the CESVI Lowveld project.

VAN COLLER, A.L., ROGERS, K.H. & HERITAGE, G.L. 1997. Linking riparian vegetation types and fluvial morphology along the Sabie River within the Kruger National Park, South Africa. *African Journal of Ecology*, 35:194–212.

VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. 1981. A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 1. The Higrophilous communities. *Journal of South African Botany*, 47(2):213–246.

WARD, J.V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, 82:269-278.

WEBER, H.E., MORAVEC, J. & THEURILLAT, J.P. 2000. International Code of Phytosociological Nomenclature. 3rd ed. *Journal of Vegetation Science*, 11:739–768.

WERGER, M.J.A. & COETZEE, B.J. 1978. The Sudano-Zambezian Region. (*In* Biogeography and ecology of southern Africa, Werger, M.J.A. *ed*, Junk: The Hague. p. 301–462).

ZIMMERMAN, H.G., MORAN, V.C. & HOFFMANN, J.H. 2004. Biological control in the management of invasive alien plants in South Africa, and the role of the Working for Water programme. *South African Journal of Science*, 100:34–40.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSION

9.1 Introduction

The development of alternative classification algorithms and measures to objectively identify diagnostic species in vegetation classification studies create a level of uncertainty among vegetation scientists as to whether classifications based on classical approaches are at all suitable for conservation and management applications.

The first hypothesis of the thesis states that the classical approach in vegetation classification reveals different results from the modern approach at various spatial scales within the Mopaneveld study area of southern Africa. This hypothesis, in combination with the key objective of the research, i.e. to evaluate the credibility of classical approaches in vegetation classification at various spatial scales, was successfully addressed in this thesis (Chapters 5–7) and will be discussed under section 9.2.

The second hypothesis of the thesis was successfully addressed in a complete phytosociological synthesis of the riparian vegetation of the Mopane Bioregion (Mucina & Rutherford, 2006) in South Africa (Chapter 8) and will be discussed under section 9.3.

Detailed discussions on the results are presented in the respective research chapters (Chapters 5–8) and will therefore only be culminated here, although this chapter aims to present the relevance of the research and the way forward.

9.2 The classical approach in vegetation classification and description present different results at various spatial scales

In the comparison of a broad-scale synthesis, the Modified TWINSPAN algorithm (Rolečeck *et al.*, 2009) along with statistical measures of diagnostic species identification (Chytrý *et al.*, 2002) revealed considerable differences in terms of classification hierarchy and clustering of the vegetation data as well as in the identification of diagnostic species against the results obtained through classical approaches in the study of Du Plessis (2001) and its published form, i.e. Siebert *et al.* (2003). Comparisons at an intermediate scale revealed similar patterns of discrepancies in the results obtained through classical versus modern approaches. Although there were similarities in the classification results, the Modified TWINSPAN algorithm in combination with statistical measures of diagnostic species revealed a more rigorous presentation of the vegetation in terms of its associated biophysical environment. At the local-scale, however, classification results appeared strongly similar in the assemblage of relevés into clusters, although differences in the classification hierarchy as well as in the identification of diagnostic species were evident.

These differences between the two classification algorithms are perfectly aligned with the expectations of the Modified TWINSPAN set by Roleček *et al.* (2009), although the improved algorithm was not previously tested extensively at various spatial scales. The Modified TWINSPAN algorithm does not alter the logic of the classical TWINSPAN classification, although it changes the hierarchy of divisions, avoiding imposed divisions of homogeneous clusters at higher levels of the classification hierarchy while it increases the flexibility of the classical TWINSPAN classification (Roleček *et al.*, 2009). At the broad-scale synthesis (i.e. the synthesis of Mopaneveld in selective countries in southern Africa, Chapter 5), the Modified TWINSPAN revealed a more plausible classification hierarchy of the Mopaneveld vegetation particularly through the avoidance of imposed divisions. The Modified TWINSPAN revealed a hierarchy of Mopaneveld vegetation across diverse landscapes and climatic patterns that are less correlated with biogeographical distribution as initially presented in Siebert *et al.* (2003) and clustering that is more associated with the biophysical environment. At the intermediate spatial scale analysis (i.e. the synthesis of the South African Lowveld Mopaneveld, Chapter 6) the avoidance of imposed divisions of homogeneous clusters by the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) is best portrayed in the non-division of the ‗Mixed Mopane savanna‘ (i.e. the *Tragus berteronianus* – *Terminalia prunioides* Mixed Lowveld Mopane woodland), a vegetation unit expected to be floristically heterogeneous. The local-scale classification outcomes confirm that the Modified TWINSPAN could change the classification hierarchy without altering the logic of the classical TWINSPAN, which is consistent with the predictions by Roleček *et al.* (2009).

The Modified TWINSPAN algorithm is therefore considered to be particularly efficient for the classification of vegetation at various spatial scales, ultimately presenting more rigorous results than the classical TWINSPAN classification. The application of the classical TWINSPAN algorithm at broader and intermediate scales has therefore been proved to be inefficient, although no strong evidence has been revealed to refrain from using the classical TWINSPAN hierarchy at the local scale.

The concept of diagnostic species has long been considered important (e.g. Braun-Blanquet, 1932; Westhoff & Van der Maarel, 1973; Barkman, 1989; Dufrêne & Legendre, 1997), although its objective application in vegetation science has only been addressed in recent years (Botta-Dukát & Borhidi, 1999; Bruelheide, 2000; Chytrý *et al.*, 2002). The development of statistical measures of species fidelity enabled an evaluation of the credibility of traditionally used approaches to identify diagnostic species at various spatial scales. A comparison between groups of diagnostic species which resulted from the different measures of diagnostic species revealed large discrepancies between the classical and statistical approaches. Despite an overlap between identified diagnostics, many species that were considered ‗general' species in the classical approaches gained diagnostic status after statistical measures have been applied.

Considerable differences in diagnostic species groups at the different spatial scales were perceived through the comparisons of approaches. It is, however, expected that diagnostic species would be inconsistent through various scales since many species which appear to be faithful to a community at a local scale study have a wider ecological optimum at the broader scale (Chytry *et al.*, 2002).

Although the application of statistical measures of species fidelity proved to efficiently identify diagnostic species at the various spatial scale studies, the application of these measures at a fine scale (i.e. local scale) should be considered with care (Chytrý *et al.*, 2002) and certainly in combination with the field knowledge of the observer.

9.3 The modern approach reveals distinctly different plant communities at an intermediate-scale synthesis of the riparian vegetation in the Mopane Bioregion

Proven to be an efficient classification algorithm at an intermediate-scale vegetation synthesis, the Modified TWINSPAN algorithm was applied to the riparian vegetation in the Mopaneveld of South Africa. The selection of diagnostic species was done through statistical measures of fidelity according to Chytry *et al.* (2002). Based on this approach distinctly different riparian plant communities were identified that represent a unique combination of plant species. To strengthen the descriptions of these entities, diagnostic species were reported along with constant and dominant species. Species diversity indices were applied for each plant community, which revealed considerable variation in species diversity and evenness. Highest species diversity was recorded for the *Combretum apiculatum* – *Colophospermum mopane* dry riparian uplands, a typical transition between terrestrial uplands and riparian fringes. The sampling of this ecotone is unusual since the majority of phytosociological data are sampled within homogeneous units with the particular avoidance of boundaries. Most of the data that contributed to this synthesis was, however, sampled specifically for riparian vegetation classifications, hence the inclusion of the transition zone. The spatial scale at which data are being recorded to meet the specific aims of a study therefore may affect the end-results. Due to the subjective, preferential method of field sampling used in the Braun-Blanquet approach, in combination with different objectives at different spatial scales, the suitability of phytosociological data for floristic diversity estimates is therefore considered severely limited, similar to the findings by Chytrý (2001). The distortion of species diversity and evenness

9.4 Future research

Despite its useful application to compare classification results obtained from similar classical approaches, the Modified TWINSPAN algorithm (Roleček *et al.*, 2009) is not necessarily considered the ultimate for vegetation classifications and syntheses. For an even more objective approach in vegetation classification, the application of OptimClass (Tichý *et al.*, 2009) could be investigated to the extensive Mopaneveld vegetation data set. OptimClass evaluates the relative performance of different numerical classification techniques without subjective interference.

A complete synthesis of all available vegetation data on southern African Mopaneveld is still awaiting consideration. Although vegetation data across its entire distribution range is severely limited, there are numerous vegetation data sets (see section 2.3.6) that were not included in the synthesis of Siebert *et al*. (2003) that could be considered for analyses through modern approaches. General limitations in accompanied environmental data, however, hinder the application of direct and indirect ordinations and hence, the ecological explanations of plant community distributions and consequently also the distribution pattern of *Colophospermum mopane* in southern Africa. Although attempts have been made to explain the distribution of *Colophospermum mopane* according to environmental factors (e.g. Okitsu, 2005), the specific drivers for its distribution is still vaguely known.

9.5 Conclusion

The effective depiction of vegetation relies on robust classifications at an appropriate scale. The results presented here suggest that the credibility of classical approaches seem to be highly limited for vegetation classification and descriptions at broader spatial scales. At a local scale however, no substantiation of the inefficiency of classical approaches could be perceived. While the results presented here cannot be regarded as sufficient to finally establish the most desirable approach for vegetation syntheses across various spatial scales, they do permit valuable discussion of the credibility of using classical approaches and similar improvements of numerical classification techniques.

The Braun-Blanquet approach has been criticized widely (see section 2.1.2) although some issues have been addressed directly, and others indirectly through the research presented here. Such concerns include scale, the use of outdated numerical-analytical techniques, such as the classical TWINSPAN algorithm and the subjectivity towards diagnostic species identification and subsequent naming of plant communities.

To conclude, recent developments in numerical-analytical approaches for vegetation classification should be acknowledged and applied where possible. However, although it may assist in the more objective treatment of data, the judgement on its significance still remains subjective.

9.6 References

BARKMAN, J.J. 1989. Fidelity and character-species, a critical evaluation. *Vegetatio,* 85:105–116.

BOTTA-DUKÁT, Z. & BORHIDI, A. 1999. New objective method for calculating fidelity. Example: the Illyrian beechwoods. *Annali di Botanica*, 57:73–91.

BRAUN-BLANQUET, J. 1932. Plant Sociology. The Study of Plant Communities. Authorized English translation of 'Pflanzensoziologie' (Fuller, G.D. & Conard, H.S. *eds*. New York: McGraw-Hill).

BRUELHEIDE, H. 2000. A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science,* 11:167–178.

CHYTRÝ, M. 2001. Phytosociological data give biased estimates of species richness. *Journal of Vegetation Science,* 12:439–444.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science,* 13:79–90.

DUFRÊNE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67(3):345–366.

DU PLESSIS, F. 2001. A Phytoociologial Synthesis of Mopaneveld. Pretoria: UP (Dissertation, MSc) 193p.

MUCINA, L. & RUTHERFORD, M.C. *eds*. 2006. The vegetation of South Africa, Lesotho and Swaziland. Pretoria: South African National Biodiversity Institute. *Strelitzia*, 19. 807p.

OKITSU, S. 2005. Factors controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs (supplementary issue)*, 30:135–151.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science,* 20:596–602.

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia,* 33(1):121–134.

TICHÝ, L., CHYTRÝ, M., HÁJEK, M., TALBOT, S. & BOTTA-DUKÁT, Z. 2009. OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science,* 21:287–299.

WESTHOFF, V. & VAN DER MAAREL, E. 1978. The Braun-Blanquet approach. (*In* Whittaker, R.H. *ed*., Classification of plant communities. Junk: De Hague, p. 289–374).

APPENDICES

APPENDIX 5-1

Reference document to Chapter 5

Siebert *et al*. (2003)

Bothalia 33,1: 121–134 (2003)

A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe

F. SIEBERT*, G.J. BREDENKAMP* and S.J. SIEBERT*[†]

Keywords: *Colophospermum mopane*, DECORANA, event-driven system, Mopani Veld, phytosociology, savanna, species richness, TWINSPAN, vegetation type

ABSTRACT

Data from fifteen phytosociological studies were merged and classified to describe and compare the vegetation of geographically separated and climatically different Mopaneveld types in South Africa, Namibia and Zimbabwe. Seven vegetation types and ten major plant communities were identified using TWINSPAN. Vegetation types were separated according to geographical regions. There were significant floristic affinities even though there were geological and climatic differences between the regions. Plant communities were described according to vegetation structure, habitat and floristic composition. Although environmental data were not adequate for a detailed ordination, DECORANA reflected the distribution of vegetation types and major plant communities along environmental gradients. Limitations of large phytosociological syntheses were also addressed. Species richness (alpha diversity) was calculated for each geographical region. The Musina (Messina) region north of the Soutpansberg, South Africa, has the highest species richness, and Kaokoland, Namibia, the lowest. Due to irregular annual rainfall patterns in semi-arid Mopaneveld, it is suggested that variance in species richness is associated with temporal vegetation states induced by rainfall events. Species richness of Mopaneveld was further compared with other savanna types.

INTRODUCTION

Colophospermum mopane (Kirk ex Benth.) Kirk ex J.Léonard, commonly termed Mopane, is a xeric woody savanna species of south tropical Africa where it occurs in a wide range of vegetation types (Timberlake 1995), collectively referred to as Mopaneveld or Mopani Veld. As the name suggests, *C. mopane* is the dominant, as well as the character species of this extensive veld type (Winterbach *et al.* 2000). Floristically, Mopaneveld occurs within the Zambezian Regional Centre of Endemism (Z), Karoo-Namib Regional Centre of Endemism (KN) and Kalahari-Highveld Regional Transition Zone (KH) (White 1983). According to the structural classification by White (1983), Mopaneveld is considered as Woodland (Z) and Scrub Woodland (Z & KH), as well as Karoo Riparian Scrub Forest and Bushland (KN).

Colophospermum mopane-dominated vegetation types (Mopaneveld) occur between 10°00′ and 24°30′ latitude (Figure 1) within the 300 m to 1 000 m altitudinal range (Madams 1990; Mapaure 1994; Timberlake 1995). Mopaneveld stretches inland from the eastern escarpment to the west coast of southern Africa and covers ± 555 000 km² (Mapaure 1994; Timberlake 1999). It is prominent in the drier savanna zone of southern Africa, which coincides with mean annual maximum temperatures between 28°C and 35°C (Werger & Coetzee 1978; Timberlake 1995) with little or no frost incidence in winter. Mopaneveld is associated with fine-textured soils in hot, dry valley bottoms and adjacent plains of large rivers, such as the Limpopo, Save, Shire, Okavango, Luangwa, Zambezi and Cunene (Wild & Barbosa 1967; Werger & Coetzee 1978; Cole 1986; Mapaure 1994). *Colophospermum mopane* can tolerate extreme environmental conditions (Timberlake 1999). In the southwestern limits of its distribution range in Namibia, Mopaneveld occurs in areas receiving 150 mm or less per annum, while in its southeastern distribution range it receives more than 800 mm per annum in some areas. These nonspecific sets of environmental conditions reflect the distribution of a single species, *C. mopane*, but little is known of the associated vegetation within the distribution range of Mopaneveld (Acocks 1953). However, since 1967, small-scale phytosociological studies have contributed to the knowledge of vegetation in some parts of the southern Mopaneveld (Table 1). Fifteen data sets were available for this study, and considering the distance between east and west, this was still insufficient for the typification of Mopaneveld across its range. However, the available information was regarded as baseline data whereby the associated vegetation of Mopaneveld could be compared for the first time.

The main objective of this study was therefore to classify, describe and compare the major plant communities of Mopaneveld in three geographically separated and climatically different areas of its distribution range to gain a better understanding of the species assemblages and richness of this vegetation type. These three regions include (1) arid to semi-arid Namibian, (2) semi-arid to sub-humid South African, and (3) sub-humid Zimbabwean Mopaneveld types.

METHODS

The first step in the synthesis of Mopaneveld vegetation was to initiate and create a database with compatible phytosociological data sets from South Africa, Namibia and Zimbabwe. All the available data sets that were considered reliable were included in the database. Reliable data sets had to consist of a detailed floristic survey of both the woody and herbaceous strata. Adequate envi-

---

* African Vegetation and Plant Diversity Research Centre, Department of Botany, University of Pretoria, 0002 Pretoria.

[†] Present address: SABONET, National Botanical Institute, Private Bag X101, 0001 Pretoria.

MS. received: 2002-09-02.

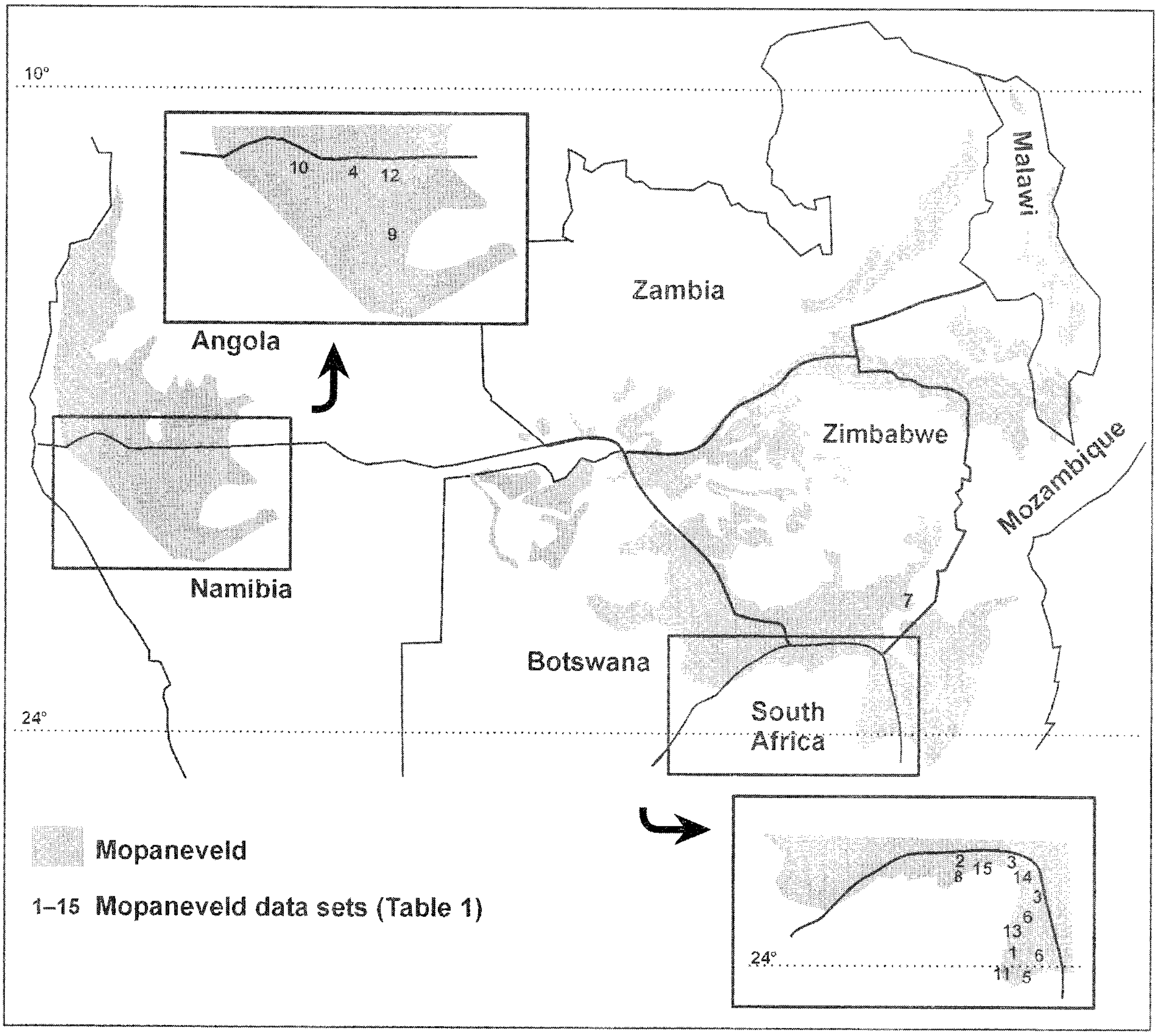


FIGURE 1.—*Colophospermum mopane*-dominated vegetation types in southern Africa (from Mapaure 1994) and approximate location of data sets in the study area.

TABLE 1.—Mopaneveld data sets used for TWINSPAN analysis

Data set no.	Author	Date	Location	No. relevés
1	Beck, N.G.	1998	Foskor, PMC & Shiela Mines, Phalaborwa, South Africa	114
2	Dekker, B.	1995	Messina Experimental Farm, South Africa	148
3	Du Plessis, F.	1998	Kruger National Park & N of Soutpansberg, South Africa	19
4	Du Plessis, F.	1998	Cuvelai Delta, Namibia	17
5	Gertenbach, W.P.D.	1987	Southern distribution of Mopaneveld, Kruger National Park, South Africa	248
6	Gertenbach, W.P.D.	1976	Central district, Kruger National Park, South Africa	343
7	Hin, C.	1999	Sango Ranch, Save River Valley, Zimbabwe	230
8	Kelly, L. & Parker, G.	1996	Pylkop, N of Soutpansberg, South Africa	62
9	Le Roux, C.J.G.	1976	Etosha National Park, Namibia	204
10	NOLIDEP	1998	Kaokoland, Namibia	34
11	Purchase, A.	1997	Hoedspruit-Klaserie-Timbavati-Umbabat Nature Reserves, South Africa	374
12	Ströhbach, B.	1998	Cuvelai Delta, Namibia	40
13	Swart, H.B.	1998	Letaba Ranch, South Africa	200
14	Van Rooyen, N.	1978	Punda Milia-Pafuri-Wambiya, Kruger National Park, South Africa	196
15	Visser, N.	1996	Honnet Nature Reserve, Tshipise, South Africa	57

ronmental data for each data set should have been a criterion for inclusion. However, due to limited environmental data available from the selected studies, this could not be implemented.

Compatible vegetation data on Mopaneveld were obtained from 15 phytosociological studies (Table 1). A total of ten data sets were selected from South Africa (1 761 relevés), four from Namibia (295 relevés) and one from Zimbabwe (230 relevés) (Figure 1). The phytosociological data, consisting of 2 286 relevés (of equal size, ± 200 m^2) and 1 465 species, were incorporated into a vegetation database created in TURBOVEG (Hennekens 1996a). Due to taxonomic disaccord in the acceptance of infraspecific taxa, only generally used subspecies and varieties were included in the data set. Infraspecific taxa not generally used were combined under the relevant species name.

The first approximation of a vegetation classification, based on this total floristic data set, was obtained by the application of Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979a) at a single division level in MEGATAB (Hennekens 1996b). Lowest TWINSPAN cutlevels (0-5-50 option) were optimal for separating distinct vegetation units in the data set. Azonal vegetation (e.g. wetlands) in the data set was separated from Mopaneveld vegetation by this single division procedure. This procedure was repeated until all azonal types were identified. Forty azonal relevés were omitted from the data set and stored in a separate database for possible future analysis. TWINSPAN was applied to the remaining 2 246 relevés (0-5-25-50 cutlevels, 6 levels of division). Forty-three vegetation clusters were separated by TWINSPAN. A synoptic table was constructed to facilitate refinement of the table by means of Braun-Blanquet procedures in MEGATAB (Hennekens 1996b). A species was excluded if it had a frequency of less then 10%, and a synrelevé was excluded if it consisted of less than 5 relevés. The refinement resulted in 29 synrelevés, grouped into ten noda (Table 2), which represent seven vegetation types and ten major plant communities. A vegetation type and a major community probably represent syntaxa on order or alliance levels respectively. The hierarchical relationships between the vegetation units are illustrated in Figure 2. The final synoptic table (Table 2) contains the constancy values of the species given in percentages. As higher syntaxa cannot be typified before the lower syntaxa are formally described, no attempt was made here to fix syntaxon names according to the International Code for Syntaxonomical Nomenclature.

Probable environmental gradients were determined by applying Detrended Correspondence Analysis (DCA) to the floristic data set in the DECORANA computer programme (Hill 1979b). DCA was applied to 29 synrelevés without data transformation (this was done before reducing the synrelevés to 10 noda). Rare species were downweighted. Due to inadequate environmental data available from the selected data sets, interpretation of the results could not be quantified.

A basic floristic analysis was undertaken to investigate species richness and is presented as mean species number per relevé for each region (Table 3). Species richness of Mopaneveld was also compared with other savanna vegetation types: 1, microphyllous thornveld (*Acacia tortilis*-dominated); 2, mixed bushveld; and 3, broad-leaved savanna (*Combretum* spp.-dominated). This data was obtained from the savanna vegetation data base housed at the University of Pretoria.

RESULTS AND DISCUSSION

Application of TWINSPAN resulted in the following hierarchical classification of the selected data sets into 10 noda:

1. *Digitaria milanjiana–Colophospermum mopane* Vegetation Type
1.1 *Justicia flava–Colophospermum mopane* Major Community
1.2 *Setaria sphacelata–Colophospermum mopane* Major Community
2. *Croton megalobotrys–Colophospermum mopane* Vegetation Type
3. *Cissus cornifolia–Colophospermum mopane* Vegetation Type
4. *Ptycholobium contortum–Colophospermum mopane* Vegetation Type
5. *Enneapogon scoparius–Colophospermum mopane* Vegetation Type
6. *Boscia foetida–Colophospermum mopane* Vegetation Type
6.1 *Eragrostis viscosa–Colophospermum mopane* Major Community
6.2 *Leucosphaera bainesii–Colophospermum mopane* Major Community
7. *Bauhinia petersiana–Colophospermum mopane* Vegetation Type
7.1 *Philenoptera nelsii–Colophospermum mopane* Major Community
7.2 *Asparagus nelsii–Colophospermum mopane* Major Community

Vegetation Type 1 represents Zimbabwean Mopaneveld, Types 2 to 4, South African Mopaneveld, and Types 6 and 7 represent Namibian Mopaneveld. The *Enneapogon scoparius–Colophospermum mopane* Vegetation Type (Type 5) probably represents a degraded type.

Description of vegetation types

Mopaneveld is often associated with the constant presence, mostly with high abundance values, of *Colophospermum mopane*, *Dichrostachys cinerea*, *Tragus berteronianus*, *Grewia bicolor* and *Commiphora africana* (species group A, Table 2). Other woody species that are consistently associated with *Colophospermum mopane* over much of its range include *Acacia nigrescens*, *Adansonia digitata*, *Combretum elaeagnoides*, *C. hereroense*, *Commiphora* spp., *Diospyros quiloensis*, *Grewia* spp., *Terminalia prunioides*, *T. stuhlmannii* and *Ximenia americana* (Timberlake 1999). The Mopaneveld in South Africa and southeastern Zimbabwe is clearly separated from the Namibian Mopaneveld by the presence of species in species groups K and M (Table 2). Species of signifi-

TABLE 2.—Abbreviated synoptic table of Mopaneveld vegetation types in the study area

Vegetation type Number of relevés	1.1 *71*	1.2 *131*	2 *92*	3 *1375*	4 *157*	5 *68*	6.1 *144*	6.2 *147*	7.1 *51*	7.2 *10*
Species group A										
Colophospermum mopane	69	20	55	58	91	75	67	61	45	80
Dichrostachys cinerea	25	29	22	52	53	57	19	41	71	10
Tragus berteronianus	68	5	2	50	79	43	21	15	2	20
Grewia bicolor	40	11		59	84		23	40	39	30
Commiphora africana	9	4		22	9	13	7	6	29	10
Grewia flavescens	7	37	1	14		30	12	4	10	40
Evolvulus alsinoides	8	5		34	70		12	6	8	10
Species group B										
Cyathula uncinulata	70	48								
Indigofera varia	45	20	2			1	6	2	2	
Cucumis zeyheri	44	31								
Digitaria milanjiana	44	75					1			
Diospyros quiloensis	35	33								
Dactyloctenium giganteum	34	11	1	3						
Abutilon grandiflorum	27	11			1					
Species group C										
Justicia flava	61	4	2	10	1		1			
Sporobolus nitens	52	8		10					2	
Oropetium capense	52	1		11	33			13		
Cissus rotundifolia	40	6		1						
Aristida junciformis	34	9					2	1		
Hemizygia bracteosa	27	8		4						
Thilachium africanum	24	4		1						
Zanthoxylum capense	21	1		1						
Boscia mossambicensis	20	8	1							
Enteropogon monostachys	20	8								
Stylochiton natalensis	18	6		3						
Plectranthus neochilus	18	1								
Plectranthus caninus	14	3								
Dactyloctenium australe	11	2								
Species group D										
Setaria sphacelata	3	24	2	1	1					
Vigna frutescens	1	18								
Cucumis metuliferus	7	17							2	
Phyllanthus reticulatus	3	14	1	1						
Species group E										
Sporobolus fimbriatus			64	7	1	22	1			
Spirostachys africana			40	5		6	1	8		
Croton megalobotrys		1	34							
Ficus sycomorus			21							
Flaveria bidentis			20							
Panicum deustum			20	2		6				
Phragmites australis			19							
Hyphaene coriacea			8		3					
Phoenix reclinata			8							
Species group F										
Cissus cornifolia				54						
Tephrosia polystachya				48			1			
Corchorus asplenifolius				34				2		
Aristida congesta subsp. *congesta*			2	32	2		8			
Melhania forbesii	14	8	3	28			4	6	16	
Waltheria indica				28			2			
Solanum panduriforme		5	7	28			10			
Dalbergia melanoxylon		9	1	27						
Clerodendrum ternatum				27			1	7	16	
Acacia exuvialis				25						
Limeum fenestratum				24			2		4	
Ruellia patula				24						
Themeda triandra			4	23						
Indigofera vicioides				22						
Bothriochloa radicans			1	22				12		
Acalypha indica			4	21	1			3		
Flueggea virosa		2	2	20	7		2	9		
Asparagus setaceus				20	1		1			
Lantana rugosa	3	1		20			3			
Chamaecrista mimosoides				19						
Ceratotheca triloba				16			4			
Indigofera rhytidocarpa				16						
Bothriochloa insculpta			2	16	2	1				
Tragia dioica				16						
Endostemon tereticauli				16						
Ormocarpum trichocarpum			1	16						
Cyperus rupestris				15						
Kohautia virgata				15						
Maytenus heterophylla		2		15		1		1		
Vernonia fastigiata				15						
Sesamum alatum				15						
Blepharis integrifolia				14				1		
Talinum caffrum				14			2			
Ipomoea crassipes				14						
Vigna unguiculata				13						

TABLE 2.—Abbreviated synoptic table of Mopaneveld vegetation types in the study area (cont.)

Vegetation type	1.1	1.2	2	3	4	5	6.1	6.2	7.1	7.2
Number of relevés	*71*	*131*	*92*	*1375*	*157*	*68*	*144*	*147*	*51*	*10*
Chamaesyce neopolycnemoides				13			2			
Crabbea velutina				13						
Indigofera bainesii				13					2	
Grewia hexamita				12	1	1	3			
Sida dregei			1	12			1			
Andropogon gayanus				12						
Species group G										
Combretum hereroense		4	45	21	1	5	5	8		
Euclea divinorum		1	23	18			2	6		
Cymbopogon plurinodis			20	18	1	32		1		
Cassia abbreviata		1	15	11	2	3				
Species group H										
Eragrostis rigidior	38	32	5	36		3	1		2	
Species group I										
Ptycholobium contortum					78					
Tephrosia purpurea					73		1	2	6	
Commicarpus fallacissimus					68			1		
Acalypha villicaulis					63		8			
Achyranthes aspera			5	7	63	1	8	5	6	
Amaranthus schinzianus					61					
Cleome angustifolia				3	51		1			
Calostephane divaricata			1	4	47	1		4	2	
Indigofera heterotricha				6	44					
Kirkia acuminata		10		2	40	1	1	4		
Neuracanthus africanus			1	5	34					
Monechma debile				5	33				4	
Asparagus suaveolens					33					
Kohautia cynanchica					33					
Indigofera nebrowniana					33					
Indigofera trita					32			2	2	
Limeum sulcatum				2	28		1	4		
Ocimum americanum				7	28		7			
Jatropha spicata					27					
Grewia villosa	3	1		9	26		3	16		
Solanum coccineum			1	9	25		1			
Geigeria acaulis					25		3	8		
Justicia protracta				4	25					
Commiphora tenuipetiolata					23					
Sesamum triphyllum		1			22		2	1		
Commiphora edulis		9			21					
Leucas sexdentata					21					
Sterculia rogersii		1		2	21					
Pavonia columella			1	1	18					
Gardenia resiniflua		10		1	18		1			
Eragrostis biflora					16			1		
Digitaria velutina					15	1	1			
Adansonia digitata	1				15					
Acacia erubescens	1	7		2	15		1			
Blepharis diversispina					13				6	
Megalochlamys kenyensis					13					
Priva africana					12					
Species group J										
Bulbostylis hispidula				14	39		10		4	10
Hibiscus micranthus				47	69			12	12	
Aristida congesta subsp. *barbicollis*			1	43	50	1	1			
Heliotropium steudneri	7	3	1	29	28		1			
Dicoma tomentosa				25	69		8	7	2	
Hermannia boraginiflora				23	59		1			
Seddera capensis				22	65					
Leucas glabrata			2	19	33					
Abutilon austro-africanum			4	19	12					
Phyllanthus maderaspatensis				19	26			10	4	
Commiphora mollis		8	2	18	58	2	4	3		
Pavonia burchellii				16	30		6	4	2	
Pupalia lappacea			3	15	14		1	7	2	
Chamaecrista absus				15	30			2	4	
Mariscus rehmannianus				14	21					
Ipomoea magnusiana				13	54				2	
Hermbstaedtia odorata			1	12	21		9			
Corbichonia decumbens				10	22					
Combretum mossambicense		5	3	13	11		7	1		
Species group K										
Urochloa mosambicensis	66	67	15	54	2				2	
Maerua parvifolia	37	17	2	26	25					
Commelina benghalensis	48	39	3	26	43		1	3	4	
Kyllinga alba	37	3		9	27		3	1	6	
Grewia monticola	30	45		11	32		2			
Lannea schweinfurthii	3	13	3	22	30	6				
Philenoptera violacea	3	8	70	17	4	3				
Setaria sagittifolia	3	18	4	1	12					

TABLE 2.—Abbreviated synoptic table of Mopaneveld vegetation types in the study area (cont.)

Vegetation type Number of relevés	1.1 *71*	1.2 *131*	2 *92*	3 *1375*	4 *157*	5 *68*	6.1 *144*	6.2 *147*	7.1 *51*	7.2 *10*
Species group L										
Panicum natalense			8			29				
Sansevieria hyacinthoides			17	5	2	29				
Dicoma anomala						13	5			
Thesium utile						13	3		2	
Species group M										
Acacia nigrescens		17	45	41	30	53	1			
Eragrostis superba	1	6	15	26		25	1	4	2	
Sclerocarya birrea		3	23	32	39	28	3	2		10
Albizia harveyi		3	18	23	2	5				
Acacia gerrardii	1	2	22	8	1	44			2	
Species group N										
Triraphis purpurea						1	17	26		
Acacia nilotica			9	4			22	14	2	
Anthephora schinzii							13	21	6	
Boscia foetida			2		1		10	13	2	
Species group O										
Abutilon angulatum			3		1		15	6	4	
Eragrostis viscosa							15			
Willkommia sarmentosa							12	1		
Species group P										
Leucosphaera bainesii								62		
Enneapogon desvauxii								39	4	
Eragrostis nindensis							7	36	2	
Eragrostis echinochloidea							3	34		
Monelytrum luederitziana								25		
Hibiscus caesius								23	2	
Chascanum pinnatifidum				1			1	22	8	
Abutilon fruticosum				2	1		1	20		
Seddera suffruticosa				4			1	18	2	
Indigofera charlieriana					1		1	18	4	
Chamaesyce inaequilatera							3	17	2	
Aristida rhiniochloa				6		1	6	16		
Eragrostis porosa							5	16		
Stipagrostis hirtigluma subsp. *patula*							1	15		
Helichrysum tomentosulum								15	2	
Pegolettia senegalensis			1	2			1	15	4	
Stipagrostis hirtigluma subsp. *pearsonii*								15		
Petalidium engleranum								14	8	
Monechma genistifolium								14	4	
Gossypium triphyllum								13		
Ruelliopsis setosa								13		
Eragrostis annulata							2	13		
Hirpicium gazanioides							1	12	2	
Acacia nebrownii								12		
Species group Q										
Acacia senegal				1	11		8	11	2	
Species group R										
Combretum apiculatum	4	44	27	64	85	84	9	33	6	
Cenchrus ciliaris		1	28	11	11	24	6	50		
Enneapogon scoparius			49	10	3	52	6	10		
Combretum imberbe	3	5	56	14	5	6	9	7		
Species group S										
Terminalia sericea			1	12		5	5	1	47	100
Tephrosia dregeana							2	3	25	40
Rhus tenuinervis							3	1	20	50
Bauhinia petersiana							0		19	20
Combretum collinum				6			1		10	60
Species group T										
Acacia fleckii							3	7	49	
Philenoptera nelsii								4	49	
Merremia tridentata				7				1	49	
Elephantorrhiza suffruticosa								6	45	
Acanthosicyos naudinianus							3		43	
Requienia sphaerosperma							1		41	
Acacia ataxacantha							3	1	31	
Commiphora angolensis							1	7	31	
Albizia anthelmintica	8			1			7	7	31	
Maerua juncea			3	1			1	8	29	
Indigofera colutea								2	23	
Merremia palmata				3			2	4	22	
Harpagophytum procumbens									18	
Ipomoea verbascoidea								1	18	
Kohautia caespitosa				1			1	1	17	
Clerodendrum dekindtii								1	16	
Petalidium coccineum								1	14	
Triraphis schinzii								4	14	
Vernonia poskeana				5			3	6	14	
Oxygonum dregeanum									12	
Eragrostis dinteri							1	4	12	

TABLE 2.—Abbreviated synoptic table of Mopaneveld vegetation types in the study area (cont.)

Vegetation type Number of relevés	1.1 *71*	1.2 *131*	2 *92*	3 *1375*	4 *157*	5 *68*	6.1 *144*	6.2 *147*	7.1 *51*	7.2 *10*
Species group T (continued)										
Melinis nerviglumis	3	5					1	5	12	
Species group U										
Catophractes alexandri						1	5	45	16	
Anthephora pubescens							3	34	57	
Acacia reficiens							3	26	44	
Montinia caryophyllacea							1	25	25	
Otoptera burchellii							1	25	57	
Helinus integrifolius								23	12	
Heliotropium ovalifolium							3	17	18	
Cephalocroton mollis				1				16	10	
Hermannia modesta				2			3	15	22	
Blepharis obmitrata								15	10	
Grewia retinervis							3	15	49	
Acacia mellifera							1	14	35	
Ehretia rigida			1	9			1	13	26	
Barleria lancifolia				3	18		1	13	20	
Species group V										
Schmidtia pappophoroides				54	11	5	15	15	75	
Brachiaria deflexa			4	30	93	18	3	1	2	
Stipagrostis uniplumis			1	2	58	35	24	48	78	
Boscia albitrunca	1			5	67	3	22	30	61	
Grewia flava	3				77	6	5	19	49	
Monechma divaricatum				2	12	1	19	27	16	
Commiphora pyracanthoides				5	6	5	6	33	26	
Species group W										
Enneapogon cenchroides		6	30	52	97	71	40	61	31	
Terminalia prunioides	1		25	18	81	18	43	41	24	
Eragrostis lehmanniana			36	6	55	25	26	7	76	
Melinis repens			15	29	49	43	9	47	30	
Digitaria eriantha			12	62	10	21	1		6	
Ozoroa paniculosa			7	2	1	18	2	1	22	
Species group X										
Panicum maximum	26	72	36	68	19	21	5		14	
Acacia tortilis	20	22	10	10	20	6	10	3	4	
Species group Y										
Asparagus nelsii							6			60
Dicoma schinzii							3		4	60
Ozoroa schinzii							1			50
Requienia pseudosphaerosperma							1			40
Talinum arnotii							3		2	40
Aristida stipoides							15		6	40
Stipagrostis uniplumis var. *uniplumis*							6			30
Ochna pulchra							0		4	30
Hyphaene petersiana							5		2	20
Peltophorum africanum			4	12			2		4	20
Harpagophytum zeyheri				1			3			20
Tragus racemosus							6			20
Dichapetalum cymosum										20
Cyperus margaritaceus							1			20
Cleome rubella							3	1		20
Acrotome inflata							3		2	20
Psydrax livida							1			20
Species group Z										
Schmidtia kalihariensis							13	13	29	60
Pogonarthria fleckii							14	19	18	10
Pechuel-Loeschea leubnitziae							17	9	4	30
Acacia erioloba						1	6	1	51	30
Mundulea sericea				7			3	12	10	80
Rhigozum brevispinosum							4	19	73	10
Croton gratissimus				1	2		9	22	47	70
Urochloa brachyura				4			6	23	10	10
Species group AA										
Aristida adscensionis			32	24	80	35	16	74	12	10
Eragrostis trichophora			1	2	62	35	43	13	6	90

cant differential value include woody species such as *Grewia monticola*, *Lannea schweinfurthii*, *Philenoptera violacea*, *Maerua parvifolia* (species group K, Table 2), *Acacia nigrescens*, *Sclerocarya birrea*, *Albizia harveyi* and *Acacia gerrardii* (species group M, Table 2). Important species in the herbaceous layer include *Urochloa mosambicensis*, *Commelina benghalensis* (species group K, Table 2) and *Eragrostis superba* (species group M, Table 2). The Namibian Mopaneveld differs from the eastern Mopaneveld by species in species group Z, such as *Schmidtia kalihariensis*, *Pogonarthria fleckii* and *Acacia erioloba*. Differences in geological substrates as well as annual precipitation are the major factors driving floristic dissimilarities between the eastern and western Mopaneveld (Figure 2: Du Plessis 2001). Despite their differences, floristic affinities can be observed in the

TABLE 3.—Species richness for Mopaneveld and other savanna types presented as the mean number of species per relevé

	Species richness
Mopaneveld regions	
Save River Valley	16
Musina [Messina]	45
Honnet Nature Reserve	15
Punda Milia-Pafuri, KNP*	25
Southern limit of Mopaneveld, KNP*	39
Central district, KNP*	41
Owamboland	18
Kaokoland	12
Etosha	28
Other savanna types	
Microphyllous thornveld	30
Mixed bushveld	42
Broad-leaved savanna	27

* KNP, Kruger National Park

non-specific distribution of certain species, such as those listed in species groups A, R, V, W and X (Table 2).

Vegetation types proved sufficiently homogeneous at the scale of this study to be regarded as single units. The description of the seven proposed Mopaneveld vegetation types follows as an amplification of the suggested *Commiphoro mollis–Colophospermetea mopani* of the Central Savanna Biome, South Africa (Winterbach *et al.* 2000).

1. *Digitaria milanjiana–Colophospermum mopane* Vegetation Type

Data set 7 (Table 1).

This vegetation type represents southeastern Zimbabwean Mopaneveld of the Save River Valley. TWINSPAN distinctly separated it from the South African and Namibian Mopaneveld (Table 2; Figure 2). This type is associated with areas receiving ± 530 mm rainfall per annum. A detailed classification and description of this vegetation type was prepared by Hin (2000). Diagnostic species are listed in species group B (Table 2). High constancy values in species group C resulted in a division of this vegetation type into two major communities: the *Justicia flava–Colophospermum mopane* Major Community (Type 1.1) on deep, alluvial soils, and the *Setaria sphacelata–Colophospermum mopane* Major Community (Type 1.2) on shallow soils of rocky outcrops and inselbergs. Species richness of this plant community is low in comparison with other Mopaneveld regions (Table 3).

1.1 *Justicia flava–Colophospermum mopane* Major Community

Vegetation of this community is confined to valleys and depressions, typically those found in the Save River Valley, Zimbabwe. This tall valley bushveld on clayey alluvium is characterized by woody species such as *Zanthoxylum capense* and *Boscia mossambicensis* (species group C). The tree layer is well developed (75% cover in certain areas) with individuals of *Colophospermum mopane* (species group A) reaching heights of 16–20 m (Hin 2000). The shrub layer is less conspicuous. Herbaceous cover is high with dominant grass species such as *Sporobolus nitens* and *Enteropogon monostachys* (species group C, Table 2). Diagnostic species are listed in species group C (Table 2) and consist mostly of herbaceous species.

1.2 *Setaria sphacelata–Colophospermum mopane* Major Community

This major community is associated with disturbed land, rocky outcrops and inselbergs on well-drained, shallow, coarse sandy soils derived mainly from gneiss. The shrub layer is better developed than that of the *Justicia*

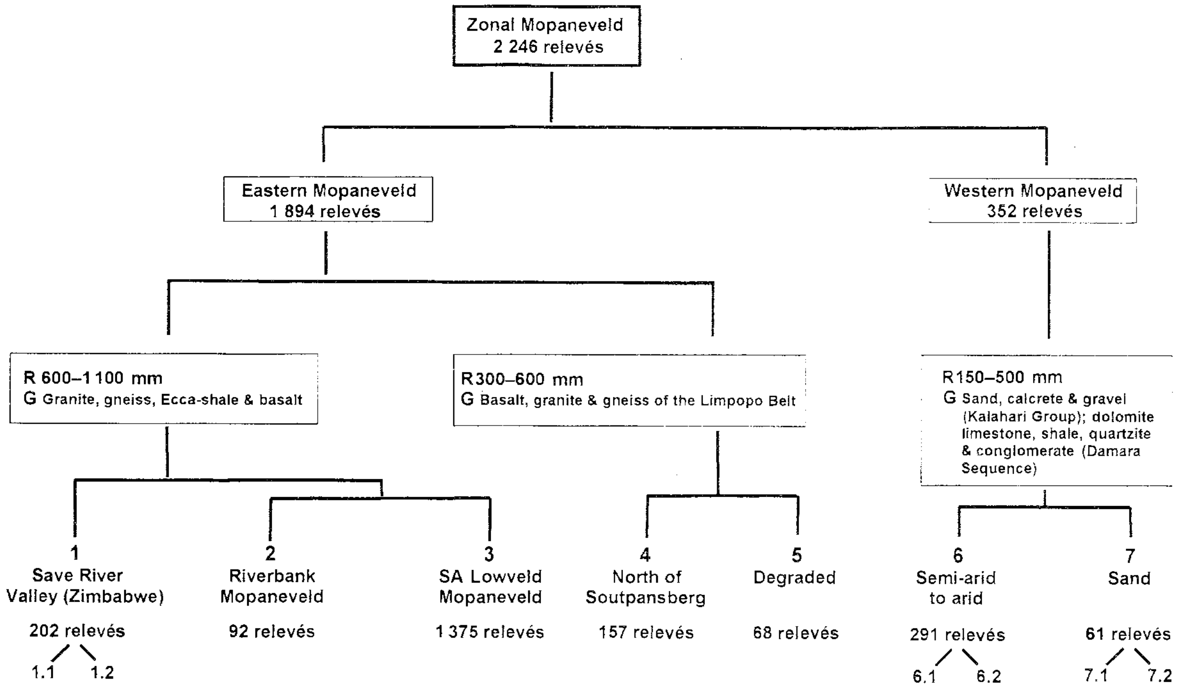


FIGURE 2.—Dendrogram depicting the TWINSPAN division of Mopaneveld vegetation in the study area. R, annual rainfall; G, major rocks.

flava–Colophospermum mopane Major Community. Tree species reach heights of 15–25 m, making it closed woodland. The herbaceous layer is well developed with dominant grass species such as *Digitaria milanjiana* (species group B) and *Setaria sphacelata* (species group D).

Although this community is not characterized by a strong diagnostic species group, its existence is supported by the very low constancy of species characteristic of the *Justicia flava–Colophospermum mopane* Major Community (species group C) and a high frequency of species such as *Setaria sphacelata* (species group D). Some diagnostic species for this community, such as the shrub *Phyllanthus reticulatus* (species group D), is representative of riparian habitats. Floristic relationships between savanna vegetation of rocky hills and riverbanks have been recorded before in the arid Lowveld vegetation of South Africa (Bredenkamp & Deutschländer 1995).

2. *Croton megalobotrys–Colophospermum mopane* Vegetation Type

Data sets 1, 3, 6, 7, 11 & 14 (Table 1).

This vegetation type is associated with South African and Zimbabwean riparian vegetation on alluvium, although it does not represent typical azonal (riparian) vegetation due to the high abundance of terrestrial plant species such as *C. mopane* (species group A). Mopane is known to grow on a wide variety of soils, including 'wet' soils of alluvial origin (Van Rooyen 1978; Biggs 1979; O'Connor & Campbell 1986). This type therefore represents a transition between true terrestrial and riparian vegetation. Annual rainfall varies between 350 and 800 mm. The tree layer is well developed and often forms tall, closed woodland (Van Rooyen 1981). Woody plant species of floodplains and riverbanks, such as *Croton megalobotrys*, *Ficus sycomorus*, *Hyphaene coriaceae*, *Phoenix reclinata* and *Spirostachys africana* (species group E) are abundant. Grass species adapted to moist conditions, such as *Sporobolus fimbriatus* (species group E), characterize this vegetation type.

Diagnostic species are listed in species group E (Table 2). This vegetation type shows little relationship with the western (Namibian) Mopaneveld.

3. *Cissus cornifolia–Colophospermum mopane* Vegetation Type

Data sets 1, 3, 5, 6, 11, 13 & 14 (Table 1).

A large number of relevés (1 375) were classified under this vegetation type, which is predominantly found in the South African Lowveld Mopaneveld, covering an area of ± 7 250 km^2 (Gertenbach 1987). Most of the relevés of this vegetation type were taken from studies in the Kruger National Park, South Africa (e.g. data sets 3, 5, 6 & 14, Table 1). It is comparable to Broad-Sclerophyll Arid Bushveld (Werger & Coetzee 1978) with an annual rainfall of 350–600 mm (Gertenbach 1980).

The structure of this community varies according to geology—from tall woodland (on shale) to dwarf shrub (on basalt). Diagnostic species are listed in species group F (Table 2). Other species commonly associated with this vegetation type include *Combretum apiculatum* (species group R), *Grewia bicolor*, *Commiphora africana* (species group A), and *Schmidtia pappophoroides* (species group V) in Mopane Bushveld, and *Acacia nigrescens* (species group M), *Dalbergia melanoxylon* (species group F), *Combretum imberbe* (species group R), *Themeda triandra* and *Bothriochloa radicans* (species group F) in Mopane Shrubveld (Low & Rebelo 1996). Species richness varies between values of 25 in the northern, sandy areas to 41 in the central district on clayey soil (Table 3). This vegetation type has a poor floristic affinity with the Namibian Mopaneveld (Table 2; Figure 2) due to higher annual rainfall and differences in geological substrates (Figure 2).

4. *Ptycholobium contortum–Colophospermum mopane* Vegetation Type

Data sets 1, 2, 3 & 15 (Table 1).

This vegetation type is confined to the Mopaneveld north of the Soutpansberg in the Limpopo River Valley, South Africa. The vegetation of the Messina Experimental Farm (Dekker & Van Rooyen 1995, Data set 2) is well represented in this vegetation type. This low, open to closed woodland type covers an area of 2 037 km^2 between 300 and 780 m altitude (Louw 1970) and receives ± 350 mm rainfall per annum. The geology of this area comprises mosaic formations of metamorphic rocks belonging to the Archaean Complex.

Several *Commiphora* species are known to be diagnostic for this Mopaneveld (Louw 1970), of which *C. tenuipetiolata*, *C. edulis* (species group I), *C. mollis* (species group J) and *C. africana* (species group A) are abundant. Another conspicuous feature of this vegetation type is the scattered stands of *Adansonia digitata* (species group I) on sandy, undulating plains derived from granite and gneiss (Dekker & Van Rooyen 1995). Diagnostic species are listed in species group I (Table 2). The highest species richness values in the study area of Musina (Messina) (Table 3) were recorded for this vegetation type. Floristically it is related to the *Cissus cornifolia–Colophospermum mopane* Vegetation Type (species group J), although it has a more diverse floristic composition, especially in the woody component. Although this vegetation type occurs under the most arid conditions for Mopaneveld in South Africa, it is not similar to the Namibian Mopaneveld.

5. *Enneapogon scoparius–Colophospermum mopane* Vegetation Type

Data sets 1, 8 & 15 (Table 1).

Relevés delineating this vegetation type were sampled in areas that were overgrazed, used for military training and as dumping sites (Beck 1998). In addition, some relevés were sampled during sustained drought conditions. Based on general climatic conditions and location, it was expected that these data sets (data sets 1, 8 & 15,

Table 1) would be classified under the *Ptycholobium contortum–Colophospermum mopane* Vegetation Type, but due to harsh environmental conditions it represents seral communities in semi-arid South African Mopaneveld. Diagnostic species are listed in species group L (Table 2). Especially grass species are conspicuous and include *Panicum natalense* (species group L), *Enneapogon scoparius* (species group R), *Stipagrostis uniplumis* (species group V), *Enneapogon cenchroides*, *Melinis repens* (species group W), *Aristida adscensionis* and *Eragrostis trichophora* (species group AA). These species are generally unpalatable grasses, typically associated with disturbed areas.

6. *Boscia foetida–Colophospermum mopane* Vegetation Type

This vegetation type represents the semi-arid to arid Mopaneveld of Namibia. It is strongly associated with harsh environments on mainly sand, gravel and calcrete of the Kalahari Group and dolomites, limestone, shale, quartzite and conglomerate of the Damara Sequence. This shrubveld to open tree savanna is characterized by species group N (Table 2). The conspicuous tree, *Boscia foetida*, which is known for its association with semi-arid environments, is diagnostic for this community.

6.1 *Eragrostis viscosa–Colophospermum mopane* Major Community

Data sets 3, 4, 8, 9, 10, 12 & 15 (Table 1).

Although this community is differentiated only by three species (species group O), it comprises elements of extreme habitats such as Mopaneveld of the Cuvelai Delta on aeolian sands of the Kalahari Group (Owamboland, Namibia) and the arid Kaokoland (northern Namibia). Soils are generally sandy with a clayey or calcareous subsoil and include mopane shrubveld (Owamboland, 500 mm rainfall/annum) and open tree/ shrub savanna (Kaokoland, 200 mm rainfall/annum). Relevés from the Honnet Nature Reserve, north of the Soutpansberg, South Africa (Visser *et al.* 1996) are more associated with this community than with its nearest neighbour, the *Ptycholobium contortum–Colophospermum mopane* Vegetation Type (type 4).

Tree species such as *Boscia albitrunca* (species group V) and *Terminalia prunioides* (species group W) dominate the tree layer, whereas *Stipagrostis uniplumis* (species group V), *Enneapogon cenchroides* (species group W) and *Eragrostis trichophora* (species group AA) are dominant grass species.

This community needs refinement on a smaller scale, because heterogeneous combinations could not be clearly expressed by TWINSPAN procedures on the large scale of this study. Species richness of the Kaokoland parts of this community is the lowest for the study area (i.e. 12, Table 3) and moderate to low (18, Table 3) in the Owamboland region.

6.2 *Leucosphaera bainesii–Colophospermum mopane* Major Community

Data sets 9 & 10 (Table 1).

This dry, deciduous tree savanna (300–450 mm annual rainfall) is found in the Etosha National Park and surrounding areas in Namibia and occurs on calcareous ridges and plains of the Kalahari Group. Diagnostic species are listed in species group P (Table 2), including the prominent *Leucosphaera bainesii*, which is known to be associated with calcareous soils. *Colophospermum mopane* individuals on these sodium-rich soils are usually only 2–6 m tall and are associated with a poorly developed herbaceous layer (Le Roux 1980; Timberlake 1995). On very shallow lithosols of calcrete substrates, *C. mopane* is accompanied by *Acacia reficiens* (species group U) and *Terminalia prunioides* (species group W) in the tree stratum, and *Boscia foetida* (species group N). *Monechma genistifolium* and *Petalidium engleranum* (species group P) in the shrub stratum. In sites where aeolian sands cover calcrete boulders, *Catophractes alexandri*, *Otoptera burchellii* (species group U), *Rhigozum brevispinosum* and *Mundulea sericea* (species group Z) become prominent. The herbaceous layer is well developed and includes species such as *Anthephora schinzii* (species group N), *Enneapogon desvauxii*, *Stipagrostis hirtigluma* (species group P) and *Enneapogon cenchroides* (species group W). Lithosols derived from andesites are relatively fertile and produce a heterogeneous vegetation type on this hilly landscape. The herbaceous stratum is perennial with *Eragrostis nindensis* (species group P) being very prominent (Le Roux *et al.* 1988).

This community is distinctly separated from community 6.1 and shares a number of species with the *Philenoptera nelsii–Colophospermum mopane* Major Community (Type 7.1) (species group U). Species richness for this community is moderate to high (i.e. 28 species per relevé, Table 3).

7. *Bauhinia petersiana–Colophospermum mopane* Vegetation Type

This vegetation type is confined to deep Kalahari sands that are mainly of aeolian origin. Annual rainfall varies between 300 mm and 400 mm. This sandy, dry bushveld is best represented in the sandveld areas of Etosha National Park, Namibia. Diagnostic species are listed in species group S (Table 2). Although *Colophospermum mopane* is often associated with heavier, clayey soils in higher rainfall areas, it is also well represented within this vegetation type (species group A).

7.1 *Philenoptera nelsii–Colophospermum mopane* Major Community

Data sets 4 & 9 (Table 1).

This community represents vegetation associated with Kalahari sands of aeolian origin within the arid Namibian Mopaneveld. Several species indicative of soils containing a high sandy content characterize this community (species group T) and include *Philenoptera nelsii*, *Acanthosicyos naudinianus*, *Requienia sphaerosperma* and *Harpagophytum procumbens*. Habitats typical of this community include Kowares Sandy Mopane Shrubveld (Kaokoland section, Etosha National Park) and the Sandy Shrub Mopaneveld (Sandveld areas, Etosha National Park), often overlying calcrete (Le Roux 1980). The floristic component of calcareous substrates links this community to the *Leucosphaera bainesii–Colophospermum mopane* Major Community (species group U). Species in species group V links this community to the South African Mopaneveld types. Species richness for this community is 35 (Table 3), which is moderate to high when compared to other types.

7.2 *Asparagus nelsii–Colophospermum mopane* Major Community

Data sets 10 & 12 (Table 1).

This unique community of only 10 relevés represents the moister northeastern Namibian Mopaneveld, adjacent to the Caprivi. These mopane woodlands lie in an area of old river drainage lines, which are covered by aeolian sand deposits (Mendelsohn & Roberts 1997). This dry, early-deciduous savanna woodland includes species that prefer deep sandy soils, such as *Requienia pseudosphaerosperma*, *Hyphaene petersiana*, *Harpagophytum zeyheri* and *Dichapetalum cymosum* (species group Y). Other diagnostic species are listed in species group Y. It shows a strong floristic affinity with the *Philenoptera nelsii–Colophospermum mopane* Major Community (Type 7.1). The environmental conditions of this community are different from any other vegetation type or major plant community. Although it represents moister Namibian Mopaneveld, moisture conditions are still low and erratic, which probably relate it to the *Philenoptera nelsii–Colophospermum mopane* Major Community. Species richness is low (i.e. 18, Table 3), especially when compared with community 7.1.

Evaluation of vegetation types

Although the Zimbabwean data set from the Save River Valley provided baseline information for the identification of the *Digitaria milanjiana–Colophospermum mopane* Vegetation Type and a comparison with other Mopaneveld types, comprehensive vegetation studies of other types in Zimbabwean Mopaneveld would need to be included for a more detailed account.

The *Croton megalobotrys–Colophospermum mopane* Vegetation Type does not include riparian vegetation from Namibia. In Namibia, Mopaneveld is restricted to the upper clayey soils where the rivers are deeply incised. Shallow rivers tend to dry out seasonally, which consequently gives *C. mopane* the ability to inhabit these dry, sandy washes. In the Cuvelai Delta, northern Namibia, isolated patches of Mopaneveld are often associated with upland islands within the broad, sandy, calcareous shores. Local-scale studies on Namibian Mopaneveld could separate these discontinuous Mopaneveld patches within the Cuvelai Delta.

The *Cissus cornifolia–Colophospermum mopane* Vegetation Type is more diverse than what is obvious in Table 2. These 1 375 relevés of the South African Lowveld Mopaneveld were classified independently (Du Plessis 2001), and revealed the identification of at least four different major plant communities on different geological substrates, namely the (a) *Terminalia sericea–Colophospermum mopane* Community on sandy soils derived from alluvium, shale, andesite and the Malvernia Formation; (b) *Acacia nigrescens–Colophospermum mopane* Community on heavy clays derived from basalt and gabbro; (c) *Euclea divinorum–Colophospermum mopane* Community on clayey soils derived from shale of the Ecca Group; and (d) *Combretum apiculatum–Colophospermum mopane* Community on coarse, well-drained, sandy soils derived from granite and gneiss. Differentiation in geological parent material is responsible for the distinct physiognomical variance typically associated with the South African Lowveld Mopaneveld: Mopane Shrubveld and Mopane Bushveld (Low & Rebelo 1996, types 9 & 10). Mopane Shrubveld occurs on flat plains of vertic or near-vertic clays derived mainly from igneous gabbro and basalt. The shrubveld type is generally dominated by a stunted and multi-stemmed shrubby growth of *Colophospermum mopane*. In contrast with Mopane Shrubveld, Mopane Bushveld is characterized by a fairly dense growth of *C. mopane* trees occurring on undulating landscapes derived from basalt, shale, solonetzes and coarse, sandy soils derived from granite (Van Rooyen & Bredenkamp 1998).

The area north of the Soutpansberg is associated with a diversity of geological substrates. However, the *Ptycholobium contortum–Colophospermum mopane* Vegetation Type was not separated into lower syntaxa. A further classification of Mopaneveld vegetation data from this region should reveal the identification of different plant communities based on geology. More data sets would be needed for a detailed synthesis.

As a seral vegetation unit, it may be questioned whether the *Enneapogon scoparius–Colophospermum mopane* Vegetation Type carries sufficient weight to be treated as an independent vegetation type. Seral communities are temporal variations of 'true' communities and can therefore be regarded as a variant of such communities. On a scale as large as the Mopaneveld, it can, however, be valued as a vegetation type since it is likely to be repeated spatially. On a local scale, it should rather be considered a variant.

Colophospermum mopane-dominated vegetation of Namibia is more differentiated than Giess (1998) suggested (Table 2). Mopane savanna in Namibia comprises elements of Dry Early-Deciduous Shrub Savanna (Wild & Barbosa 1967), elements of the Early-Deciduous Savanna Woodland and an Intermediate Deciduous Savanna (Timberlake 1995). According to descriptions of *Colophospermum mopane*-dominated vegetation in Namibia (Giess 1998), the *Boscia foetida–Colophospermum mopane* Vegetation Type represents the intermediate lower, sparser Dry Deciduous Mopane Savanna.

The *Eragrostis viscosa–Colophospermum mopane* Major Community, Type 6.1, comprises communities that are not reflected at this scale: Owamboland and Kaokoland. Owamboland (northern Namibia) is a broad plain about 1 100 m above sea level. Aeolian Kalahari sands of varying depth cover the area with scattered patches of calcareous substrates. Oshanas are seasonally flooded watercourses of the Cuvelai Delta in Owamboland. Mopaneveld occurs as interfaces on slightly elevated terraces between the oshanas. Dominant trees include

Colophospermum mopane, several species of *Acacia*, *Combretum* and *Commiphora*, the palm *Hyphaene petersiana*, *Adansonia digitata*, *Terminalia prunioides* and *T. sericea*. However, in the dry, central parts of the Kaokoland escarpment, an open tree savanna predominates at an altitude between 700 m and 1 100 m. Being the dominant woody species for this open savanna, *Colophospermum mopane* occurs here as a small tree (height of 2.5 m). Accompanying species in this savanna type include *Catophractes alexandri*, *Terminalia prunioides*, *Combretum apiculatum*, *Euphorbia damarana*, *Ceraria longipedunculata*, *Commiphora multijuga*, *C. virgata*, *C. africana*, *Maerua schinzii* and *Sesamothamnus guerichii* (Werger & Coetzee 1978). The herbaceous stratum is poorly developed, with *Schmidtia kalihariensis* (species group Z) the dominant grass. The strange grouping of relevés from Honnet Nature Reserve (South Africa) with the *Eragrostis viscosa–Colophospermum mopane* Major Community (Namibia) can probably be explained by the dry conditions under which sampling were undertaken. At the time of sampling (1995), the vegetation of the Honnet Nature Reserve was in a degraded state, especially the herbaceous component, which relates it to a certain state in the semi-arid/arid Namibian Mopaneveld.

The *Bauhinia petersiana–Colophospermum mopane* Vegetation Type is different from all other Mopaneveld types in that it is associated with sandy, rather than clayey soil. The *Philenoptera nelsii–Colophospermum mopane* Major Community, Type 7.1, is floristically linked to other types across the Mopaneveld range (species groups V, W & X) due to its calcareous substrate. Deep Kalahari sand on which the *Asparagus nelsii–Colophospermum mopane* Major Community, Type 7.2, occurs, makes it is floristically poorly related to other Mopaneveld types. Its relationship with Namibian Mopaneveld (species group Z) is due to similar climatic conditions. Despite these poor relationships and the high sand content of the soil, *Colophospermum mopane* has a frequency of 80% in this type, which suggests a sandy topsoil, underlain by clayey subsoil.

Ordination

Vegetation types and major plant communities along the first and third axes of a Detrended Correspondence Analysis (DECORANA) scatter diagram is shown in Figure 3. Due to insufficient environmental data available, no clear explanation could be found for the distribution of the vegetation types along environmental axes. The ordination, however, supports the geographical and climatic (mean annual rainfall) separations between Zimbabwe (far left), South Africa (middle) and Namibia (far right) (Axis 1, Figure 3). The distribution of vegetation types and major plant communities along the vertical axis from bottom to top (Axis 3) probably follows a decrease in soil depth and an increase in clay content (Figure 3). Soil moisture availability is a major factor that determines the distribution of Mopaneveld vegetation types (Timberlake *et al.* 1993). Although all interacting factors determining soil moisture availability were not assessed (i.e. rainfall, topography, soil texture and depth, drainage and rooting habit), the interaction of soil depth, soil texture and annual rainfall had a significant influence on the distribution of vegetation types along a soil moisture availability gradient (Figure 3).

Species richness

There are distinct differences in species richness within Mopaneveld of different regions (Table 3). Despite its higher rainfall, Zimbabwean Mopaneveld has lower species richness than South Africa. Kaokoland (Namibia) has the lowest species richness in Mopaneveld, whereas Musina (Messina) has the highest. Etosha has the highest species richness in Namibia, probably due to the diversity in landscapes. Species richness in the South African Mopaneveld varies considerably (from 15 to 45). However, the data sets selected for species richness calculation of Mopaneveld in South Africa were sampled during different rainfall conditions. For instance, the area north of the Soutpansberg normally receives ± 350 mm rainfall per annum, but Honnet

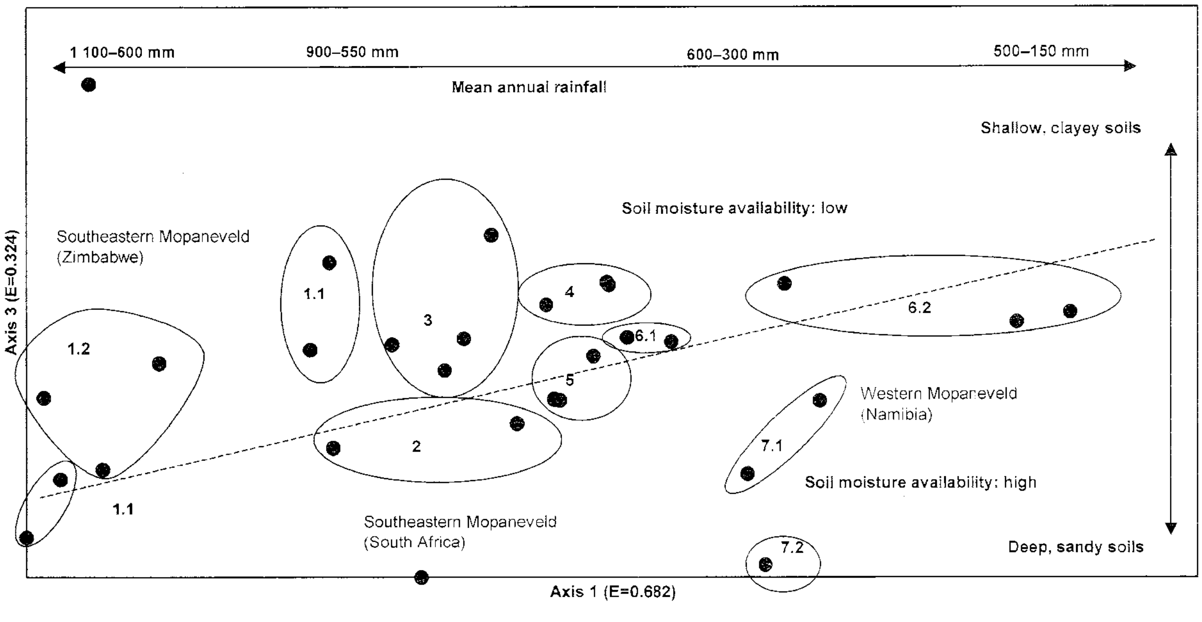


FIGURE 3.—Ordination diagram of axes 1 and 3 illustrating the distribution of Mopaneveld vegetation types along environmental gradients.

Nature Reserve (15, Table 3) was surveyed during a drought year (rainfall less than 100 mm/annum), and Musina (Messina) (45, Table 3) was surveyed during a wetter year after a drought (>200 mm/annum). It has been shown that perennial herbaceous species disappear after a drought event in a semi-arid savanna, but are replaced by annuals after the first rainfall event (O'Connor 1999). According to Oelofse *et al.* (2000), Mopaneveld vegetation follows a 'state-and-transition' model for vegetation change, which suggests that the herbaceous layer dies back after an event such as overgrazing, fire or drought, but responds rapidly to an event such as rainfall. The response to rainfall is usually a dense cover of many different annual species, which temporarily induces an increase in plant species richness. Furthermore, species richness in Mopaneveld is often dependent on the cover of *Colophospermum mopane*. High cover of *C. mopane* results in low species richness, whereas a higher species richness is noted in areas with low *C. mopane* cover (O'Connor 1992). It can therefore be suggested that high annual rainfall and high tree cover (e.g. Zimbabwean Mopaneveld) do not induce species richness, but rather unpredictable rainfall events and low tree cover in semi-arid areas such as the Musina (Messina) region.

When species richness of other savanna types are compared with Mopaneveld types, Mopaneveld appears to be richer than expected (Table 3). This comparison of species richness (alpha-diversity), however, does not suggest high species diversity. According to Timberlake (1995) Mopaneveld has a low gamma diversity due to typically associated species being common and present in most vegetation types across its range. These typical tree species include *Acacia nigrescens*, *A. nilotica*, *Adansonia digitata*, *Albizia harveyi*, *Balanites* spp., *Combretum apiculatum*, *C. hereroense*, *Commiphora* spp., *Dalbergia melanoxylon*, *Diospyros quiloensis*, *Erythroxylum zambesiacum*, *Kirkia acuminata*, *Sclerocarya birrea*, *Terminalia prunioides*, *T. stuhlmannii* and *Ziziphus mucronata*. Shrubs include *Combretum elaeagnoides*, *Dichrostachys cinerea*, *Gardenia resiniflua*, *Grewia* spp., *Ximenia americana* and species of the family Capparidaceae. Mopaneveld is therefore species rich, but low in species diversity.

Limitations

Broad-scale phytosociological syntheses have limitations, which should not be ignored:

1. Adequate phytosociological data sets were limited for Zimbabwe and Namibia. These regions are therefore weakly represented in this comparative study. Consequently, this study only touches on differences and associations between the geographically separated Mopaneveld regions and is not a detailed account of the region.

2. Limited environmental data were available from the selected studies, which influenced the interpretation of results (e.g. ordination). Dealing with this constraint emphasized the need for the collection of detailed environmental data, which include, amongst others, Global Positioning System (GPS) readings for each sample plot.

3. Mopaneveld is considered an event-driven system (Du Plessis 2001) and is characterized by highly dynamic, unstable vegetation states. Vegetation classification of such systems is intricate due to temporal and spatial relationships between communities. This dynamic character of Mopaneveld vegetation, especially in the field layer, causes a major constraint in phytosociological syntheses in that plant communities are irregularly separated or combined by TWINSPAN procedures. Plant community descriptions are therefore not accurate and it is suggested that plant community descriptions in semi-arid regions should focus only on perennial herbaceous and woody species rather than a total floristic composition.

4. Although the objectives of this study were to identify major vegetation types, too little variation could be derived from TWINSPAN classification on the regional scale. It therefore became evident that detailed phytosociological syntheses should also be undertaken on a local scale. For instance, Becker & Jürgens (2000) identified a total of four major vegetation units along a decreasing moisture gradient in Kaokoland. This kind of variance is easily overlooked on a regional scale.

5. Differences in mean annual rainfall appears to be one of the major driving forces on a regional scale, but on a local scale soil character plays an important role. The Zimbabwean vegetation type was separated into two major communities based on soil and topography. In the Namibian Mopaneveld, the *Boscia foetida–Colophospermum mopane* Vegetation Type, as well as the *Bauhinia petersiana–Colophospermum mopane* Vegetation Type, was subdivided into two major types based on soil type. The *Eragrostis viscosa–Colophospermum mopane* Major Community, Type 6.1, occurs on clayey soil with a thin sand deposit, whereas the *Leucosphaera bainesii–Colophospermum mopane* Major Community, Type 6.2, is characterized by calcareous substrates. Although the South African Lowveld Mopaneveld was not separated during the classification of the entire data set, separate classification procedures revealed distinct major plant communities according to soil type (Du Plessis 2001).

6. Vegetation types represent broad units with some variation in environmental conditions, which therefore constitute different habitats, with different plant communities of lower rank. Certain species are confined to these plant communities (habitats), though will not have any influence on a synoptic table, as these communities are all consolidated into the single synrelevé. Such species of limited distribution often have low frequency values and may not be included in the synoptic table. The vegetation types may therefore be floristically and environmentally much more diverse than indicated by the table and descriptions.

CONCLUSIONS

Despite the limitations associated with a phytosociological synthesis, this classification and description revealed a discernible difference between Mopaneveld vegetation of South Africa, Namibia and Zimbabwe. Although Mopaneveld vegetation varies between different geographical regions, there is a relationship between Zimbabwean and South African Mopaneveld. The Namibian Mopaneveld displays few relationships with the eastern Mopaneveld, although the dynamics of the herbaceous layer in Mopaneveld vegetation may induce temporal shifts in plant communities towards spatial affinities. Species richness in Mopaneveld is therefore a weak indication of species diversity due to the dynamic shifts in the field layer. This study makes Mopaneveld floristically and on plant community levels far more extensive than was previously thought.

ACKNOWLEDGEMENTS

Our appreciation to all the researchers who made their data available for this project, although in some cases the data have not been published. Mr Ben Ströhbach from the National Botanical Research Institute in Windhoek, Namibia is gratefully acknowledged for his valuable input and assistance with field work in Namibia. Mr Jacques Gerber is thanked for proofreading the manuscript. The National Research Foundation and the University of Pretoria funded this research project. An anonymous reviewer provided constructive comments on the manuscript.

REFERENCES

ACOCKS, J.P.H. 1953. Veld types of South Africa, edn 1. *Memoirs of the Botanical Survey of South Africa* No. 28: 1–192.

BECK, N.D. 1998. *A wildlife management plan involving ecological studies of plant communities and animal populations for Foskor mine, Phalaborwa.* B.Sc.(Hons.) project, University of Pretoria, Pretoria.

BECKER, T. & JÜRGENS, N. 2000. Vegetation along climate gradients in Kaokoland, North-West Namibia. *Phytocoenologia* 30: 543–565.

BIGGS, R.C. 1979. *The ecology of Chief's Island and the adjacent floodplains of the Okavango Delta, Botswana.* M.Sc. thesis, University of Pretoria, Pretoria.

BREDENKAMP, G.J. & DEUTSCHLÄNDER, M.S. 1995. New azonal syntaxa from the hills and river banks of the Manyeleti Game Reserve, Northern Transvaal Province, South Africa. *Koedoe* 38: 41–58.

COLE, M.M. 1986. *The savannas: biogeography and geobotany.* Academic Press, London.

DEKKER, B. & VAN ROOYEN, N. 1995. The physical environment and plant communities of the Messina Experimental Farm. *South African Journal of Botany* 61: 158–167.

DU PLESSIS, F. 2001. *A phytosociological synthesis of Mopaneveld.* M.Sc. thesis, University of Pretoria, Pretoria.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 26: 9–121.

GERTENBACH, W.P.D. 1987. *'n Ekologiese studie van die suidelikste Mopanieveld in die Nasionale Krugerwildtuin.* D.Sc. thesis, University of Pretoria, Pretoria.

GIESS, W. 1998. A preliminary vegetation map of Namibia. *Dinteria* 4: 5–112.

HENNEKENS, S.M. 1996a. *TURBOVEG: software package for input, processing and presentation of phytosociological data.* IBN-DLO, Wageningen, University of Lancaster.

HENNEKENS, S.M. 1996b. *MEGATAB: a visual editor for phytosociological tables.* Giesen & Geurts, Ulft.

HILL, M.O. 1979a. *TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes.* Cornell University, Ithaca, New York.

HILL, M.O. 1979b. *DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Cornell University, Ithaca, New York.

HIN, C.J. 2000. *A natural resource inventory of Sango Ranch, Save Valley Conservancy, Zimbabwe.* M.Sc. thesis, University of Pretoria, Pretoria.

LE ROUX, C.J.G. 1980. *Vegetation classification and related studies in the Etosha National Park.* D.Sc. thesis, University of Pretoria, Pretoria.

LE ROUX, C.J.G., GRUNOW, J.O., MORRIS, J.W., BREDENKAMP, G.J. & SCHEEPERS, J.C. 1988. A classification of the vegetation of the Etosha National Park. *South African Journal of Botany* 54: 1–10.

LOUW, A.J. 1970. *'n Ekologiese studie van die Mopanie-veld noord van die Soutpansberg.* D.Sc. thesis, University of Pretoria, Pretoria.

LOW, A.B. & REBELO, A.G. (eds). 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

MADAMS, R.W. 1990. *The biogeography of* Colophospermum mopane *(Kirk ex Benth.) Kirk ex J. Léonard at its distribution limits in eastern Botswana.* Ph.D. thesis, University of London, UK.

MAPAURE, I. 1994. The distribution of mopane. *Kirkia* 15: 1–5.

MENDELSOHN, J. & ROBERTS, C. 1997. *An environmental profile and atlas of Caprivi.* Environmental Profiles project, Directorate of Environmental Affairs, Namibia.

O'CONNOR, T.G. 1992. Woody vegetation—environment relations in a semi-arid savanna in the northern Transvaal. *South African Journal of Botany* 58: 268–274.

O'CONNOR, T.G. 1999. Impact of sustained drought on a semi-arid *Colophospermum mopane* savanna. *African Journal of Range and Forage Science* 15: 83–91.

O'CONNOR, T.G. & CAMPBELL, B.M. 1986. Classification and condition of the vegetation types of the Nyahungwe area on the Lundi River, Gonarezhou National Park, Zimbabwe. *South African Journal of Botany* 52: 117–123.

OELOFSE, J., BROCKETT, B.H., BIGGS, H.C. & EBERSOHN, C. 2000. The effect of drought and post-fire grazing on the herbaceous layer of shrub-mopane veld on basalt in the Kruger National Park, South Africa. *Sixth International Rangeland Congress Proceedings* 1: 505–507.

TIMBERLAKE, J.R. 1995. *Colophospermum mopane*: annotated bibliography and review. *The Zimbabwean Bulletin of Forestry Research* 11: 1–49.

TIMBERLAKE, J.R. 1999. *Colophospermum mopane*: an overview of current knowledge. In J.R. Timberlake & S. Kativu, *African plants: biodiversity, taxonomy and uses*: 565–571. Royal Botanic Gardens, Kew.

TIMBERLAKE, J.R., NOBANDA, N. & MAPAURE, I. 1993. Vegetation survey of the communal lands—north and west Zimbabwe. *Kirkia* 14: 171–270.

VAN ROOYEN, N. 1978. *'n Ekologiese studie van die plantgemeenskappe van die Punda Milia-Pafuri-Wambiyagebied in die Nasionale Krugerwildtuin.* M.Sc. thesis, University of Pretoria, Pretoria.

VAN ROOYEN, N. 1981. A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa: 3. The *Colophospermum mopane* communities. *Journal of South African Botany* 47: 585–626.

VAN ROOYEN, N. & BREDENKAMP, G.J. 1998. Mopane Shrubveld, Mopane Bushveld. In A.B. Low & A.G. Rebelo, *Vegetation of South Africa, Lesotho and Swaziland*: 9, 10. Department of Environmental Affairs & Tourism, Pretoria.

VISSER, N., VAN HOVEN, W. & THERON, G.K. 1996. The vegetation of the Honnet Nature Reserve, Northern Province, South Africa. *Koedoe* 39: 25–42.

WERGER, M.J.A. & COETZEE, B.J. 1978. The Sudano-Zambezian Region. In M.J.A. Werger, *Biogeography and ecology of southern Africa*: 301–462. Junk, The Hague.

WHITE, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. *Natural Resources Research* 20: 1–356.

WILD, H., & BARBOSA, L.A.G. 1967. Supplement of the vegetation map of the *Flora zambesiaca* area. In H. Wild & A. Fernandes, *Vegetation map of the* Flora zambesiaca *region.* Harare, Zimbabwe.

WINTERBACH, R., BREDENKAMP, G.J., DEUTSCHLÄNDER, M.S. & MUCINA, L. 2000. Preliminary syntaxonomic scheme of vegetation classes for the Central Bushveld of South Africa. In P.S. White, L. Mucina, J.S. Leps & E. van der Maarel, *Proceedings IAVS Symposium*: 123–147. Opulus Press, Uppsala.

APPENDIX 5-2

Fidelity syntable of the broad-scale Mopaneveld vegetation synthesis after the application of the Modified TWINSPAN algorithm

Appendix 5-2

Percentage Phi-coefficient fidelity syntable (Chapter 5).

Species names are coded according to JUICE 7.0 (Tichý & Holt, 2006)

Species used in plant community names (Chapter 5) are shaded in grey

	1	2.1	2.2	3	4	5.1.1	5.1.2	5.2	6.1	6.2
	67	45	176	508	111	43	93	105	65	1049
Species group 1 [1]										
ERAGECH	78.2	---	---	---	---	---	---	---	---	---
LEURBAI	74	---	14.3	---	---	---	---	---	---	---
ENNEDES	72.4	---	2.9	---	---	---	---	---	---	---
MONLLUE	62.2	---	---	---	---	---	---	---	---	---
ERAGANN	48.4	---	---	---	---	---	---	---	---	---
RUEISET	47.1	---	---	---	---	---	---	---	---	---
CHASINA	46.3	---	---	---	---	---	---	---	---	---
INDGCHA	43.7	---	5.4	---	---	---	---	---	---	---
PETLENG	41.7	---	4.4	---	---	---	---	---	---	---
GEIGODO	41.5	---	---	---	---	---	---	---	---	---
ACACNEB	41.2	---	---	---	---	---	---	---	---	---
HIRPGAZ	40.8	---	---	---	---	---	---	---	---	---
AIZNVIR	39.5	---	---	---	---	---	---	---	---	---
CYAHLAN	37.9	---	---	---	---	---	---	---	---	---
APTOLIN	33.6	---	---	17.8	---	---	---	---	---	12.9
AIZODIN	20.1	---	---	---	---	---	---	---	---	---
MONEGEN	38.8	---	4.2	---	---	---	---	---	---	---
ERAGGLA	37.7	---	---	---	---	---	---	---	---	---
HELRLIN	36.3	---	---	---	---	---	---	---	---	---
KOHAAZU	35.8	---	---	---	---	---	---	---	---	---
HERMMOD	34.7	---	9.8	---	---	---	---	---	---	---
STIRH-E	32.2	---	7.9	---	---	---	---	---	---	---
PTYHBIF	26.9	---	7.6	---	---	---	---	---	---	---
ERAGPOR	25	---	9	---	---	---	---	---	---	---
ACALSEG	20.1	---	9.7	---	---	---	---	---	---	---
SPORSPI	24.9	---	---	---	---	---	---	---	---	---
STIRHIR	23.3	---	---	---	---	---	---	---	---	---
LYCIBOS	23.2	---	---	---	---	---	---	---	---	---
SETAVER	22.4	---	---	---	---	---	---	---	---	---
SALSTUB	20.1	---	---	---	---	---	---	---	---	---
ERAGSAB	20.1	---	---	---	---	---	---	---	---	---
STIRHOC	22.6	---	7.9	---	---	---	---	---	---	---
SPORACI	22	---	---	---	---	---	---	---	---	---
BRACMAL	21.4	---	---	---	---	---	---	---	---	---
Species group 2 [2]										
SCHFKAL	---	36.3	24.3	---	---	---	---	---	---	---
POGOFLE	---	37.7	25.4	---	---	---	---	---	---	---
CRONGRA	---	12.7	33.2	---	---	---	---	---	---	---
Species group 3 [2.1]										
ERAGTRI	---	70.8	---	12.5	---	---	---	---	---	---
ERAGVIS	---	59.6	---	---	---	---	---	---	---	---

ARITSTI	---	56	---	---	---	---	---	---	---	---
WILKSAR	---	44	---	---	---	---	---	---	---	---
HYPNPET	---	38.9	---	---	---	---	---	---	---	---
ASPRNEL	---	36.4	---	---	---	---	---	---	---	---
ACACH-T	---	36.2	---	---	---	---	---	---	---	---
TRASRAC	---	36.2	---	---	---	---	---	---	---	---
DICMSCH	---	34.5	---	---	---	---	---	---	---	---
ACACNIL	---	34	8.4	---	---	---	---	---	---	---
ASPRPEA	---	31.8	---	---	---	---	---	---	---	---
REQUPSE	---	30.8	---	---	---	---	---	---	---	---
STIRU-U	---	30.1	---	---	---	---	---	---	---	---
ACACARE	---	29.8	---	---	---	---	---	---	---	---
GISEAFR	---	29.4	---	18.5	---	---	---	---	---	---
ALOEEXC	---	28.4	---	---	---	---	---	---	---	---
APTODEC	---	24.4	---	---	---	---	---	---	---	---
KOHACIC	---	24.1	---	---	---	---	---	---	---	---
KLEILON	---	22.4	---	---	---	---	---	---	---	---
CLEORUB	---	20.7	---	---	---	---	---	---	---	---
XERPHUM	---	20.2	---	---	---	---	---	---	---	---
GEIGSCH	---	20	---	---	---	---	---	---	---	---
LIMEMYO	---	20	---	---	---	---	---	---	---	---
DICACYM	---	20	---	---	---	---	---	---	---	---
OPHIPOL	---	20	---	---	---	---	---	---	---	---
Species 4										
GEIGORN	28.9	33.3	---	---	---	---	---	---	---	---
ODYSPAU	27.3	14.6	---	---	---	---	---	---	---	---
IPOMADE	10.2	17	---	---	---	---	---	---	---	---
Species group 5 [2.2]										
ANTPPUB	---	---	54.7	---	---	---	---	---	---	---
RHIOBRE	---	---	54	---	---	---	---	---	---	---
OTOPBUR	---	---	49.1	---	---	---	---	---	---	---
GREWRET	---	---	45.1	---	---	---	---	---	---	---
ACACFLE	---	---	41.8	---	---	---	---	---	---	---
MONGCAR	---	---	41.6	---	---	---	---	---	---	---
LONCNEL	---	---	38.5	---	---	---	---	---	---	---
ARITMER	---	---	36	---	---	---	---	---	---	---
ELEPSUF	---	---	35.8	---	---	---	---	---	---	---
COMPPYR	---	---	34.5	---	---	---	---	---	---	---
BOSCALB	---	---	34.2	9.8	---	---	---	---	---	---
REQUSPH	---	---	33.4	---	---	---	---	---	---	---
ACACERI	---	---	32.1	---	---	---	---	---	---	---
TRIbRAM	---	---	32	---	---	---	---	---	---	---
HELHTOM	---	---	31.5	---	---	---	---	---	---	---
ACACATA	---	---	31	---	---	---	---	---	---	---
MELBLON	---	---	27.8	---	---	---	---	---	---	---
INDGCOL	---	---	27.8	---	---	---	---	---	---	---
SEDDSUF	---	---	27.5	---	---	---	---	---	---	7.1
CYPEFUL	---	---	27.1	---	---	---	---	---	---	---
ACATNAU	---	---	25.9	---	---	---	---	---	---	---
MEGAMAR	---	---	24.9	---	---	---	---	---	---	---

ACACSEN	---	---	22.8	5.6	---	---	---	---	---	---
IPOMVER	---	---	22.7	---	---	---	---	---	---	---
SIDAOVA	---	---	22	---	---	---	---	---	---	---
MAERJUN	---	---	21.9	---	---	---	---	---	---	---
COMPANG	---	---	21.9	---	---	---	---	---	---	---
CLEDDEK	---	---	21.5	---	---	---	---	---	---	---
ABUTANG	---	---	20.1	---	---	---	---	---	---	---
Species group 6 [Western]										
PECHLEU	14.4	35.3	4	---	---	---	---	---	---	---
ANTPSCH	16.2	25.2	15.8	---	---	---	---	---	---	---
CATOALE	38.2	---	33.7	---	---	---	---	---	---	---
ERAGNIN	32.1	---	25.7	---	---	---	---	---	---	---
UROHBRA	25.9	---	12.1	---	---	---	---	---	---	---
ARITADS	37.8	---	19.6	---	---	---	---	---	---	---
MONEDIV	29.6	---	20.3	---	---	---	---	---	---	---
STIRUNI	18.2	---	41.3	14.4	---	---	---	---	---	---
CHACPIN	17.3	---	27.2	---	---	---	---	---	---	---
BOSCFOE	16.8	---	22.1	---	---	---	---	---	---	---
ACACMEI	12.6	---	31.4	---	---	---	---	---	---	---
HELROVA	23.4	---	13.3	---	---	---	---	---	---	---
HIBICAE	26.2	---	20.8	---	---	---	---	---	---	---
HELNINT	14.9	---	31.3	---	---	---	---	---	---	---
STIRH-P	16.7	---	21.1	---	---	---	---	---	---	---
TRIbPUR	20.3	---	17.4	---	---	---	---	---	---	---
ACACREF	17.5	---	36.8	---	---	---	---	---	---	---
BLEPOBM	18.5	---	21.8	---	---	---	---	---	---	---
Species group 7 [3]										
ARITCON	---	---	---	67.7	---	---	---	---	---	---
BRACDEF	---	---	---	55.2	---	---	---	---	---	---
PTYHCON	---	---	---	47.1	---	---	---	---	---	---
COMPMOL	---	---	---	44.3	---	---	---	---	---	---
TEPHPUR	---	---	---	41.9	---	---	---	---	---	---
AMARSCH	---	---	---	41.6	---	---	---	---	---	---
ACALVIL	---	---	---	40.8	---	---	---	---	---	---
LIMEFEN	---	---	---	40	---	---	---	---	---	---
COMIFAL	---	---	---	39.9	---	---	---	---	---	---
CLEOANG	---	---	---	39.1	---	---	---	---	---	---
MICHCAF	---	---	---	37.4	---	---	---	---	---	---
SESMALA	---	---	---	33.1	---	---	---	---	---	---
TRASBER	---	---	---	32.8	---	---	---	---	---	16.7
MELMGLA	---	---	---	32.1	---	---	---	---	---	---
INDGNEB	---	---	---	30.5	---	---	---	---	---	---
KOHACYN	---	---	---	30.2	---	---	---	---	---	---
LANNDIS	---	---	---	27.8	---	---	---	---	---	---
ASPRSUA	---	---	---	27.5	---	---	---	---	---	---
JATRSPI	---	---	---	26.1	---	---	---	---	---	---
ASPRAFR	---	---	---	26.1	---	---	---	---	---	---
COMPTEN	---	---	---	25.7	---	---	---	---	---	---
BULSHIS	---	---	---	25.5	---	---	---	---	---	---
INDGTRA	---	---	---	24.8	---	---	---	---	---	---

LEUSSEX	---	---	---	24	---	---	---	---	---	---
INDGHER	---	---	---	23.5	---	---	---	---	---	---
ARITBIP	---	---	---	22.9	---	---	---	---	---	---
CALHDIV	---	---	---	22	---	---	---	---	---	---
MELHREH	---	---	---	21.8	---	---	---	---	---	---
DIGIVEL	---	---	---	21.3	---	---	---	---	---	---
ACHYASP	---	---	---	20.9	---	---	---	---	---	---
SESMTRI	---	---	---	20.7	---	---	---	---	---	---
HYPAANA	---	---	---	20.4	---	---	---	---	---	---
Species group 8										
TERMPRU	---	---	28.3	22.3	---	---	---	---	---	---
MELBREP	---	---	28.1	21.7	---	---	---	---	---	14.5
GREWFLA	---	---	27.5	23.1	---	---	---	---	---	---
ERAGLEH	---	---	25.8	20.5	---	---	---	---	---	---
Species group 9 [4]										
CUCMZEY	---	---	---	---	53.6	---	---	17.7	---	---
VIGNFRU	---	---	---	---	42.4	---	---	---	---	---
SETASPH	---	---	---	---	37.4	---	---	---	---	---
SETASAG	---	---	---	---	32	---	---	---	---	---
MILLSUT	---	---	---	---	27.1	---	---	---	---	---
PHYARET	---	---	---	---	22.3	---	---	---	13.9	---
DACLAUS	---	---	---	---	21.7	---	---	---	---	---
PLETNEO	---	---	---	---	21.8	---	---	9.7	---	---
GREWCAF	---	---	---	---	22.1	---	---	---	---	---
ENTEMON	---	---	---	---	37.2	---	---	---	---	---
CYAHUNC	---	---	---	---	55.4	---	---	34	---	---
Species group 10										
DIGIMIL	---	---	---	---	49.7	---	---	45.5	---	---
DACLGIG	---	---	---	---	23.5	---	---	23.7	---	---
JUSTFLA	---	---	---	---	20	---	---	21.6	---	6.2
THILAFR	---	---	---	---	21	---	---	18.6	---	---
CISUROT	---	---	---	---	30.3	---	---	18.4	---	---
GREWMON	---	---	---	---	39.1	---	---	13.5	---	---
ZANHCAP	---	---	---	---	17.5	---	---	11.8	---	---
Species group 11 [5.1]										
PHILVIO	---	---	---	---	---	26.3	48.9	---	---	---
COMRIMB	---	---	---	---	---	36	36.8	---	---	---
Species group 12 [5.1.1]										
SETAINC	---	---	---	---	---	80	---	---	---	---
TEPHMUL	---	---	---	---	---	52.4	---	---	---	---
PANICOL	---	---	---	---	---	45.4	---	---	---	7.9
NEORAMB	---	---	---	---	---	45.2	---	---	---	2.6
SORHVER	---	---	---	---	---	40.1	---	---	---	1.1
JATRZEY	---	---	---	---	---	36.9	---	---	---	2.9
RHYHMIN	---	---	---	---	---	33.5	---	---	---	1.2
HYBAENN	---	---	---	---	---	29.4	---	---	---	5.4
EHRERIG	---	---	15.2	---	---	29.1	---	---	---	5.9
INDGSCI	---	---	---	---	---	27.8	---	---	---	5
ISCHAFR	---	---	---	---	---	24.8	---	---	---	---

ACACBOR	---	---	---	---	---	22.7	---	---	---	---
IPOMERI	---	---	---	---	---	21.7	---	---	---	---
HELHMIC	---	---	---	---	---	20.5	---	---	---	---
HYPARUF	---	---	---	---	---	20.5	---	---	---	---
Species group 13										
CEPLMOL	---	---	20.8	---	---	16	---	---	---	---
COLPMOP	---	24.9	---	19	---	21.5	---	---	---	---
CENCCIL	25.7	---	6	---	---	36.8	---	---	---	---
Species group 14 [5.1.2]										
CRONMEG	---	---	---	---	---	---	51.1	---	---	---
SPORFIM	---	---	---	---	---	---	45.3	---	---	---
FICUSYC	---	---	---	---	---	---	43.6	---	---	---
FLAVBID	---	---	---	---	---	---	41.4	---	---	---
SPISAFR	---	---	---	---	---	---	38.5	---	---	---
PHOEREC	---	---	---	---	---	---	34	---	---	---
PANIDEU	---	---	---	---	---	---	28	---	---	---
EUCLCRI	---	---	---	---	---	---	26.1	---	---	---
ENNESCO	---	---	---	---	---	---	25.6	---	---	9.2
ACACROU	---	---	---	---	---	---	25	---	---	---
MAYTSEN	---	---	---	---	---	---	24.8	---	---	---
ABUTRAM	---	---	---	---	---	---	23.9	---	---	---
PHRGAUS	---	---	---	---	---	---	23.7	---	---	---
DIOPMES	---	18.7	---	---	---	---	23.2	---	---	---
XANHZAM	---	---	---	---	---	---	22.4	---	---	---
Species group 15 [5.2]										
SPORNIT	---	---	---	---	---	---	---	38.8	---	9.8
ACACTOR	---	---	---	---	---	---	---	32.9	---	---
BOSCMOS	---	---	---	---	8.2	---	---	31.3	---	---
ALBIANT	---	---	17.2	---	---	---	---	22.6	---	---
KALALAN	---	---	---	---	---	---	---	21.8	---	---
Species group 16 [6]										
DIGIERI	---	---	---	---	---	---	---	---	52.5	37.1
PANIMAX	---	---	---	---	---	---	---	---	26.6	28
POGOSQU	---	---	---	---	---	---	---	---	32.9	31.2
CROTSPH	---	---	---	---	---	---	---	---	29.1	15.5
IPOMMAG	---	---	---	13.6	---	---	---	---	35	12.1
Species group 17 [6.1]										
PSELMAP	---	---	---	---	---	---	---	---	57	---
STRYMAD	---	---	---	---	---	---	---	---	55.6	4.8
COMRZEY	---	---	---	---	---	---	---	---	53.9	2.7
PTELMYR	---	---	---	---	---	---	---	---	53.5	---
GUIBCON	---	---	---	---	---	---	---	---	53.3	---
VIGNUNG	---	---	---	---	---	---	---	---	53.2	10
PEROPAT	---	---	---	---	---	---	---	---	48.9	8.6
DIPRCON	---	---	---	---	---	---	---	---	47.3	---
MERRTRI	---	---	11.8	---	---	---	---	---	47.1	---
TERMSER	---	---	8.6	---	---	---	---	---	46.3	2.6
ERAGPAL	---	---	---	---	---	---	---	---	46	---
HYMEULM	---	---	---	---	---	---	---	---	44.4	---

COMRCOL	---	---	---	---	---	---	---	---	44.7	---
TAREZYG	---	---	---	---	---	---	---	---	44.4	---
SPEMSEN	---	---	---	---	---	---	---	---	42	---
PHYABUR	---	---	---	---	---	---	---	---	41.9	---
BURKAFR	---	---	---	---	---	---	---	---	41.8	---
HEXLMON	---	---	---	---	---	---	---	---	41.6	---
HERMGLN	---	---	---	---	---	---	---	---	41	---
RHYHRES	---	---	---	---	---	---	---	---	41	---
CHASTET	---	---	---	---	---	---	---	---	40.9	---
MONBJUN	---	---	---	---	5.1	---	---	---	40.4	---
BRACNIG	---	---	---	---	---	---	---	---	40.1	7.7
ALCOLAX	---	---	---	---	---	---	---	---	39.1	---
CHEIVIR	---	---	---	---	---	---	---	---	38.7	---
TEPHELO	---	---	---	---	---	---	---	---	37.4	---
STRYDEC	---	---	---	---	---	---	---	---	36	---
HIBIENG	---	---	---	---	---	---	---	---	36	---
HOLAPUB	---	---	---	---	---	---	---	---	33.5	---
CORCKIR	---	---	---	---	---	---	---	---	32.6	---
TRIhPEN	---	---	---	---	---	---	---	---	32.6	---
AFZEQUA	---	---	---	---	---	---	---	---	30.6	---
BAUHGAL	---	---	---	---	---	---	---	---	30.6	---
BAPHMAS	---	---	---	---	---	---	---	---	31.7	---
VITXFER	---	---	---	---	---	---	---	---	31	---
COMMERE	---	---	---	---	---	---	---	---	30.8	10.9
ARITSTP	---	---	---	1	---	---	---	---	30.1	---
VANGINF	---	---	---	---	---	---	---	---	29.8	---
ARITMOL	---	---	---	---	---	---	---	---	29.4	7.6
STRIASI	---	---	---	---	---	---	---	---	29.4	---
INDGINH	---	---	---	---	---	---	---	---	29	---
HUGOORI	---	---	---	---	---	---	---	---	29	---
TEPHLON	---	---	---	---	---	---	---	---	28.9	4.4
MAYTMOS	---	---	---	---	---	---	---	---	28.8	---
COMRCEL	---	---	---	---	---	---	---	---	28.8	---
ARTABRA	---	---	---	---	---	---	---	---	28.4	---
PELLCAL	---	---	---	---	---	---	---	---	28.3	---
RHYHVEU	---	---	---	---	---	---	---	---	28.3	---
CELOTRI	---	---	---	---	---	---	---	---	28.3	---
BLEPMAD	---	---	---	---	---	---	---	---	27.8	---
CATUSPI	---	---	---	---	---	---	---	---	27.3	---
GREWMIC	---	---	---	---	---	---	---	---	26.4	---
LIMEDIN	---	---	---	---	---	---	---	---	26.4	---
TRICJUN	---	---	---	---	---	---	---	---	26.4	---
HIPCCRE	---	---	---	---	---	---	---	---	26	---
POLGWIL	---	---	---	---	---	---	---	---	26	---
LEPTDEL	---	---	---	---	---	---	---	---	26	---
OCHNPUL	---	---	---	---	---	---	---	---	25.4	---
MONEDEB	---	---	---	12.1	---	---	---	---	25.2	---
CRONPSE	---	---	---	---	---	---	---	---	25.1	---
HEMZBRA	---	---	---	---	---	---	---	---	24.9	8.5
IPOMPE-	---	---	---	---	---	---	---	---	23.2	---

PTECANG	---	---	---	---	---	---	---	---	23.2	---
ARITJUN	---	---	---	---	---	---	---	---	23	---
XERDSTU	---	---	---	---	---	---	---	---	21.7	---
MARGDIS	---	---	---	---	---	---	---	---	20.2	---
PTAEOBL	---	---	---	---	---	---	---	---	20.2	---
LEONNEP	---	---	---	---	---	---	---	---	20.7	---
MACYAXI	---	---	---	---	---	---	---	---	20.1	---
CLESSCH	---	---	---	---	---	---	---	---	20.4	---
HEINCRI	---	---	---	---	---	---	---	---	20.4	---
Species group 18										
VEROFAS	---	---	---	---	---	30.9	---	---	26.8	9.9
Species group 19 [6.2]										
TEPHPOL	---	---	---	---	---	---	---	---	---	59.2
ACACEXU	---	---	---	---	---	---	---	---	---	54.4
ARITC-B	---	---	---	---	---	---	---	---	---	50
HIBIMIC	---	---	---	---	---	---	---	---	---	47.8
CISUCOR	---	---	---	---	---	---	---	---	---	47.6
RUELPAT	---	---	---	---	---	---	---	---	---	46.2
CORCASP	---	---	---	---	---	---	---	---	---	45.4
TRAGDIO	---	---	---	---	---	---	---	---	---	43.6
MELHFOR	---	---	---	---	---	---	---	---	---	43
BLEPINT	---	---	---	---	---	---	---	---	---	39.8
CERHTRI	---	---	---	---	---	---	---	---	---	39.6
ENDSTER	---	---	---	---	---	---	---	---	---	39.5
ABUTAUS	---	---	---	---	---	---	---	---	---	38.9
CHASNEO	---	---	---	---	---	---	---	---	---	38.8
ASPRSET	---	---	---	---	---	---	---	---	---	38.7
WALTIND	---	---	---	---	---	---	---	---	---	38.3
LANTRUG	---	---	---	---	---	---	---	---	---	38.2
IPOMCRA	---	---	---	---	---	---	---	---	---	38
TALICAF	---	---	---	---	---	---	---	---	---	37.3
COMMBEN	---	---	---	---	---	---	---	---	---	37.3
INDGVIC	---	---	---	---	---	---	---	---	---	37
HELRSTE	---	---	---	---	---	---	---	---	---	36.1
INDGBAI	---	---	---	---	---	---	---	---	---	35.7
CYPERUP	---	---	---	---	---	---	---	---	---	35.5
MELHDID	---	---	---	---	---	---	---	---	---	35.4
KOHAVIR	---	---	---	---	---	---	---	---	---	35.1
PHYAASP	---	---	---	---	---	---	---	---	---	34.9
HERMBOR	---	---	---	---	---	---	---	---	---	33.9
EVOLALS	---	---	---	---	---	---	---	---	---	33.8
INDGFIP	---	---	---	---	---	---	---	---	---	33.6
SEDDCAP	---	---	---	---	---	---	---	---	---	33.5
MARIREH	---	---	---	---	---	---	---	---	---	33.4
ACACNIG	---	---	---	---	---	---	---	---	---	33.1
ERAGRIG	---	---	---	---	---	---	---	---	---	32.7
CLEDTER	---	---	---	---	---	---	---	---	---	32.2
SIDADRE	---	---	---	---	---	---	---	---	---	31.8
GREWSUB	---	---	---	---	---	---	---	---	---	31.6
ORNISEI	---	---	---	---	---	---	---	---	---	31.3

MELHPRO	---	---	---	---	---	---	---	---	---	31.1
BRACXAN	---	---	---	---	---	---	---	---	---	30.9
ACALIND	---	---	---	---	---	---	---	---	---	30.7
CHAAMIM	---	---	---	---	---	---	---	---	---	30.6
ARITC-O	---	---	---	---	---	---	---	---	---	30.3
SCHFPAP	---	---	---	---	---	---	---	---	---	29.8
CRABVEL	---	---	---	---	---	---	---	---	---	29.7
MAYTHET	---	---	---	---	---	---	---	---	---	29.6
CYMOPLU	---	---	---	---	---	---	---	---	---	29.4
GREWBIC	---	---	---	---	---	---	---	---	---	29.3
LEUSGLA	---	---	---	---	---	---	---	---	---	29.1
LEUSNEU	---	---	---	---	---	---	---	---	---	29.1
HIBIPUS	---	---	---	---	---	---	---	---	---	28.9
SCLCBIR	---	---	---	---	---	---	---	---	---	28.8
TRIEMON	---	---	---	---	---	---	---	---	---	28
SOLNPAN	---	---	---	---	---	---	---	---	---	28.3
POLGSPH	---	---	---	---	---	---	---	---	---	28.6
TRIRGRA	---	---	---	---	---	---	---	---	---	27.8
ALBIHAR	---	---	---	---	---	---	---	---	---	27.8
RHYHTOT	---	---	---	---	---	---	---	---	---	27.6
HETGCON	---	---	---	---	---	---	---	---	---	27.5
COMPAFR	---	---	---	---	---	---	---	---	---	27.1
ORMOTRI	---	---	---	---	---	---	---	---	---	27
CHLRGAL	---	---	---	---	---	---	---	---	---	27
INDGRHY	---	---	---	---	---	---	---	---	---	26.6
EHREAMO	---	---	---	---	---	---	---	---	---	25.5
COMMAFR	---	---	---	---	---	---	---	---	---	25.1
PHYAINC	---	---	---	---	---	---	---	---	---	24.9
BOTHRAD	---	---	---	---	---	---	---	---	---	24.8
FIMBCOM	---	---	---	---	---	---	---	---	---	24.8
CORBDEC	---	---	---	---	---	---	---	---	---	24.7
PAVOBUR	---	---	---	---	---	---	---	---	---	24.6
BOLSSPE	---	---	---	---	---	---	---	---	---	24.4
PHYAMAD	---	---	---	---	---	---	---	---	---	24.1
LANNSCW	---	---	---	---	---	---	---	---	---	23.9
SIDACHR	---	---	---	---	---	---	---	---	---	23.9
PHYAPEN	---	---	---	---	---	---	---	---	---	23.8
CROTSCH	---	---	---	---	---	---	---	---	---	23.6
PORUKER	---	---	---	---	---	---	---	---	---	23.6
HIBISID	---	---	---	---	---	---	---	---	---	23.3
MONSANG	---	---	---	---	---	---	---	---	---	23.2
FLUEVIR	---	---	---	---	---	---	---	---	---	23.1
CUCMAFR	---	---	---	---	---	---	---	---	---	23.1
RHINXER	---	---	---	---	---	---	---	---	---	23.1
MONSBUR	---	---	---	---	---	---	---	---	---	22.8
CHAAABS	---	---	---	---	---	---	---	---	---	22.6
IPOMOBS	---	---	---	---	---	---	---	---	---	22.5
ARITSCA	---	---	---	---	---	---	---	---	---	22.5
ERAGSUP	---	---	---	---	---	---	---	---	---	22.4
ANDPGAY	---	---	---	---	---	---	---	---	---	22.4

ORTSSUF	---	---	---	---	---	---	---	---	---	22.1
CHACHED	---	---	---	---	---	---	---	---	---	21.8
IPOMCOP	---	---	---	---	---	---	---	---	---	21.7
JUSTANA	---	---	---	---	---	---	---	---	---	21.7
SOLNCOC	---	---	---	---	---	---	---	---	---	21.6
TRIJLAC	---	---	---	---	---	---	---	---	---	21.6
CROTVIG	---	---	---	---	---	---	---	---	---	21.2
TRIJGLA	---	---	---	---	---	---	---	---	---	21
COCCREH	---	---	---	---	---	---	---	---	---	20.9
INDGLUP	---	---	---	---	---	---	---	---	---	20.9
ARITS-G	---	---	---	---	---	---	---	---	---	20.7
ASPRBUC	---	---	---	---	---	---	---	---	---	20.3
OZORENG	---	---	---	---	---	---	---	---	---	20.3
CUCMHIR	---	---	---	---	---	---	---	---	---	20.1
Species group 20										
MAERPAR	---	---	---	---	---	---	---	24.6	---	21.3
UROHMOS	---	---	---	---	18.7	---	---	39.1	---	21.4
Species group 21										
EUCLDIV	---	---	---	---	---	---	27.2	---	---	20.4
COMRHER	---	---	---	---	---	---	32.7	---	---	15.3
Species group 22										
THEMTRI	---	---	---	---	---	58.8	---	---	---	21.1
BOTHINS	---	---	---	---	---	46	---	---	---	17.9
DALBMEL	---	---	---	---	---	31.6	---	---	---	18
Species group 23										
DICMTOM	---	---	---	27.8	---	---	---	---	---	23.9
KYPHANG	---	---	---	27.5	---	---	---	---	---	36.3
COMRAPI	---	---	---	30.4	---	---	---	---	---	24.4
ENNECEN	---	---	---	33.1	---	---	---	---	---	16.4
GREWHEX	---	---	---	19.4	---	---	---	---	---	15.4
OCIMAME	---	---	---	18.7	---	---	---	---	---	15.8
Species group 24										
SPORSAL	16.4	---	---	---	---	---	---	---	---	---
IPOMSIN	16.5	---	---	---	---	---	---	---	---	---
CROTDAM	19.4	---	---	---	---	---	---	---	---	---
VEROCIN	19.2	---	10.2	---	---	---	---	---	---	---
MONETON	19.9	---	---	---	---	---	---	---	---	---
STIGHER	16.4	---	---	---	---	---	---	---	---	---
ORNTCAL	16.4	---	---	---	---	---	---	---	---	---
HELRGIE	18.7	---	---	---	---	---	---	---	---	---
ATRPLIN	16.4	---	---	---	---	---	---	---	---	---
LYCIOXY	16.4	---	---	---	---	---	---	---	---	---
GOSYTRI	18.8	---	16.2	---	---	---	---	---	---	---
ERAGMIC	16.4	---	---	---	---	---	---	---	---	---
ACACM-D	19	---	10.1	---	---	---	---	---	---	---
FELICLA	16.4	---	---	---	---	---	---	---	---	---
SUAEART	16.4	---	---	---	---	---	---	---	---	---
TEPHDRE	---	16	19.2	---	---	---	---	---	---	---
MERRPAL	---	---	16.8	---	---	---	---	---	---	---
STRIGES	---	---	13	---	---	---	---	---	---	---

APPENDIX 7-1

Reference document to Chapter 7

Siebert *et al*. (2010)

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

Authors:
Frances Siebert[1]
Holger C. Eckhardt[2]
Stefan J. Siebert[1]

Affiliations:
[1]School of Environmental Sciences and Development, North-West University, South Africa

[2]Scientific Services, South African National Parks, South Africa

Correspondence to:
Frances Siebert

email:
frances.siebert@nwu.ac.za.

Postal address:
School of Environmental Sciences and Development, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa

Keywords:
biodiversity; Letaba River; Mopaneveld; riparian vegetation; savanna; vegetation mapping

Dates:
Received: 27 May 2009
Accepted: 24 Nov. 2009
Published: 21 June 2010

How to cite this article:
Siebert, F., Eckhardt, H.C. & Siebert, S.J., 2010, 'The vegetation and floristics of the Letaba exclosures, Kruger National Park, South Africa', *Koedoe* 52(1), Art. #777, 12 pages. DOI: 10.4102/koedoe.v52i1.777

This article is available at:
http://www.koedoe.co.za

ABSTRACT

The construction of exclosures 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 is affected by fire, flood and herbivory. To assist this research programme, vegetation surveys were conducted within exclosures along the Letaba River to classify and map the vegetation of the area. The history and experimental design of the Letaba exclosures are similar to that of the Nkhuhlu exclosures along the Sabie River, which is directly related to questions surrounding elephant management. The main difference between the Nkhuhlu and Letaba exclosures 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 exclosures. 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 exclosures, 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 exclosures were constructed in 2002. For the same reason and purpose as the Nkhuhlu exclosures, 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 exclosures are similar to those of the Nkhuhlu exclosures (O'Keefe & Alard 2002), which is directly related to questions surrounding elephant management. The different treatment blocks at the Letaba exclosures vary in size, with 42 ha, 51 ha and 36 ha respectively, for the full exclosure, partial exclosure and unfenced area. The main difference between the Nkhuhlu and Letaba exclosures 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'Keeffe & Rogers 2003). The lower mean annual rainfall (approximately 400 mm), compared to the annual 560 mm at Nkhuhlu, drives a different fire regime and mammal concentrations. These not only translate into less obvious differences between the different treatments at the Letaba exclosures, 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 dramatica 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 exclosures have not received the same degree of attention from researchers as the Nkhuhlu exclosures. 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 exclosures are situated approximately 5 km upstream of the Mingerhout Dam, along the northern bank of the Letaba River in the Kruger National Park. The exclosures 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

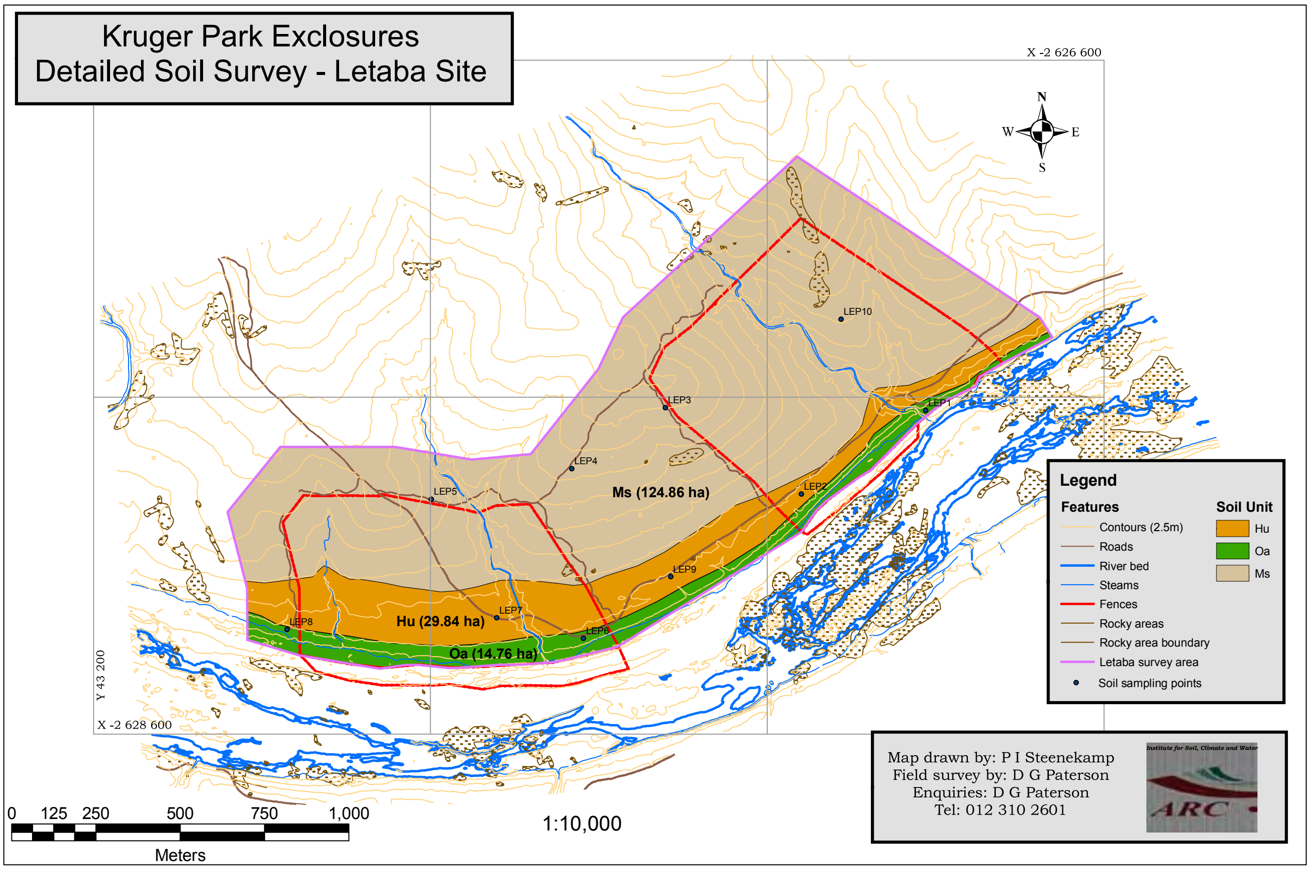


FIGURE 1

Soil map of the Letaba exclosures study site (courtesy of ARC-Institute of Soil, Climate and Water, Paterson and Steenekamp 2003)

- a partially fenced area (51 ha) excluding only elephant and giraffe, also divided into a burn (3) and no-burn (4) block
- (5) an unfenced area protected from fire only (36 ha)
- (6) a 400 m wide buffer area that is subjected to fire and herbivory.

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 midslopes 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 1983) 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 AZa7 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 cornifolia* – *Colophospermum mopane* vegetation type (Siebert, Bredenkamp & 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 Bredenkamp 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 megalobotrys*, *Nuxia oppositifolia*, *Gymnosporia senegalensis*, *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 cornifolia*, *Commiphora mollis*, *C. africana*, *Grewia bicolor*, *Combretum imberbe*, *Acacia nigrescens*, *Acacia exuvialis* and *Rhigozum zambeziacum*. Grasses, such as *Panicum coloratum*, *Schmidtia pappophoroides*, *Melinis repens*, *Bothriochloa radicans*, and forbs such as *Crabbea velutina*, *Ocimum americanum*, *Phyllanthus maderaspatensis*, *Pavonia burchellii*, *Hibiscus micranthus* and *Jasminum stenolobum*, characterise the field layer.

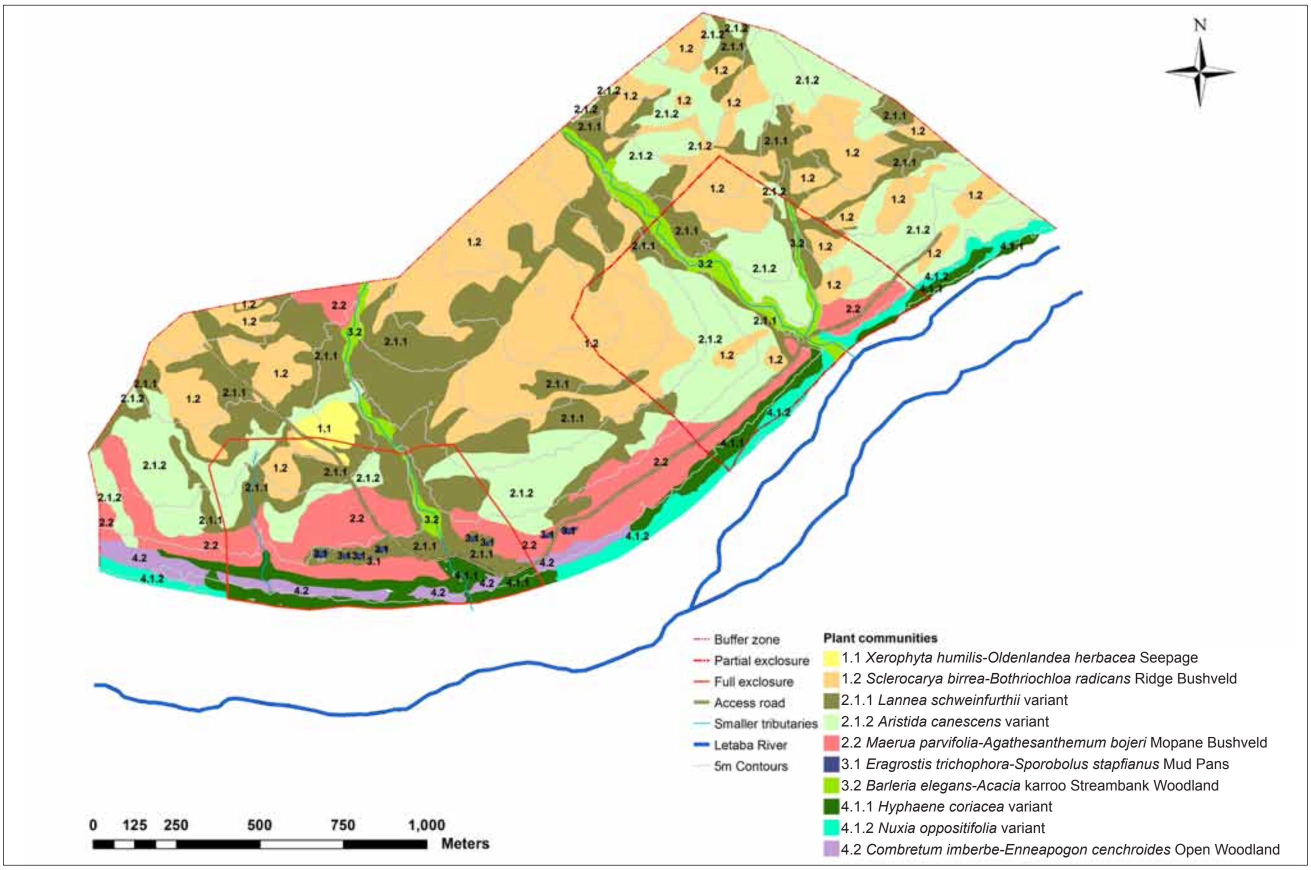


FIGURE 2
Vegetation map of the Letaba exclosures study site

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

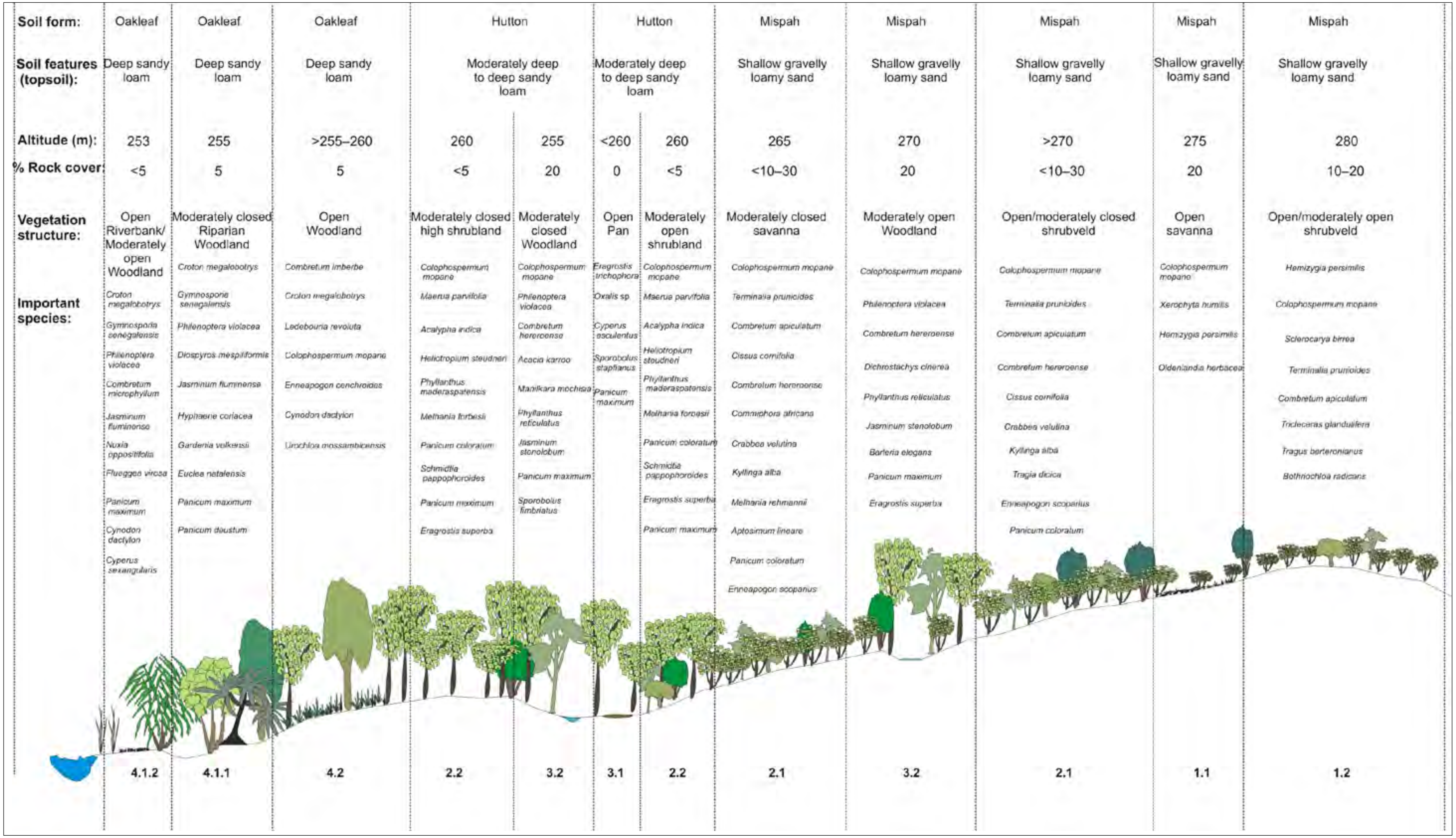
Floristic data were analysed to allow floristic comparison across mapping units and were therefore presented on variant level where appropriate. The approach for floristic comparison followed the method used for the Nkhuhlu exclosures (Siebert & Eckhardt 2008), which entailed the use of Shanon-Wiener 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 *Co lophospermum 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* crest savannah
1.1 *Xerophyta humilis*
– *Oldenlandia herbacea* seepage
1.2 *Sclerocarya birrea* – *Bothriochloa radicans* ridge bushveld
1.2.1 *Senna italica* variant
1.2.2 Typical variant
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 *Philenoptera violacea* – *Jasminum fluminense* riverbank woodland
4.1.1 *Hyphaene coriacea* variant
4.1.2 *Nuxia oppositifolia* variant



Soil form:	Oakleaf	Oakleaf	Oakleaf	Hutton		Hutton		Mispah	Mispah	Mispah	Mispah	Mispah
Soil features (topsoil):	Deep sandy loam	Deep sandy loam	Deep sandy loam	Moderately deep to deep sandy loam		Moderately deep to deep sandy loam		Shallow gravelly loamy sand	Shallow gravelly loamy sand	Shallow gravelly loamy sand	Shallow gravelly loamy sand	Shallow gravelly loamy sand
Altitude (m):	253	255	>255–260	260	255	<260	260	265	270	>270	275	280
% Rock cover:	<5	5	5	<5	20	0	<5	<10–30	20	<10–30	20	10–20
Vegetation structure:	Open Riverbank/ Moderately open Woodland	Moderately closed Riparian Woodland	Open Woodland	Moderately closed high shrubland	Moderately closed Woodland	Open Pan	Moderately open shrubland	Moderately closed savanna	Moderately open Woodland	Open/moderately closed shrubveld	Open savanna	Open/moderately open shrubveld
Important species:	*Croton megalobotrys* *Gymnospoda senegalensis* *Philenoptera violacea* *Combretum microphyllum* *Jasminum fluminense* *Nuxia oppositifolia* *Flueggea virosa* *Panicum maximum* *Cynodon dactylon* *Cyperus sexangularis*	*Croton megalobotrys* *Gymnosporia senegalensis* *Philenoptera violacea* *Diospyros mespiliformis* *Jasminum fluminense* *Hyphaene coriacea* *Gardenia volkensii* *Euclea natalensis* *Panicum maximum* *Panicum deustum*	*Combretum imberbe* *Croton megalobotrys* *Ledebouria revoluta* *Colophospermum mopane* *Enneapogon cenchroides* *Cynodon dactylon* *Urochloa mossambicensis*	*Colophospermum mopane* *Maerua parvifolia* *Acalypha indica* *Heliotropium steudneri* *Phyllanthus maderaspatensis* *Melhania forbesii* *Panicum coloratum* *Schmidtia pappophoroides* *Panicum maximum* *Eragrostis superba*	*Colophospermum mopane* *Philenoptera violacea* *Combretum hereroense* *Acacia karroo* *Manilkara mochisia* *Phyllanthus reticulatus* *Jasminum stenolobum* *Panicum maximum* *Sporobolus fimbriatus*	*Eragrostis trichophora* *Oxalis* sp. *Cyperus esculentus* *Sporobolus stapfianus* *Panicum maximum*	*Colophospermum mopane* *Maerua parvifolia* *Acalypha indica* *Heliotropium steudneri* *Phyllanthus maderaspatensis* *Melhania forbesii* *Panicum coloratum* *Schmidtia pappophoroides* *Eragrostis superba* *Panicum maximum*	*Colophospermum mopane* *Terminalia prunioides* *Combretum apiculatum* *Cissus cornifolia* *Combretum hereroense* *Commiphora africana* *Crabbea velutina* *Kyllinga alba* *Melhania rehmannii* *Aptosimum lineare* *Panicum coloratum* *Enneapogon scoparius*	*Colophospermum mopane* *Philenoptera violacea* *Combretum hereroense* *Dichrostachys cinerea* *Phyllanthus reticulatus* *Jasminum stenolobum* *Barleria elegans* *Panicum maximum* *Eragrostis superba*	*Colophospermum mopane* *Terminalia prunioides* *Combretum apiculatum* *Combretum hereroense* *Cissus cornifolia* *Crabbea velutina* *Kyllinga alba* *Tragia dioica* *Enneapogon scoparius* *Panicum coloratum*	*Colophospermum mopane* *Xerophyta humilis* *Hemizygia persimilis* *Oldenlandia herbacea*	*Hemizygia persimilis* *Colophospermum mopane* *Sclerocarya birrea* *Terminalia prunioides* *Combretum apiculatum* *Triceratas glandulifera* *Tragus berteronianus* *Bothriochloa radicans*
	4.1.2	4.1.1	4.2	2.2	3.2	3.1	2.2	2.1	3.2	2.1	1.1	1.2

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

4.2 *Combretum imberbe* – *Enneapogon cenchroides* open woodland. The identified plant assemblages 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* (2.1.1) and *Aristida canescens* (2.1.2) variants of the *Melhania rehmannii* – *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 catena. 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 megalobotrys* 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* – *Bothriochloa radicans* ridge bushveld (1.2) and a unique, localised seepage (1.1) (Figure 3).

Floristic analysis

Compared to the Nkhuhlu exclosures, the plant richness per area of the Letaba exclosures is low (Figure 4), due to *Colophospermum mopane* dominating the tree and shrub layers (O'Connor 1992; Du Plessis 2001). The overall plant richness per area, of both the Nkhuhlu and Letaba exclosures, is above average for the Kruger National Park (Figure 4).

At community level, the *Schmidtia 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.

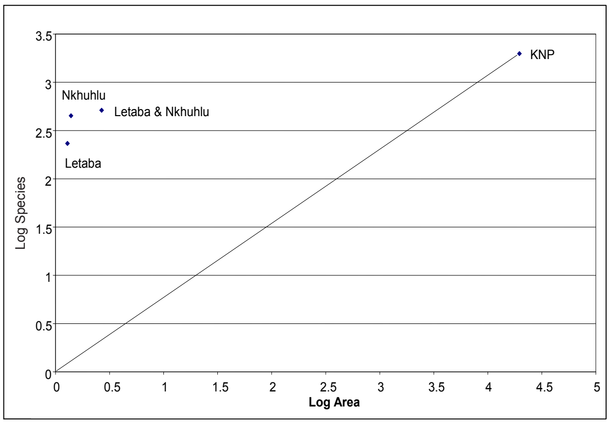


FIGURE 4
Species richness per area of the Nkhuhlu and Letaba exclosures respectively as well as pooled (Letaba & Nkhuhlu) in relation to the species richness of the entire Kruger National Park (KNP)

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 Nkhuhlu exclosures.

DISCUSSION

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 site 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 Mispah 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 1 (see online Appendix), which includes *Acacia exuvialis* in the woody layer, and *Hemizygia bracteosa* and *Tricliceras 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 radicans*, *Tragus berteronianus* (species group 3), *Schmidtia pappophororoides* (species group 5) and *Enneapogon scoparius* (species group 10), whereas *Evolvulus alsinoides*, *Clerodendrum ternatum* (species group 10), *Lantana rugosa*, *Ceratotheca 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 and Poaceae (Table 2) floristically dominate the crest savanna.

The crest savanna contains elements of the '*Combretum* spp. / *Colophospermum mopane* landscape' (Landscape 22, Gertenbach 1983) in the field layer, but not typically in the woody layer, except for common trees such as *Colophospermum mopane*, *Terminalia sericea*, *Acacia exuvialis*, *Combretum apiculatum* and

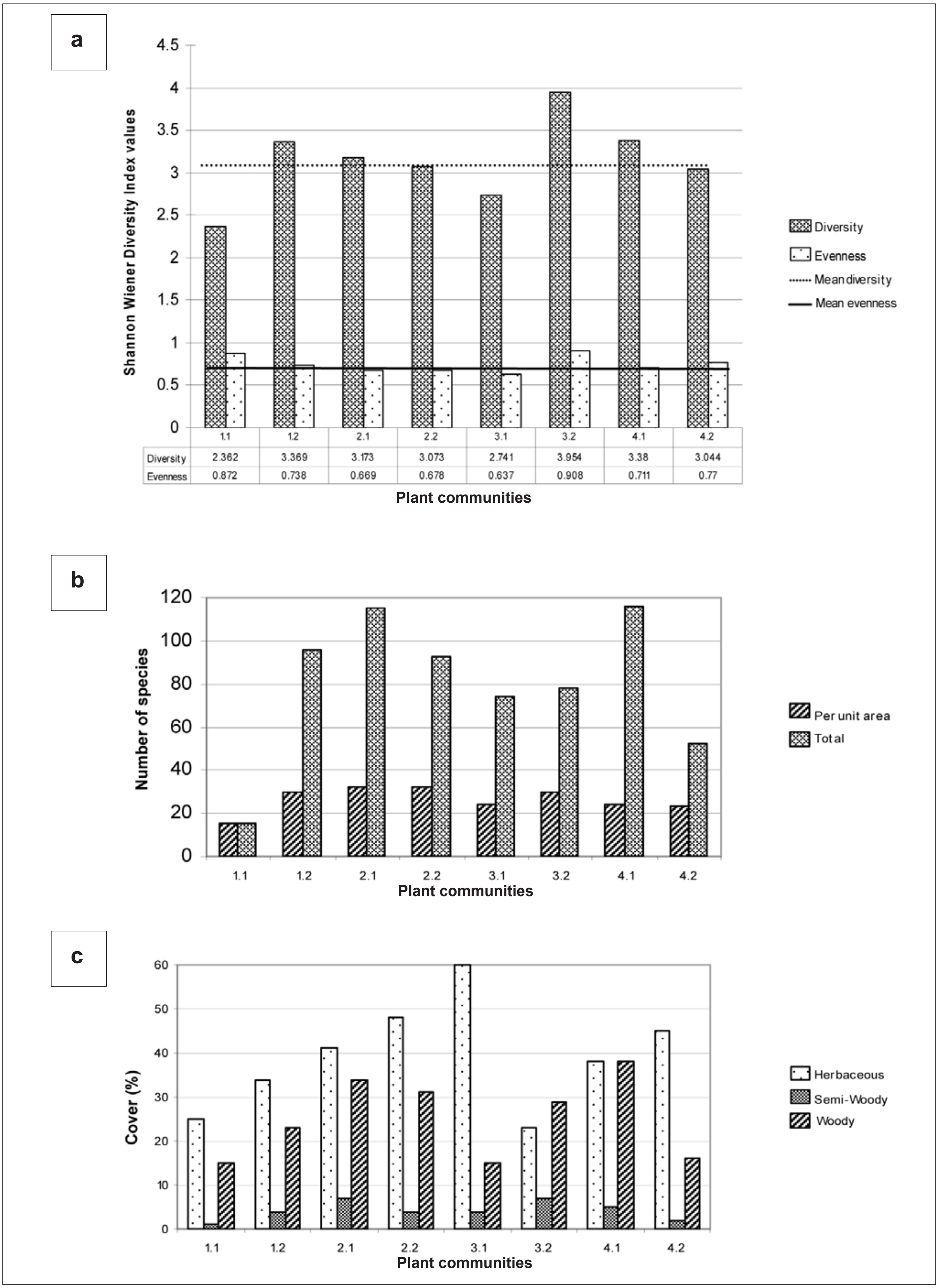


FIGURE 5

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 exuvialis* crest savanna:

1.1 *Xerophyta humilis – Oldenlandia 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), *Schmidtia pappophoroides* (species group 5) and *Panicum coloratum* (species group 14) occur, but with low percentage cover. Prominent forbs include, other than *Xerophyta humilis* and *Oldenlandia herbacea* (species group 2), *Kohautia virgata* (species group 9), *Evolvulus alsinoides* (species group 10), *Tephrosia purpurea* and *Ceratotheca 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 *Sclerocarya birrea – 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 bufferzone (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 23% of the area (Figure 5).

This ridge bushveld is characterised by species group 3 (see online Appendix) and include *Sclerocarya birrea* 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 *Rhigozum 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 triloba*, *Hibiscus micranthus*, *Lantana rugosa*, *Melhania acuminata*, *Ocimum americanum*, *Pavonia burchellii*, *Phyllanthus incurvus* and *Phyllanthus maderaspatensis* (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 moderately open to open shrubveld on slightly elevated crests on shallow soils of the Mispah soil form. It is less stoney 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*, *Heliotropium ovalifolium*, *Boerhavia diffusa*, *Corbichonia 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 bufferzone. 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 exuvialis* (species group 1), *Sclerocarya birrea* (species group 3), *Rhigozum zambesiacum* (species group 10), *Terminalia prunioides*, *Combretum apiculatum*, *Acacia nigrescens* and *Dichrostachys cinerea* (species group 14). Other species present in the herbaceous layer are grasses such as *Bothriochloa radicans* (species group 3), *Schmidtia pappophoroides* (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 indica* (species group 21).

2. *Schmidtia pappophoroides – 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 areas. Its nearest counterpart in plant communities, as have been described previously, is the *Colophospermum mopane – Combretutum 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 *Schmidtia pappophoroides* (species group 5). The grasses *Enneapogon scoparius* (species group 10), *Eragrostis superba* and *Panicum maximum* (species group 21) are prominent. Forbs such as *Crabbea velutina*, *Hibiscus praeteritus*, *Ruellia cordata* (species group 5), *Evolvulus alsinoides*, *Limeum fenestratum*, *Talinum caffrum*, *Clerodendrum ternatum* (species group 10), *Ocimum americanum*, *Phyllanthus maderaspatensis*, *Lantana rugosa*, *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

TABLE 1
Richness, Shanon-Wiener diversity and evenness at plant community level of the Letaba exclosures study site

	Plant communities				
	1	2	3	4	Total
Richness	96	141	119	131	233
Spp/400 m^2	22	32	27	24	-
Diversity	3.414	3.267	3.585	3.609	-
Evenness	0.748	0.66	0.75	0.74	-

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 *Melhania rehmannii – Enneapogon scoparius* mixed bushveld: Mixed bushveld of the Letaba exclosures site is typically associated with midslopes 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 species group 6 (see online Appendix) characterise the floristic composition of this sub-community and include *Melhania rehmannii*, *Aptosimum lineare*, *Asparagus setaceus*, *Abutilon angulatum*, *Becium filamentosum*, *Dumasia villosa* and *Coccinia adoensis*, all of which are representative of the forb layer. Conspicuous woody species include *Cissus cornifolia* (species group 5), *Colophospermum mopane*, *Combretum apiculatum*, *Dichrostachys cinerea* (species group 14), *Cassia abbreviata* (species group 20) and *Combretum hereroense* (species group 21). Prominent forbs, other than the character species, are *Crabbea velutina*, *Ruellia cordata* (species group 5), *Evolvulus alsinoides*, *Dicoma tomentosa*, *Clerodendrum ternatum* (species group 10), *Ocimum americanum*, *Lantana rugosa*, *Melhania acuminata*, *Phyllanthus incurvus*, *Pavonia burchellii*, *Hibiscus micranthus*, *Tragia dioica* (specis group 14), *Kyllinga alba* and *Waltheria indica* (species group 21). In the grass layer, *Pogonarthria squorrosa*, *Schmidtia pappophoroides* (species group 9), *Digitaria eriantha* (species group 16), *Panicum maximum* and *Tragus beteronianus* (species group 28) are most common.

This sub-community contains the highest number of graminoids, forbs and dwarf shrubs (Table 3), which explains its high species richness (115 taxa, Figure 5), the second highest for the Letaba exclosures site. Mean species per sampling plot is 32. Diversity is average for the Letaba study area, whereas the evenness is below average as a result of the dominance of *Colophospermum mopane* (Figure 5).

Two variants were identified that are easily be differentiated in the field, due to the difference in vegetation structure. Although species composition does not vary significantly between these two variants, they alternate along the midslopes and footslopes of the landscape.

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 *Commiphora africana*. The herbaceous layer is characterised by the climbers *Vigna luteola* and the forbs *Indigofera nebrowniana*, *I. cryptantha* and *Ocimum gratissimum*. The vegetation is dominated by the tree *Colophospermum mopane* (species group 14) and the grasses *Enneapogon 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 maximum* (species group 21) and the forbs, *Kyllinga alba* and *Waltheria indica* (species group 21). Other woody species present, include *Maerua parvifolia* (species group 9), *Philenoptera violacea* (species group 16), *Cassia abbreviata* (species group 20) and *Combretum hereroense* (species group 21). Forb species such as *Crabbea velutina* (species group 5), *Evolvulus alsinoides*, *Commelina 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 totta*, *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 maderaspatensis*, *Ceratotheca triloba* and *Phyllanthus incurvus* (species group 21). *Schmidtia pappophoroides* (species group 5), *Enneapogon scoparius* (species group 10), *Panicum coloratum* (species group 14), *Eragrostis superba*, *Urochloa mosambicensis* and *Panicum maximum* (species group 21) are the most conspicuous grasses.

2.2 *Maerua parvifolia – 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 midslopes 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 parvifolia* and the forbs *Acalypha indica* and *Heliotropium steudneri* are the most prevalent. It has floristic affinities to the *Lannea schweinfurthii* variant, of which *Maerua parvifolia*, *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 parvifolia* (species group 9), *Rhigozum zambesiacum* (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* *praeteritus* (species group 5), *Evolvulus alsinoides*, *Commelina africana*, *Limeum fenestratum* (species group 10), *Panicum coloratum*, *Ocimum americanum*, *Phyllanthus maderaspatensis*, *Pavonia burchellii*, *Jasminum stenolobum*, (species group 14), *Eragrostis superba*, *Kyllinga alba*, *Waltheria indica*, *Melhania forbesii* and *Panicum maximum* (species group 21).

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 93 and the number of species recorded per sampling plot is 32, which is an average count 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 fimbriatus* – *Grewia 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 group 11 (see online Appendix) contains the diagnostic species for this community, including only *Grewia bicolor* in the woody layer and forbs, such as *Justicia flava*, *Hibiscus calyphyllus* and the fern *Cheilanthes viridis*. The grasses *Sporobolus fimbriatus* (species group 11), *Eragrostis superba* and *Panicum maximum* (species group 21) are typically found in the field layer. Other prominent species associated with this community include *Colophospermum mopane* (species group 14), that occurs as large individuals on the perimeter of the mud pans and on the streambank. Species of lesser abundance, but of value to differentiate this community, include *Cissus cornifolia* (species group 5), *Terminalia prunioides*, *Combretum apiculatum*, the climber *Jasminum stenolobum* (species group 14) and the woody shrub *Flueggea 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 zoogenic mud pans that are scattered in the Letaba exclosure site. The four most prominent mud pans are located in the full exclosure on the bottomlands 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*, *Hemizygia bracteosa*, *Sporobolus africanus*, *Urochloa panicoides*, *Sesbania bispinosa* and *Polygala sphenoptera*. Along the edges of the open mud pans are trees and shrubs, for example *Terminalia prunioides*, *Combretum apiculatum*, *Jasminum stenolobum* (species group 14) and *Flueggea 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).

TABLE 2

Species counts for the 11 most dominant plant families recorded in the four major plant communities of the Letaba exclosures study site

Family	Plant communities				Letaba exclosures site
	1	2	3	4	
Fabaceae	16	23	16	18	34
Poaceae	13	16	18	15	30
Malvaceae	3	9	6	7	11
Cucurbitaceae	1	3	7	6	8
Lamiaceae	5	6	2	1	8
Rubiaceae	2	3	3	4	8
Acanthaceae	3	6	6	4	7
Asteraceae	2	2	0	6	7
Combretaceae	3	5	4	5	7
Cyperaceae	3	4	5	4	7
Euphorbiaceae	4	2	4	6	7
Number of species	55	79	71	76	134
Percentage of total (233 spp)	23	34	30	33	57

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 is overlain 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 buxifolia*, *Acacia karroo*, *Tricalysia lanceolata* and *Euclea divinorum. 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 fimbriatus* (species group 11), *Lantana rugosa*, *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 mespiliformis* (species group 16), *Phyllanthus reticulatus*, *Combretum microphyllum*, *Cassia abbreviata*, *Cocculus hirsutus* and *Momordica foetida* (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 this woodland type, with an average of 30 species per 400 m^2 (Figure 5). Species diversity and evenness is the highest of all communities that occur at the Letaba exclosures 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 capassa* (= *Philenoptera violacea*) –*Croton megalobotrys* – *Colophospermum mopane* Dry Riparian Woodland', the '*Croton megalobotrys* – *Maytenus senegalensis* (= *Gymnosporia senegalensis*) Riparian Forest' and the '*Phragmites mauritianus* – *Cynodon dactylon* Reed Communities'. According to the description of the Subtropical Alluvial Vegetation (AZa7), given by Mucina 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 *Cynodon 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 & Steenekamp 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 nature, it harbours the highest number of tree and shrub taxa in the study area (Table 3). The field layer is dominated by forbs and annuals. Species group 15 (see online Appendix) floristically characterises this woodland, of which *Croton megalobotrys* and *Gymnosporia senegalensis* are most prolific in the woody layer. *Panicum deustum* and *Indigofera tinctoria* are prominent characteristic species in the field layer. The tree *Philenoptera violacea* (species group 16) is also conspicuously present in this woodland.

The total species count for this community is 131, the second highest at the Letaba exclosures 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 exclosure types, as well as in the buffer zone. The dominant soil form underlying this sub-community is Oakleaf (Paterson & Steenekamp 2003). It is structurally classified as moderately closed woodland, where the trees and shrubs reach their maximum heights at the Letaba exclosures 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*, *Trichilia emetica*, *Philenoptera violacea*, *Nuxia oppositifolia* and *Diospyros mespiliformis*.

Species from species group 16 (see online Appendix) characterise the floristic composition of this sub-community and include *Philenoptera violacea*, *Diospyros 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 *Cynodon 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 conspicous than others. They include *Phyllanthus reticulatus*, *Combretum mossambicense* and *Cassia abbreviata* in the woody layer and lianas such as *Cocculus hirsutus* 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 *Melhania forbesii* and *Waltheria indica* (species group 21) are the only 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 (1993). 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 at the Letaba exclosures 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 *Diospyros 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 *Euclea natalensis*, are the major contributors to the woody cover. In the forb layer *Thunbergia neglecta* and *Tragia glabrata* 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 common 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 & Steenekamp 2003). This is well represented in all zones, including the sacrificial zone. It is better developed in the full exclosure 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 Nkhuhlu 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-Loeshea leubnitzi* and two geophytes, *Albuca setosa* and *Ledebouria revoluta*. *Croton megalobotrys* (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* – *Oldenlandea 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

Plant species richness for different growth forms in each of the plant communities and sub-communities of the Letaba exclosures study site

	Community 1			Community 2			Community 3			Community 4			Total
	1.1		1.2	2.1		2.2	3.1		3.2	4.1		4.2	
Annual	5		17	16		19	11		8	18		6	35
		21			22			15			21		
Climber	0		9 (2)	10 (2)		7 (1)	11 (1)		13 (1)	17 (1)		3	29 (3)
		9			11			9			17		
Geophyte	0		1	4		1	4		1	1		3	10
		1			4			4			3		
Graminoid	3 [1]		12 [1]	15 [1]		13 [1]	14 [1]		9	11 [2]		9 [1]	30 [3]
		15			28			17			14		
Forb	2		23	29 (2)		26	16		14	21		10	45 (2)
		25			36			24			23		
Dwarf shrub	1		12	14		9	7		5	7		3	18
		12			15			8			7		
Shrub	1		7	14		11	6		12	17		8	36
		6			16			16			21		
Tree	3		18	13		7	5		16	24		10	30
		18			15			15			22		

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

Editor: Llewellyn C. Foxcroft

REFERENCES

Barbour, M.G., Burk, J.H. & Pitts, W.D., 1987, *Terrestrial plant ecology,* Cummings, California.

Bredenkamp, G.J. & Van Rooyen, N., 1993, 'A survey of the vegetation of the Letaba River in the Kruger National Park', unpublished report, Ekotrust.

Du Plessis, F., 2001, 'A phytosociological synthesis of Mopaneveld', MSc dissertation, University of Pretoria.

Germishuizen, G. & Meyer, N.L., 2003, 'Plants of southern Africa: An annotated checklist', *Strelitzia* 14, National Botanical Institute, Pretoria.

Gertenbach, W.P.D., 1983, 'Landscapes of the Kruger National Park', *Koedoe* 26, 9–121.

Hennekens, S., 1996, *MEGATAB: A visual editor for phytosociological tables,* computer program, version 1.0, user's guide, Giesen & Geurts, Ulft.

Hill, M.O., 1979, *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two way table by classification of individuals and attributes,* computer program, Cornell University, Ithaca.

Mucina, L., Rutherford, M.C. (eds.), 2006, 'The vegetation of South Africa, Lesotho and Swaziland', *Strelitzia* 19, South African National Biodiversity Institute, Pretoria.

Mueller-Dombois, D. & Ellenberg, H., 1974, *Aims and methods of vegetation ecology*, Wiley, New York.

O'Connor, T.G., 1992, 'Woody vegetation-environment relations in a semi-arid savanna in the northen Transvaal', *South African Journal of Botany* 58(4), 268–274.

O'Keeffe, T. & Alard G., 2002, *Field operations manual for herbivore & fire exclosures on the Sabie and Letaba Rivers in the Kruger National Park*, viewed n.d. April 2009, from http://www.sanparks.org/parks/kruger/conservation/scientific/exclosures/Exclosure_Field_Manual.pdf

O'Keeffe, J. & Rogers K.H., 2003, 'Heterogeneity and management of the Lowveld rivers' in J.T. du Toit, K.H. Rogers & H.C. Biggs (eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*, pp. 41–58, Island Press, Washington.

Parsons, M., McLoughlin, C.A., Kotschy, K.A., Rogers, K.H. & Rountree, M.W., 2005, 'The effects of extreme floods on the biophysical heterogeneity of river landscapes', *Frontiers in Ecology and the Environment* 3, 487–494.

Paterson, D.G. & Steenekamp, P.I., 2003, 'Soil survey of Letaba exclosure', ISCW Report No. GW/A/2003/38, ARC – Institute for Soil, Climate & Water, Pretoria.

Siebert, F., Bredenkamp, G.J. & Siebert, S.J., 2003, 'A comparison of mopaneveld vegetation in South Africa, Namibia and Zimbabwe', *Bothalia* 33(1), 121–134.

Siebert, S.J., Van Wyk, A.E., Bredenkamp, G.J. & Siebert, F., 2003, 'Vegetation of the rock habitats of the Sekhukhuneland Centre of Plant Endemism, South Africa', *Bothalia* 33(2), 207–228.

Siebert, F. & Eckhardt, H.C., 2008, 'The vegetation and floristics of the Nkhuhlu exclosures, Kruger National Park', *Koedoe* 50(1), 126–144.

Van Rooyen, N., Theron, G.K. & Grobbelaar, N., 1981, 'A floristic description and structural analysis of the plant communities of the Punda–Milia–Wambiya area in the Kruger National Park, Republic of South Africa: 3. The *Colophospermum mopane* communities', *Journal of South African Botany* 47(4), 585–626.

Visser, D.J.L., Coertze, F.J. & Walraven F., 1989, *Explanation of the 1:1000000 geological map, fourth edition, 1984: The geology of the Republics of South Africa, Transkei, Bophuthatswana, Venda and Ciskei and the Kingdoms of Lesotho and Swaziland,* Government Printer, Pretoria.

Weather Bureau, 1986, *Climate of South Africa. Pretoria, South Africa*, Department of Environmental Affairs, Weather Bureau Publication No. 40.

APPENDIX 8-1

Riparian vegetation synthesis
Fidelity syntable

Azonal group

Appendix 8-1

Fidelity syntable of the vegetation of the Azonal vegetation (plant communities 1 - 3)
Only fidelity diagnostics with values >30 is considered as diagnostics in the text
Plant community numbers are in accordance to the described communities in the text

	Plant community numbers		
Species diagnostic to community 1:	1	2	3
Phragmites mauritianus	80.3	---	---
Cynodon dactylon	61.1	---	---
Pluchea dioscoridis	52	---	---
Xanthium strumarium	50.1	---	---
Sporobolus africanus	48.8	---	---
Kanahia laniflora	47	---	---
Breonadia salicina	45.5	---	---
Nuxia oppositifolia	44.3	---	---
Dichanthium annulatum	40.2	---	---
Ludwigia stolonifera	38.7	---	---
Flueggea virosa	33.6	---	---
Senna occidentalis	32.3	---	---
Aeschynomene indica	31.4	---	---
Eriochloa meyeriana	30.8	---	---
Argemone ochroleuca	30.5	---	---
Species diagnostic to community 2:			
Xanthocercis zambesiaca	---	65.9	---
Acacia schwenfurthii	---	55.8	---
Azima tetracantha	---	58.4	---
Faidherbia albida	---	54.7	---
Capparis tomentosa	---	46.2	---
Acacia xanthophloea	---	41.6	---
Acacia tortilis	---	40.3	---
Setaria verticillata	---	38.5	---
Acacia robusta	---	30.6	---
Panicum schinzii	---	30.5	---
Thilachium africanum	---	30.2	---
Species diagnostic to community 3:			
Combretum hereroense	---	---	46.6
Colophospermum mopane	---	---	40.2
Cassia abbreviata	---	---	36.3
Philenoptera violacea	---	---	35.1
Euclea natalensis	---	---	33.6
Combretum imberbe	---	---	31.9
Spirostachys africana	---	---	31.2
Species below the 30% fidelity threshold			
Gomphrena celosioides	29.1	---	---
Cyperus articulatus	29	---	---
Ficus capreifolia	28.8	---	---

Cyperus sexangularis	28.4	---	---
Cyperus esculentus	26.3	---	---
Eichhornia crassipes	26.1	---	---
Cyperus longus	24.6	---	---
Echinochloa colona	23.9	---	---
Hleiotropium ovalifolium	22.8	---	---
Cissampelos mucronata	22.4	---	---
Indigofera cryptantha	22	---	---
Combretum erythrophyllum	21.3	---	---
Paspalum dilatatum	19.3	---	---
Secamone alpinii	19.3	---	---
Cocculus hirsutus	---	29.8	---
Grewia flavescens	---	29.7	---
Garcinia livingstonei	---	26.9	---
Setaria sagittifolia	---	26	---
Abutilon grandiflorum	---	26	---
Hibiscus micranthus	---	24.6	---
Leptochloa panicea	---	24.4	---
Ximenia americana	---	24.2	---
Adansonia digitata	---	22.6	---
Schotia brachypetala	---	21.6	---
Hyphaene petersiana	---	21.1	---
Leucas sexdentata	---	21.1	---
Boerhavia diffusa	---	19.9	---
Limeum sulcatum	---	19.2	---
Eragrostis heteromera	---	---	29.2
Sporobolus fimbriatus	---	---	28.1
Enneapogon cenchroides	---	---	27.1
Flaveria bidentis	---	---	26.5
Acanthospermum hispidum	---	---	26.4
Eragrostis lehmanniana	---	---	26
Sclerocarya birrea	---	---	24.1
Sesamum alatum	---	---	24.1
Acacia nigrescens	---	---	23.9
Schmidtia pappophoroides	---	---	21.6
Terminalia prunioides	---	---	22.7
Abutilon grantii	---	---	22
Euclea divinorum	---	---	21.4
Enneapogon scoparius	---	---	21.1
Eragrostis superba	---	---	20.9
Pupalia lappacea	---	---	20.7
Grewia monticola	---	---	19.2
Crotalaria sphaerocarpa	---	---	18.2

JUICE codes of species with no fidelity to communities 1, 2 or 3

SOLNPAN	---	---	---
MAYTSEN	---	---	---

SETASPH	---	---	---
PANIMAX	---	---	---
BECIFIL	---	---	---
MELHREH	---	---	---
CRONMEG	---	---	---
AERVLEU	---	---	---
TRAGRUP	---	---	---
CORCKIR	---	---	---
CHLOGAY	---	---	---
CYPEFEN	---	---	---
DIOPMES	---	---	---
UROHMOS	---	---	---
COMRMOS	---	---	---
COMRMIC	---	---	---
TRIHEME	---	---	---
ZIZIMUC	---	---	---
TRILTER	---	---	---
ACHYASP	---	---	---
RHIOZAM	---	---	---
JASMFLU	---	---	---
BERCDIS	---	---	---
PHYARET	---	---	---
BRIDCAT	---	---	---
ALBU/SP	---	---	---
CISUCOR	---	---	---
COMMBEN	---	---	---
LANNSCW	---	---	---
PAVOBUR	---	---	---
SIDADRE	---	---	---
TRAGDIO	---	---	---
COCCREH	---	---	---
COMPAFR	---	---	---
PANICOL	---	---	---
ABUTGUI	---	---	---
ACALIND	---	---	---
MELHFOR	---	---	---
PAVECAO	---	---	---
TRICJUN	---	---	---
MANLMOC	---	---	---
HIPCLON	---	---	---
THUNNEG	---	---	---
ABUTAUS	---	---	---
BOLSSPE	---	---	---
TERMSER	---	---	---
PANIDEU	---	---	---
WALTIND	---	---	---
EHREAMO	---	---	---

BARLELE	---	---	---
HYPNCOR	---	---	---
GARDVOL	---	---	---
RUELCOR	---	---	---
TRAGGLA	---	---	---
VIGNFRU	---	---	---
MOMOFOE	---	---	---
LIPPJAV	---	---	---
LAGESPH	---	---	---
CHAAABS	---	---	---
COMPMOL	---	---	---
RHOCREV	---	---	---
MARKZAN	---	---	---
MAEREDU	---	---	---
PHYAASP	---	---	---
PORUOLE	---	---	---
HYPB/SP	---	---	---
AMARPRA	---	---	---
HERSODO	---	---	---
ERAGRIG	---	---	---
BOSCALB	---	---	---
LEONNEP	---	---	---
BIDEPIL	---	---	---
PHRGAUS	---	---	---
PHOEREC	---	---	---
SORHBIC	---	---	---
SPHEINC	---	---	---
TEPHPUR	---	---	---
SYZYGUI	---	---	---
PELTAFR	---	---	---
ACACNIL	---	---	---
BOTHRAD	---	---	---
CLEOANG	---	---	---
LAGGDEC	---	---	---
ALCOLAX	---	---	---
PILITHO	---	---	---
XYLITOR	---	---	---
ARTABRA	---	---	---
TABEELE	---	---	---
AFZEQUA	---	---	---
DIOPLYC	---	---	---
MACLAFR	---	---	---
ANTDVEN	---	---	---
EUGE/SP	---	---	---
LANTCAM	---	---	---
SETAMEG	---	---	---
HEXLMON	---	---	---

PTELMYR	---	---	---
DRYPGER	---	---	---
FICUSYC	---	---	---
STRYPOT	---	---	---
SYZYCOR	---	---	---
ACALGLB	---	---	---
CORDMON	---	---	---
OCHN/SP	---	---	---
ALBIBRE	---	---	---
STRYHEN	---	---	---
MIMSZEY	---	---	---
FICUSUR	---	---	---
TODABRE	---	---	---
AGAHBOJ	---	---	---
CUCMAFR	---	---	---
MERRPAL	---	---	---
TRIEMON	---	---	---
ACACBUR	---	---	---
ANDPGAY	---	---	---
COMMERE	---	---	---
CENCCIL	---	---	---
SENNPET	---	---	---
BOSCFOE	---	---	---
TALICAF	---	---	---
COMPGLA	---	---	---
ACALVIL	---	---	---
LIMEPAU	---	---	---
TERMPHA	---	---	---
ALTE/SP	---	---	---
PASA/SP	---	---	---
SIDACOR	---	---	---
ALTEPUN	---	---	---
CYPEDIV	---	---	---
CORBRUB	---	---	---
DATUSTR	---	---	---
CHASHIR	---	---	---
EVOLALS	---	---	---
JUSTFLA	---	---	---
SESBSES	---	---	---
PHYAINC	---	---	---
ALYSRUG	---	---	---
ABRUPRE	---	---	---
MENT/SP	---	---	---
TRASBER	---	---	---
CORCASP	---	---	---
SCHVAFR	---	---	---
HELRSTE	---	---	---

CUCUCIN	---	---	---
CHASINA	---	---	---
MOLLCER	---	---	---
RICNCOM	---	---	---
VERSENC	---	---	---
VINCMAJ	---	---	---
PASADIS	---	---	---
EKEBCAP	---	---	---
ERAGROT	---	---	---
LIPPSCA	---	---	---
ECLIPRO	---	---	---
DICSCIN	---	---	---
MAERPAR	---	---	---
CORCCON	---	---	---
DACLGEM	---	---	---
SIDAALB	---	---	---
DIGISAN	---	---	---
PHYLNOD	---	---	---
TACAAPI	---	---	---
RHYHTOT	---	---	---
JASMSTE	---	---	---
COMMDIF	---	---	---
SOLNSEA	---	---	---
CROTLAB	---	---	---
ERAGINA	---	---	---
LEONOCY	---	---	---
UROHPAN	---	---	---
CRINMAC	---	---	---
CYPEROT	---	---	---
CENECOR	---	---	---
CTEOCER	---	---	---
LAGESIC	---	---	---
SPORNIT	---	---	---
NIDOAUR	---	---	---
CYPECOM	---	---	---
THEL/SP	---	---	---
COMRAPI	---	---	---
GREWBIC	---	---	---
COMMAFR	---	---	---
ANDTJOH	---	---	---
GISEAFR	---	---	---
ABUTRAM	---	---	---
HIBICAL	---	---	---
IPOMOBS	---	---	---
VANGINF	---	---	---
ERAGCYL	---	---	---
OCIMGRA	---	---	---

DICMTOM	---	---	---
KYLLALB	---	---	---
SPORSTA	---	---	---
ACACKAR	---	---	---
HIBITRI	---	---	---
INDGZEY	---	---	---
INDGTIN	---	---	---
COMMECK	---	---	---
GOMPFRU	---	---	---
LEDEREV	---	---	---
ALBUSET	---	---	---
MAYTHET	---	---	---
ALOECHA	---	---	---
PAVEZEY	---	---	---
ARITADS	---	---	---
ALBIFOR	---	---	---
VEROGLA	---	---	---
BRACDEF	---	---	---
SPORCOS	---	---	---
GREWRET	---	---	---
GREWVIL	---	---	---
CHEDALB	---	---	---
CHEDCAR	---	---	---
CHLOVIR	---	---	---
LANN/SP	---	---	---
EUPHTIR	---	---	---
ABUTANG	---	---	---
PECHLEU	---	---	---
KIGEAFR	---	---	---
MAERANG	---	---	---
LIME/SP	---	---	---
DEINXAN	---	---	---
ALBIVER	---	---	---
KAROSPE	---	---	---
PSELMAP	---	---	---
CYPSCIR	---	---	---
GYROAME	---	---	---
ALOEDIC	---	---	---
ECHIPYR	---	---	---
CORBDEC	---	---	---
SOLNINC	---	---	---
CLEOHIR	---	---	---
ERAGBIF	---	---	---
ABUTA-M	---	---	---
EUCLCRI	---	---	---
OLAXDIS	---	---	---
STRYSPI	---	---	---

ERAGCHL	---	---	---
BERCZEY	---	---	---
DIGIERI	---	---	---
ARITCON	---	---	---
SERRSTE	---	---	---
SALBBAB	---	---	---
STRYPUN	---	---	---
FICUSTU	---	---	---
ERAGPAL	---	---	---
DOMBROT	---	---	---
HYPAHIR	---	---	---
DIGIDIA	---	---	---
DOMBCYM	---	---	---
ALBIHAR	---	---	---
PANINAT	---	---	---
OLEACAP	---	---	---
GREWSUL	---	---	---
CYMOPLU	---	---	---
DACLAEG	---	---	---
LIMEFEN	---	---	---
CARICOR	---	---	---
DACLGIG	---	---	---
ERAGRAC	---	---	---
HETGCON	---	---	---
ANDPAPP	---	---	---
SCHKPIN	---	---	---
CHLRVIS	---	---	---
MELBREP	---	---	---
FICUING	---	---	---
LOUDFIL	---	---	---
CHED/SP	---	---	---
ASPLMOS	---	---	---
HELHSTE	---	---	---
KYPHANG	---	---	---
MONEDIV	---	---	---
COMRMOL	---	---	---
DIGIVEL	---	---	---
ERAGNIN	---	---	---
HELHLIN	---	---	---
SECMPAR	---	---	---
MALACOR	---	---	---
POGOSQU	---	---	---
DICEERI	---	---	---
DALBMEL	---	---	---
FINGAFR	---	---	---
LANNDIS	---	---	---
GEIGORN	---	---	---

ALTESES	---	---	---
HERMGLN	---	---	---
MELIAZE	---	---	---
PEUC/SP	---	---	---
ERAGTRI	---	---	---
BRIDMOL	---	---	---
INDGAST	---	---	---
INDGFLV	---	---	---
SIDEINE	---	---	---
ELEUCOR	---	---	---
LIMEVIS	---	---	---
BIDEBIP	---	---	---
GALNTRA	---	---	---
ZALEPEN	---	---	---
MOMOBAL	---	---	---
ERAGCIL	---	---	---
SPORPYR	---	---	---
GREWHEX	---	---	---
XERPRET	---	---	---
TRIL/SP	---	---	---
ERYTLYS	---	---	---
HYPHDIS	---	---	---
DALEGAL	---	---	---
LEUSGLA	---	---	---
TEPHPOL	---	---	---
HELRLIN	---	---	---
IPOMSIN	---	---	---
SIDA/SP	---	---	---
THEMTRI	---	---	---
VIGNUNG	---	---	---
TETPTEN	---	---	---
BARL/SP	---	---	---
SCOLZEY	---	---	---
COMM/SP	---	---	---
ARITCAN	---	---	---
AGEACON	---	---	---
PORUKER	---	---	---
MAYTPUB	---	---	---
ASPRSET	---	---	---
RUELPAT	---	---	---
COMRPAD	---	---	---
PISTSTR	---	---	---
PROT/SP	---	---	---
ZANHCAP	---	---	---
BAUHGAL	---	---	---
RAUVCAF	---	---	---
SALBMUC	---	---	---

LITGGAR	---	---	---
PSEGLUT	---	---	---
DATUINN	---	---	---
SENEAPI	---	---	---
DOVYCAF	---	---	---
WISSROS	---	---	---
FICUNAT	---	---	---
ANSEAFR	---	---	---
VEROFAS	---	---	---
SANSPEA	---	---	---
BOTHINS	---	---	---
SIDARHO	---	---	---
FLUEV-V	---	---	---
SALVAUS	---	---	---
OROPCAP	---	---	---
PAPPCAP	---	---	---
STYONAT	---	---	---
KIRKACU	---	---	---
ASPRAFR	---	---	---
ALOESES	---	---	---
CANTSET	---	---	---
ELEPBUR	---	---	---
FICU/SP	---	---	---
HEMZPEE	---	---	---
SANSHYA	---	---	---
CISUQUA	---	---	---
CHEIVIR	---	---	---
FICUABU	---	---	---
EUPHCOF	---	---	---
SARSVIM	---	---	---
EUSTPAS	---	---	---
RHYHMIN	---	---	---
ISCHAFR	---	---	---
LEPHUNI	---	---	---
POLGHOT	---	---	---
HYPBFOR	---	---	---
BULSHIS	---	---	---
STIRUNI	---	---	---
VEROSTE	---	---	---
IPOMCOP	---	---	---
IPOMPLE	---	---	---
ADEUMUL	---	---	---
CASPGER	---	---	---
CHASNEO	---	---	---
MAERJUN	---	---	---
PLUMZEY	---	---	---
MARIREH	---	---	---

COMMLIV	---	---	---
VEROPOS	---	---	---
HIBICAN	---	---	---
LUDWOCT	---	---	---
SESBBIS	---	---	---
CASIAET	---	---	---
HETPTRI	---	---	---
INDGVIC	---	---	---
RICHBRA	---	---	---
OTTEEXS	---	---	---
CERHTRI	---	---	---
PHYAMAD	---	---	---
UROHOLI	---	---	---
TEPHMUT	---	---	---
CROTPAL	---	---	---
ARITBIP	---	---	---
KEDRAFR	---	---	---
CAPPSEP	---	---	---
TRIhPIL	---	---	---
CUCMHIR	---	---	---
SENNITA	---	---	---
CYNGLAN	---	---	---
MARISUM	---	---	---
CLEOMON	---	---	---
SENNOBT	---	---	---
EHRERIG	---	---	---
JATRVAR	---	---	---
STRYMAD	---	---	---
CRONGRA	---	---	---
ERAGCUR	---	---	---
RHYHCAR	---	---	---

APPENDIX 8-2

Riparian vegetation synthesis
Fidelity syntable

Savanna-riparian interface group

Appendix 8-2

Fidelity syntable of the vegetation of the Riparian-savanna interface vegetation (plant communitie

Only fidelity diagnostics with values >30 is considered as diagnostics in the descriptions

Plant community numbers are in accordance to the described communities in the text

	Plant community numbers		
Species diagnostic to community 4:	**4**	**5**	**6**
Diospyros mespiliformis	47.2	---	---
Euclea divinorum	46.6	---	---
Combretum hereroense	46.1	---	---
Gymnosporia senegalensis	45.3	---	---
Philenoptera violacea	42.8	---	---
Combretum imberbe	41.4	---	---
Spirostachys africana	41.2	---	---
Abutilon guineense	38.4	---	---
Euclea natalensis	36.9	---	---
Peltophorum africanum	35	---	---
Phyllanthus asperulatus	34.7	---	---
Melhania forbesii	31.7	---	---
Cucumis africanus	31.3	---	---
Species diagnostic to community 5:			
Combretum apiculatum	---	64.8	---
Terminalia prunioides	---	52.7	---
Tephrosia purpurea	---	52.6	---
Ocimum americanum	---	48.6	---
Melinis repens	---	48.1	---
Grewia flava	---	43	---
Colophospermum mopane	---	38.9	---
Panicum coloratum	---	37.7	---
Acalypha vilicaulis	---	36.6	---
Commiphora mollis	---	36.1	---
Crabbea velutina	---	35.4	---
Melhania rehmannii	---	34.7	---
Cissus cornifolia	---	34.5	---
Oropetium capense	---	33.8	---
Phyllanthus maderaspatensis	---	33	---
Kirkia acuminata	---	32.7	---
Aristida congesta	---	32.4	---
Clerodendrum ternatum	---	31.4	---
Indigofera hermannioides	---	30.9	---
Sclerocarya birrea	---	30.8	---
Enneapogon scoparius	---	30.5	---
Kyllinga alba	---	30	---
Commiphora tenuipetiolata	---	32	---
Species diagnostic to community 6:			
Abutilon grandiflorum	---	---	70.6
Salvadora australis	---	---	70.1
Acacia tortilis	---	---	69.1
Lycium cinereum	---	---	64.2
Setaria verticillata	---	---	61.3

Cucumis zeyheri	---	---	50.8
Tribilus zeyheri	---	---	48
Sida cordifolia	---	---	46.1
Pseudognaphalium luteo-album	---	---	44.6
Urochloa mosambicensis	---	---	42.8
Chloris virgata	---	---	41.5
Hydnora africana	---	---	39.5
Hypertelis salsoloides	---	---	38
Boscia foetida	---	---	37
Cucumis metuliferus	---	---	36.6
Chenopodium album	---	---	36.5
Geigeria burkei	---	---	36.5
Cyathula ornacantha	---	---	36
Echinochloa colona	---	---	35.4
Grewia subspatulata	---	---	35.2
Boerhavia diffusa	---	---	35.1
Abutilon pycnodon	---	---	34
Flueggea virosa	---	---	33.3
Leucas sexdentata	---	---	32.2
Trianthema triquetra	---	---	32.2
Hermania modesta	---	---	32.1
Litogyne gariepina	---	---	31.2
Ammania baccifera	---	---	31
Trianthema salsoides	---	---	30.1
Species below the 30% fidelity threshold			
Sporobolus fimbriatus	29.7	---	---
Flueggea virosa	28.8	---	---
Schotia brachypetala	28.4	---	---
Dalbergia melanoxylon	27.5	---	---
Ormocarpum trichocarpum	27.3	---	---
Acacia robusta	27	---	---
Panicum maximum	26.9	---	---
Albizia harveyi	26.3	---	---
Sporobolus nitens	24.6	---	---
Commelina benghalensis	24.5	---	---
Manilkara mochia	24.3	---	---
Themeda triandra	24.3	---	---
Tephrosia polystachya	24.2	---	---
Justicia flava	24.1	---	---
Rhynchosia minima	22.7	---	---
Endestemon terecaulis	22.7	---	---
Vigna unguiculata	22.4	---	---
Capparis tomentosa	21.7	---	---
Bolusanthus speciosus	21	---	---
Merremia palmata	21	---	---
Acacia butkei	21	---	---
Hibisuc calyphyllus	21	---	---
Thunbergia neglecta	21	---	---
Euclea undulata	21	---	---

Melhania didyma	21	---	---
Rhoicissus tridentata	21	---	---
Achyropsis leptostachya	21	---	---
Euclea schimperi	21	---	---
Grewia hexamita	20.7	---	---
Ximenia caffra	20.7	---	---
Eragrostis rigidior	20.6	---	---
Tribulus terrestris	19.9	---	---
Crotalaria sphaerocarpa	19.6	---	---
Dactyloctenium giganteum	19.1	---	---
Ipomoea coptica	19.1	---	---
Cynodon dactylon	18.7	---	---
Terminalia sericea	18.7	---	---
Gymnosporia buxifolia	18.6	---	---
Lannea schweinfurthii	18.5	---	---
Barleria elegans	17.9	---	---
Maerua parvifolia	17.8	---	---
Strychnos madagascariensis	17.7	---	---
Indigofera vicioides	14.4	---	---
Barleria lancifolia	---	29.9	---
Gardenia resenifolia	---	29.9	---
Ptycholobium contortum	---	29.4	---
Kyphocarpa angustifolia	---	29.6	---
Ceratotheca triloba	---	29.1	---
Calostephane divaricata	---	28.6	---
Neuracanthus africanus	---	28.3	---
Indigofera nebrowniana	---	27.9	---
Seddera capensis	---	27.8	---
Justicia protracta	---	26.1	---
Jatropha spicata	---	26.1	---
Vigna luteola	---	26.1	---
Amaranthus schinzianus	---	26.1	---
Rhynchosia totta	---	25.4	---
Phyllanthus incurvus	---	25.2	---
Evolovulus alsinoides	---	24.9	---
Asparagus suaveolens	---	24.6	---
Acacia erubescens	---	24.4	---
Acacia senegal	---	24.1	---
Ficus tettensis	---	24.1	---
Danthoniopsis dintheri	---	24.1	---
Ipomoea magnusiana	---	23.3	---
Agathesanthemum bojeri	---	23.3	---
Grewia monticola	---	23.1	---
Boscia albitrunca	---	22.9	---
Lantana rugosa	---	22.9	---
Tricholaena monachne	---	22.7	---
Commiphora africana	---	22.4	---
Waltheria indica	---	22.4	---
Hermannia boraginiflora	---	22.2	---
Dicoma tomentosa	---	22.1	---

Indigofera cryptantha	---	21.9	---
Mariscus sumatrensis	---	21.9	---
Commelina eckloniana	---	21.9	---
Hibiscus praeterites	---	21.9	---
Tricliseras glanduliferum	---	21.9	---
Hemizygia persimilis	---	21.9	---
Dumasia villosa	---	21.9	---
Indigofera trachyphylla	---	21.9	---
Commicarpus fallacissimus	---	21.9	---
Limeum fenestratum	---	21.8	---
Hibiscus micranthus	---	21.8	---
Cyperus rupestris	---	21.8	---
Cleome angustifolia	---	21.3	---
Kohautia virgata	---	21.2	---
Hexalobus monopetalus	---	21.1	---
Pavonia burchellii	---	21.1	---
Brachiaria deflexa	---	20.6	---
Eragrostis superba	---	20.6	---
Talinum caffrum	---	20.3	---
Ruellia cordata	---	20.1	---
Cassia abbreviata	---	17.2	---
Schmidtia pappophoroides	13.9	14.9	---
Commiphora mossambicensis	11.1	15.9	---
Acacia nigrescens	14.4	19	---
Digitaria eriantha	14.1	14.1	---
Barleria bremekampii	---	---	29.9
Commicarpus plumbagineus	---	---	29.9
Abutilon angulatum	---	---	29.5
Hyphaene petersiana	---	---	28.6
Alternanthera nodifolra	---	---	28.6
Tribulus zeyheri	---	---	28.6
Flaveria bidentis	---	---	28
Cordia monoica	---	---	27.4
Glinus lotoides	---	---	27.4
Indigofera sordida	---	---	27.4
Cadaba termitaria	---	---	26.7
Ocimum americanum	---	---	26.7
Hermstaedtia lineare	---	---	25.4
Maerua juncea	---	---	24.2
Cyathula lanceolata	---	---	24.2
Portulaca oleracea	---	---	24.1
Boerhavia erecta	---	---	24
Dinebra retroflexa	---	---	24
Heliotropium supinum	---	---	24
Commicarpus pilosus	---	---	21.7
Leucosphaera bainesii	---	---	20.9
Balanites pedecillaris	---	---	20.9
Acacia nebrowniana	---	---	20.9
Datura ferox	---	---	20.9
Digitaria velutina	---	---	20.4

Panicum schinzii	---	---	20.1
Hypoestis aristata	---	---	20.1
Heliotropium steudneri	---	---	19.7
Limeum sulcatum	---	---	19.3
Eragrostis lehmanniana	---	---	17.7
Erogrostis trichophora	---	---	17.3
Enneapogon cenchroides	---	---	17.1
JUICE codes of species with no fidelity to communities 4, 5 or 6			
PHRGMAU	---	---	---
NUXIOPP	---	---	---
DICHANN	---	---	---
XANTSTR	---	---	---
BERCZEY	---	---	---
GOMRCEL	---	---	---
FICUCAP	---	---	---
PLUCDIO	---	---	---
AESCIND	---	---	---
SPORAFR	---	---	---
CRONMEG	---	---	---
ERIHMEY	---	---	---
SIDADRE	---	---	---
ALTEPUN	---	---	---
SORHBIC	---	---	---
CROTLAB	---	---	---
PHYARET	---	---	---
CYPEESC	---	---	---
COCUHIR	---	---	---
CYPESEX	---	---	---
UROHPAN	---	---	---
RICNCOM	---	---	---
MOMOFOE	---	---	---
FICUSYC	---	---	---
PANIDEU	---	---	---
SOLNPAN	---	---	---
COMRMIC	---	---	---
ACAHHIS	---	---	---
LEONNEP	---	---	---
DICSCIN	---	---	---
SESBSES	---	---	---
JASMFLU	---	---	---
CISSMUC	---	---	---
LUDWSTO	---	---	---
MACLAFR	---	---	---
SESMALA	---	---	---
CTEOCER	---	---	---
ACACXAN	---	---	---
CORCCON	---	---	---
DACLGEM	---	---	---
SIDAALB	---	---	---

DIOPLYC	---	---	---
DATUSTR	---	---	---
GREWFLV	---	---	---
TRASBER	---	---	---
HELROVA	---	---	---
CORCASP	---	---	---
RHIOZAM	---	---	---
CHASINA	---	---	---
VERSENC	---	---	---
JASMSTE	---	---	---
COMMDIF	---	---	---
ZIZIMUC	---	---	---
ERAGROT	---	---	---
GARDVOL	---	---	---
HYPNCOR	---	---	---
ABUTAUS	---	---	---
MARIREH	---	---	---
INDGAST	---	---	---
PHRGAUS	---	---	---
VEROPOS	---	---	---
HIBICAN	---	---	---
SESBBIS	---	---	---
SPHEINC	---	---	---
LAGGDEC	---	---	---
FAIDALB	---	---	---
FICUING	---	---	---
PHOEREC	---	---	---
GARCLIV	---	---	---
CASIAET	---	---	---
SIDA/SP	---	---	---
CORBDEC	---	---	---
HETGCON	---	---	---
ARITADS	---	---	---
OCIMGRA	---	---	---
CLEOHIR	---	---	---
COMMERE	---	---	---
LIMEVIS	---	---	---
ACALIND	---	---	---
SCHKPIN	---	---	---
UROHOLI	---	---	---
TRAGGLA	---	---	---
CENCCIL	---	---	---
PLUMZEY	---	---	---
ERAGHET	---	---	---
GREWBIC	---	---	---
PUPALAP	---	---	---
XANHZAM	---	---	---
BERCDIS	---	---	---
ARTABRA	---	---	---
THILAFR	---	---	---

ADANDIG	---	---	---
SETASAG	---	---	---
ACACSCH	---	---	---
AZIMTET	---	---	---
GREWRET	---	---	---
GREWVIL	---	---	---
CHEDCAR	---	---	---
TRICJUN	---	---	---
XIMEAME	---	---	---
STRYPOT	---	---	---
EUPHTIR	---	---	---
PECHLEU	---	---	---
KIGEAFR	---	---	---
MAERANG	---	---	---
ALBIVER	---	---	---
PSELMAP	---	---	---
ALCOLAX	---	---	---
CYPSCIR	---	---	---
ACHYASP	---	---	---
AMARPRA	---	---	---
TABEELE	---	---	---
ECHIPYR	---	---	---
SOLNINC	---	---	---
ERAGBIF	---	---	---
ACACNIL	---	---	---
BAUHGAL	---	---	---
DATUINN	---	---	---
SENEAPI	---	---	---
DOVYCAF	---	---	---
RUELPAT	---	---	---
COMM/SP	---	---	---
AFZEQUA	---	---	---
PORUKER	---	---	---
ALBIFOR	---	---	---
RHOCREV	---	---	---
HIPCLON	---	---	---
SANSPEA	---	---	---
ASPRSET	---	---	---
ZANHCAP	---	---	---
ABUTRAM	---	---	---
SETASPH	---	---	---
BOTHINS	---	---	---
SIDARHO	---	---	---
VEROFAS	---	---	---
BOTHRAD	---	---	---
STRYSPI	---	---	---
ERAGCHL	---	---	---
ERAGPAL	---	---	---
DOMBROT	---	---	---
ACACKAR	---	---	---

CYMOPLU	---	---	---
DACLAEG	---	---	---
CARICOR	---	---	---
ERAGRAC	---	---	---
PAVO/SP	---	---	---
ANDPAPP	---	---	---
ANDTJOH	---	---	---
LOUDFIL	---	---	---
ASPLMOS	---	---	---
HELHSTE	---	---	---
ABUTGRN	---	---	---
HERSODO	---	---	---
MONEDIV	---	---	---
COMRMOL	---	---	---
ERAGNIN	---	---	---
HELHLIN	---	---	---
POGOSQU	---	---	---
DICEERI	---	---	---
FINGAFR	---	---	---
COMPGLA	---	---	---
LANNDIS	---	---	---
GEIGORN	---	---	---
HERMGLN	---	---	---
VANGINF	---	---	---
BRIDMOL	---	---	---
TRAGRUP	---	---	---
ZALEPEN	---	---	---
MOMOBAL	---	---	---
ERAGCIL	---	---	---
XERPRET	---	---	---
GISEAFR	---	---	---
DALEGAL	---	---	---
LEUSGLA	---	---	---
EHREAMO	---	---	---
IPOMSIN	---	---	---
TETPTEN	---	---	---
ARITCAN	---	---	---
PAPPCAP	---	---	---
STYONAT	---	---	---
ASPRAFR	---	---	---
OCHN/SP	---	---	---
ALOESES	---	---	---
HEMZPEE	---	---	---
SANSHYA	---	---	---
CISUQUA	---	---	---
CHEIVIR	---	---	---
FICUABU	---	---	---
EUPHCOF	---	---	---
SARSVIM	---	---	---
ISCHAFR	---	---	---

COCCREH	---	---	---
BULSHIS	---	---	---
STIRUNI	---	---	---
VEROSTE	---	---	---
CHASNEO	---	---	---
LIPPJAV	---	---	---
TRAGDIO	---	---	---
COMPAFR	---	---	---
PAVECAO	---	---	---
ERAGCUR	---	---	---
RHYHCAR	---	---	---
IPOMOBS	---	---	---
BIDEPIL	---	---	---
ALOECHA	---	---	---
ANDPGAY	---	---	---
VIGNFRU	---	---	---
BECIFIL	---	---	---
AERVLEU	---	---	---
CORCKIR	---	---	---
CHLOGAY	---	---	---
CYPEFEN	---	---	---
PILITHO	---	---	---
XYLITOR	---	---	---
CHAAABS	---	---	---
MARKZAN	---	---	---
MAEREDU	---	---	---
LAGESPH	---	---	---
PTELMYR	---	---	---
DRYPGER	---	---	---
ALBIBRE	---	---	---
KEDRAFR	---	---	---
CUCMHIR	---	---	---
SENNITA	---	---	---
CLEOMON	---	---	---
EHRERIG	---	---	---
CRONGRA	---	---	---
SPORSTA	---	---	---
HIBITRI	---	---	---
GOMPFRU	---	---	---
LEDEREV	---	---	---
ALBUSET	---	---	---
BRACNIG	---	---	---
MONEDEB	---	---	---
CHACPIN	---	---	---
LEUSNEU	---	---	---
KALAPAN	---	---	---
SIDACHR	---	---	---
ACACEXU	---	---	---
ARITC-B	---	---	---
INDGRHY	---	---	---

INDGFIP	---	---	---
CHACHED	---	---	---
TRIRGRA	---	---	---
POLGSPH	---	---	---
ACACGER	---	---	---
HELRSTR	---	---	---
MUNDSER	---	---	---
ELYTACA	---	---	---
BALAMAU	---	---	---
ARITS-G	---	---	---
MELHPRO	---	---	---
TRIJLAC	---	---	---
CASITRA	---	---	---
HIBIENG	---	---	---
CYMOEXC	---	---	---
HETPARB	---	---	---
AMARTHU	---	---	---
CARSBIS	---	---	---
RHUSGUE	---	---	---
PAVOCOL	---	---	---
RHUSDEN	---	---	---
COMRZEY	---	---	---
COMRCOL	---	---	---
FICUTHO	---	---	---
TECOCAP	---	---	---
VITXPAT	---	---	---
BECIOBO	---	---	---
BERISAL	---	---	---
HIBIPUS	---	---	---
SPORPAN	---	---	---
COCCSES	---	---	---
FLACIND	---	---	---
OPUNSTR	---	---	---
PAVEGAR	---	---	---
STACHYS	---	---	---
TINOFRA	---	---	---
GOSYHER	---	---	---
IPOMCRA	---	---	---
BLEPINT	---	---	---
SOLNCOC	---	---	---
SPORIOC	---	---	---
MONSANG	---	---	---
SETAINC	---	---	---
JUSTANA	---	---	---
BIDEBIT	---	---	---
HYPAANA	---	---	---
MICHCAF	---	---	---
ARITSCA	---	---	---
CROTPOD	---	---	---
ASPRFAL	---	---	---

INDGSWA	---	---	---
INDGLUP	---	---	---
COMMSUB	---	---	---
ENTEMAC	---	---	---
CHLOROX	---	---	---
RHINXER	---	---	---
ASPRPLU	---	---	---
PEROPAT	---	---	---
DIGIARG	---	---	---
CYPEOBT	---	---	---
IPOMERI	---	---	---
COCCADO	---	---	---
AMMOCOR	---	---	---
IPOMOBA	---	---	---
FOCKANG	---	---	---
APTOLIN	---	---	---
HEMZBRA	---	---	---
STYSFRU	---	---	---
IPOMBOL	---	---	---
ZORNGLO	---	---	---
CHAAMIM	---	---	---
CATUSPI	---	---	---
SPHDPRU	---	---	---
KOHACAE	---	---	---
RHUSPET	---	---	---
PERGDAE	---	---	---
MELHACU	---	---	---
OXYGSIN	---	---	---
MERRTRI	---	---	---
TEPHLON	---	---	---
OZORENG	---	---	---
ERAGGUM	---	---	---
STOTMON	---	---	---
BRACXAN	---	---	---
CYPSPUB	---	---	---
CROTSCH	---	---	---
OPUNFIC	---	---	---
PTECROT	---	---	---
NEORAMB	---	---	---
MERRPIN	---	---	---
NICAPHY	---	---	---
JAMEMIC	---	---	---
SENEINA	---	---	---
HIBISID	---	---	---
CUCMANG	---	---	---
OXAL/SP	---	---	---
TAGEMIN	---	---	---
IPOMARA	---	---	---
TEPHMUL	---	---	---
TURROBT	---	---	---

LAUNINT	---	---	---
CISUROT	---	---	---
KIRKWIL	---	---	---
DYSCROG	---	---	---
INDGBAI	---	---	---
SEDDSUF	---	---	---
ACACLUE	---	---	---
OCHNSER	---	---	---
PHAAELO	---	---	---
ORTSSUF	---	---	---
OXYGALA	---	---	---
RIOCTOR	---	---	---
ACACW-D	---	---	---
COMIAFR	---	---	---
MAYTTEN	---	---	---
TECLPIL	---	---	---
PHYABUR	---	---	---
TURRNIL	---	---	---
ABUTFRU	---	---	---
INDGTRS	---	---	---
PAVOSEN	---	---	---
PHYAPEN	---	---	---
ASPRBUC	---	---	---
RHYHDEN	---	---	---
PAVESCH	---	---	---
HYMEULM	---	---	---
MONBJUN	---	---	---
CRONPSE	---	---	---
TRIhPEN	---	---	---
OZORPAN	---	---	---
MAYTMOS	---	---	---
RHYHRES	---	---	---
LEPTDEL	---	---	---
TEPHELO	---	---	---
MARGDIS	---	---	---
PELLCAL	---	---	---
RHUSLEP	---	---	---
TRIhRHO	---	---	---
SOLN/SP	---	---	---
ACACATA	---	---	---
AMMASEN	---	---	---
FUIRPUB	---	---	---
MERRKEN	---	---	---
ASPRCRA	---	---	---
DIOSCOT	---	---	---
PYROHYS	---	---	---
VITXFER	---	---	---
BLAIGAY	---	---	---
DOMBKIR	---	---	---
ENTNCAU	---	---	---

PANIHET	---	---	---
CRYLOBL	---	---	---
BRIDMIC	---	---	---
JATRZEY	---	---	---
CROTPIS	---	---	---
INDGING	---	---	---
CROTVIG	---	---	---
CHLRGAL	---	---	---
CHEIINV	---	---	---
KALAROT	---	---	---
HYPEAMO	---	---	---
BLEPSUB	---	---	---
ZORN/SP	---	---	---
ARITSTP	---	---	---
SIDAOVA	---	---	---
CERUPER	---	---	---
STERROG	---	---	---
ARITMOL	---	---	---
SPEMSEN	---	---	---
GUIBCON	---	---	---
ASYSGAN	---	---	---
BAPHMAS	---	---	---
CLESSCH	---	---	---
GREWMIC	---	---	---
PTAEOBL	---	---	---
RHYHVEU	---	---	---
IPOMWIG	---	---	---
BULSBUR	---	---	---
CARIHAL	---	---	---
SCHVCAP	---	---	---
THUNDRE	---	---	---
COMPPYR	---	---	---
INDGLYD	---	---	---
FIMBCOM	---	---	---
ARITMER	---	---	---
TEPHREP	---	---	---
HERMRIG	---	---	---
SENEHAR	---	---	---
ARITRHI	---	---	---
MARICON	---	---	---
KOHACYN	---	---	---
MEGAKEN	---	---	---
ORNISEI	---	---	---
SEROREM	---	---	---
COMPMER	---	---	---
XERPHUM	---	---	---
OLDNHER	---	---	---
MONSBUR	---	---	---
ENICHYS	---	---	---
HARPZEY	---	---	---

OBETTEN	---	---	---
ALOE/SP	---	---	---
PENIANG	---	---	---
SELADRE	---	---	---
BLEPDIV	---	---	---
OCHNINE	---	---	---
BOERCOC	---	---	---
GREWTEN	---	---	---
ERAGMIC	---	---	---
CROTDUR	---	---	---
PENRINS	---	---	---
BARLAFF	---	---	---
COMPEDU	---	---	---
ACRARAC	---	---	---
SESMTRI	---	---	---
PRIVAFR	---	---	---
GNIDRUB	---	---	---
ERYTLAT	---	---	---
DIPCVIR	---	---	---
GEIGACA	---	---	---
GARDV-S	---	---	---
HEMZELL	---	---	---
BLEPASP	---	---	---
ASPASUA	---	---	---
JUSTP-H	---	---	---
PAVODEN	---	---	---
PSYDLIV	---	---	---
TEPHOXY	---	---	---
NERI/SP	---	---	---
VEREBON	---	---	---
IPOMCAI	---	---	---
STEGARA	---	---	---
TRIJSCH	---	---	---
BLEPMAD	---	---	---
CELOTRI	---	---	---
BARLMAC	---	---	---
DIPRCON	---	---	---
LANDKIR	---	---	---
TRICLAN	---	---	---
HELHCAN	---	---	---
CYCNADO	---	---	---
DOLITRI	---	---	---
MELMGLA	---	---	---
CROTDIS	---	---	---
KALABRA	---	---	---
DECOSCH	---	---	---
ZORNMIL	---	---	---
BARLCRO	---	---	---
HYBAENN	---	---	---
ACTNRAD	---	---	---

STADOPP	---	---	---
HIBIPAL	---	---	---
ERAGCII	---	---	---
PHYAPAR	---	---	---
IPOMS-B	---	---	---
COMIPEN	---	---	---
KEDRLIM	---	---	---
PERGD	---	---	---
ABUTSON	---	---	---
DICLEEN	---	---	---
DIPLFUS	---	---	---
ACACGRA	---	---	---
CLEOGYN	---	---	---
NEMEFRU	---	---	---
BRACERU	---	---	---
HELRCIL	---	---	---
INDGMEL	---	---	---
RHIOOBO	---	---	---
GEIGB-F	---	---	---
ASTRSQU	---	---	---
SONCWIL	---	---	---
UROHSTO	---	---	---
ACACMEI	---	---	---
LYCISHA	---	---	---
TERALAB	---	---	---
ALBIANT	---	---	---
WITHSOM	---	---	---
MOLLNUD	---	---	---
ERIHFAT	---	---	---
LINTNUT	---	---	---
DINER	---	---	---
PHYAANG	---	---	---
MARICYP	---	---	---
JUSTBET	---	---	---
RUELOTA	---	---	---
NIDORES	---	---	---
ERAGASP	---	---	---
MELBR-R	---	---	---
CULLOBT	---	---	---
AIZNGLI	---	---	---
UROHTRI	---	---	---
INDGDIM	---	---	---
PHATSPI	---	---	---
NESAOND	---	---	---
VEREOFF	---	---	---
NICTGLA	---	---	---
BRADELO	---	---	---
CADAAPH	---	---	---
UROHBRA	---	---	---
DICSC-A	---	---	---

DICBPET	---	---	---
PANRTEN	---	---	---
ERIHPAR	---	---	---
ERICACO	---	---	---
ERICFAU	---	---	---
KALALAN	---	---	---
TEPHRHO	---	---	---
ACRBINF	---	---	---
ASPRNEL	---	---	---
APTOLUG	---	---	---
ENDSTEN	---	---	---
VEROCIN	---	---	---
INDGPON	---	---	---
ALOEGLO	---	---	---
DENECAP	---	---	---
PHIYSCH	---	---	---
DIPCMAR	---	---	---
ERICABE	---	---	---
ACHRSTE	---	---	---
DOVYZEY	---	---	---
GEIGB-B	---	---	---
HERMODO	---	---	---
PUPAL	---	---	---
BRAEELO	---	---	---
HEREODO	---	---	---
INDGHOU	---	---	---
SOLNLIC	---	---	---
ERIPMAK	---	---	---
ERAGTEF	---	---	---
ERAGPOR	---	---	---
BOSCF-F	---	---	---
SESALUG	---	---	---
VAHLCAP	---	---	---
CELTAFR	---	---	---
BERZABR	---	---	---
CLIFACO	---	---	---
CORCTRL	---	---	---
INDGSCH	---	---	---
PSIAPUN	---	---	---
MONIWHI	---	---	---
BARLSEN	---	---	---
JUSTTHY	---	---	---
LEUOACU	---	---	---
ERICABB	---	---	---
NIDOAGR	---	---	---
CLEOOXY	---	---	---
EUPHCOO	---	---	---
BARLOVA	---	---	---
HELHARO	---	---	---
SANSAET	---	---	---