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A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe

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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 km^2 (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 non-specific 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-

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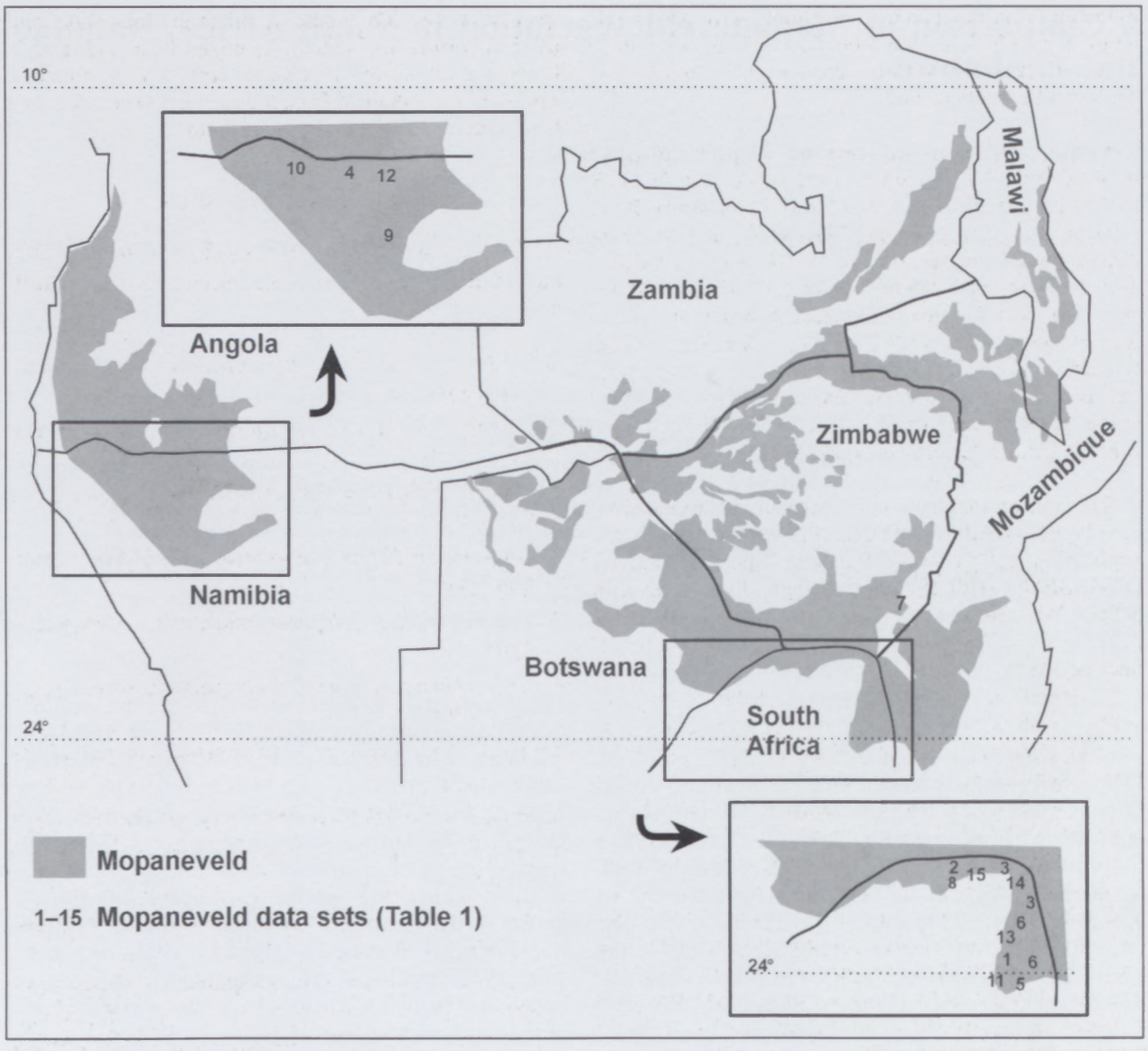

FIGURE 1.—*Colophospermum mopane*-dominated vegetation types in southern Africa (from Mapaure 1994) and approximate location of data sets in the study area.

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	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								
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			1			
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	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 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*

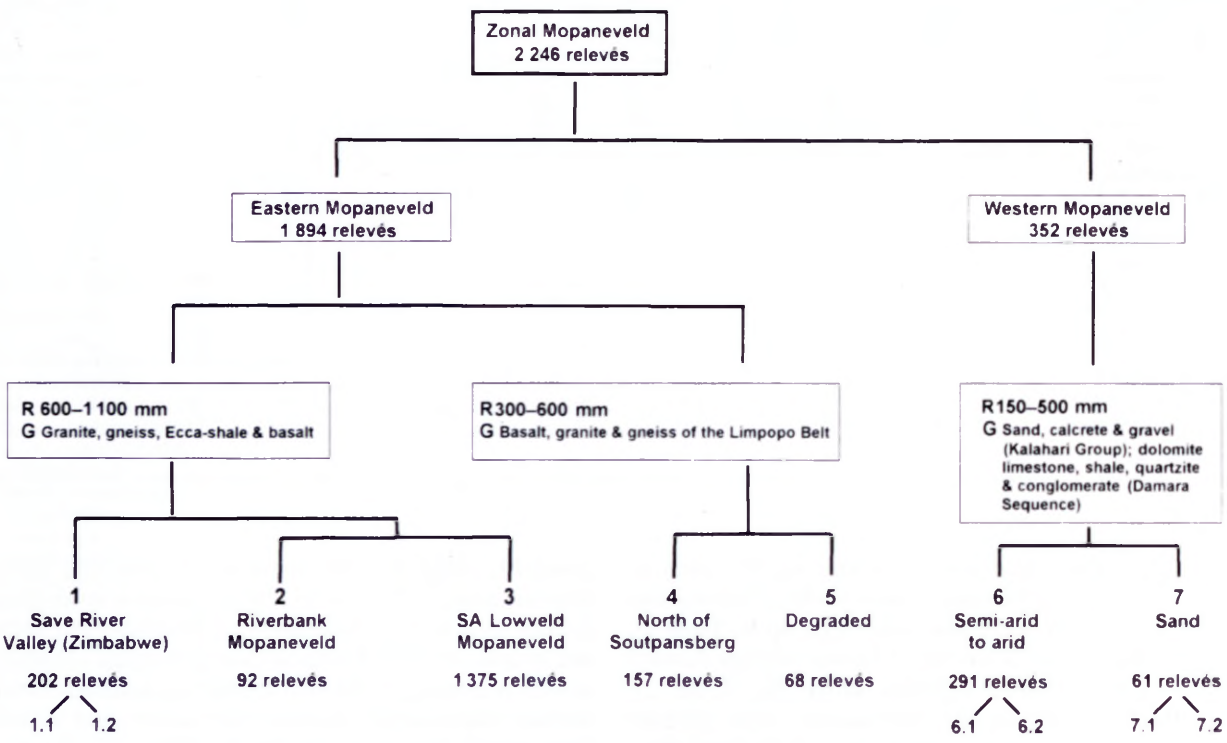

FIGURE 2.—Dendrogram depicting the TWINSPAN division of Mopaneveld vegetation in the study area. R, annual rainfall; G, major rocks.

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

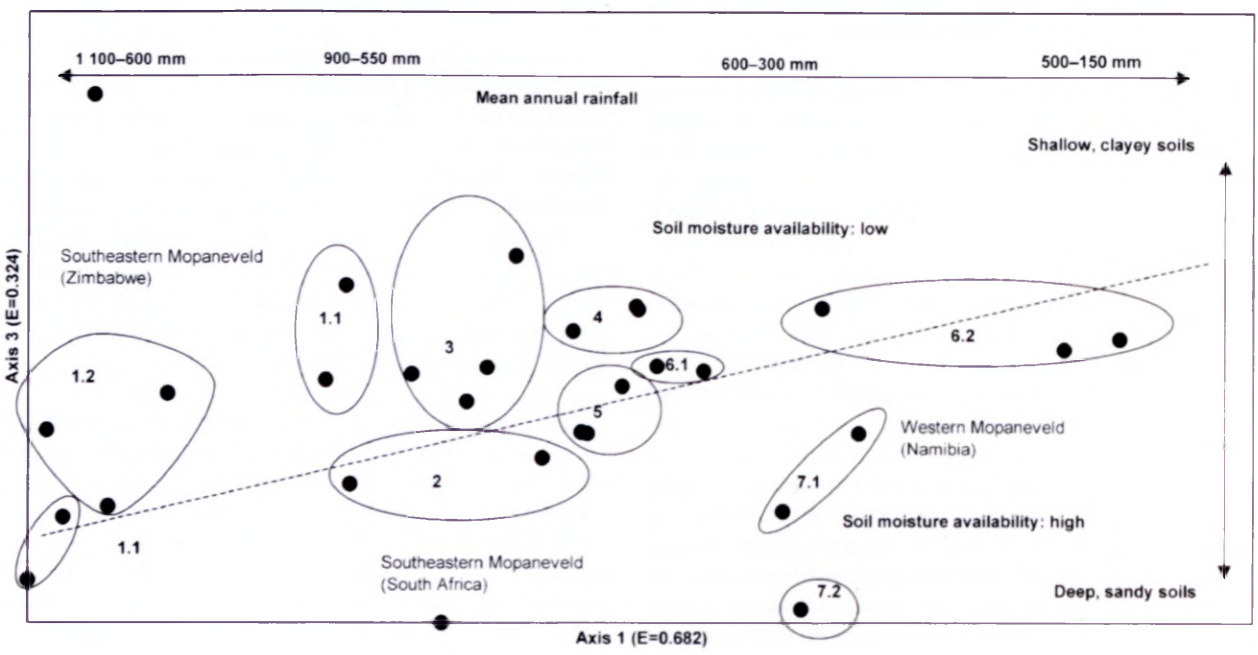

FIGURE 3.—Ordination diagram of axes 1 and 3 illustrating the distribution of Mopaneveld vegetation types along environmental gradients.

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.

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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.