CHAPTER 4

VEGETATION OF SILEZA NATURE RESERVE AND NEIGHBOURING AREAS

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Vegetation of the Sileza Nature Reserve and neighbouring areas, South Africa, and its importance in conserving the woody grasslands of the Maputaland Centre of Endemism

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Keywords: Braun-Blanquet classification, endemism, grassland, Maputaland, phytosociology, sand forest, suffrutex, synecology, vegetation, water table

ABSTRACT

An analysis of the plant communities of the Sileza Nature Reserve and surrounding areas (± 4 124 ha) is presented. The study area falls within the Maputaland Centre of Endemism, which is part of the Maputaland-Pondoland Region, a centre of plant diversity rich in endemic plants and animals. A TWINSPAN classification, refined by Braun-Blanquet procedures, revealed 12 distinct, mainly grassland plant communities. A hierarchical classification, description and ecological interpretation of these communities are presented. The level of the water table, either directly, or indirectly through its role in soil formation, is the deciding factor in defining plant communities on the geologically young sandy substrate. Fire is an essential factor, particularly in maintaining the woody grasslands, a rare vegetation type rich in geoxylic suffrutices, and unique to the Maputaland Centre. A comparison between the endemic complement in the subtropical coastal grasslands of Maputaland and the high-altitude Afromontane grasslands of the Wolkberg Centre of Endemism shows marked differences in growth form and vegetation type partitioning between the two centres. This can probably be ascribed to the relative youth (Quaternary) of the Maputaland coastal plain and its associated plant communities. Notable for their richness in Maputaland Centre endemic/near-endemic taxa, the conservation of sand forest and woody grasslands should receive high priority. Afforestation with alien trees is the most serious threat to the biodiversity of the Maputaland coastal grasslands, not only because of habitat destruction, but also through its expected negative effect on the hydrology of the region.

INTRODUCTION

Maputaland, previously known as Tongaland, comprises the northernmost sector of the Tongaland-Pondoland Regional Mosaic, one of the main African phytochoria recognised by White (1983). Most of this phytochorion falls within the Maputaland-Pondoland Region, a centre of plant endemism (Van Wyk 1994). Situated at the southern end of the tropics in Africa, emphasis on Maputaland as a region of biotic transition has largely obscured its status as a regional centre of endemism in its own right (Figure 1). Recent formal recognition of the Maputaland Centre [MC] (Van Wyk 1994, 1996) acknowledges the high levels of endemism and remarkable biodiversity of this region.

The vegetation of the MC is diverse, with at least fifteen broad vegetation types described for the KwaZulu-Natal portion of the region (Tinley 1976; Moll 1977, 1980). However, with the exception of Myre's (1964, 1971) pioneering studies on the vegetation of southern Mozambique, very little quantitative work has been done on the grasslands of the centre. The present study on the vegetation of the Sileza Nature Reserve [SNR], an area dominated by grasslands, presents more specific information on the phytosociology of one of the MC's comparatively little-known vegetation types.

With a large, impoverished and rapidly increasing human population in Maputaland, there is an urgent need to improve people's living standards by utilising the region's readily available natural resources on a sustainable basis. The SNR, an area under the control of the KwaZulu Department of Nature Conservation, is currently being developed as part of a community-driven ecotourism initiative aimed at local community upliftment and development. Also included in the project are sections of the surrounding Endlondlweni Communal Area, which comprises both undeveloped land and a section previously used for commercial plantations by the KwaZulu Department of Forestry. The bordering Nguni Cattle Area, which is being used for the breeding of pedigree Nguni cattle, will eventually be linked to form a single conservation unit that will be jointly managed by the KwaZulu Department of Nature Conservation and local communities.

Knowledge of the vegetation of a region forms the basis for understanding and managing its plant resources and other aspects of the environment. One of the main problems facing the plant conservationist is the lack of sound information on which to base conservation strategies. The present study aims to provide ecological and floristic data for the woody grasslands of Maputaland by identifying, characterising and interpreting the major vegetation units and their variations that occur in the SNR and surrounding areas. Floristically rich (high biodiversity/endemism) and interesting habitats will also be highlighted together with comment on some of the unusual structural features of the Maputaland grasslands.

STUDY AREA

Location

The location of the study area (27° 06′ S, 32° 36′ E) is shown in Figure 1. It covers ± 4 124 ha (2 124 ha of the proclaimed SNR and ± 2 000 ha of communal land), and is an extensive, low-relief, sandy plain, covered mostly by grassland with relatively small patches of

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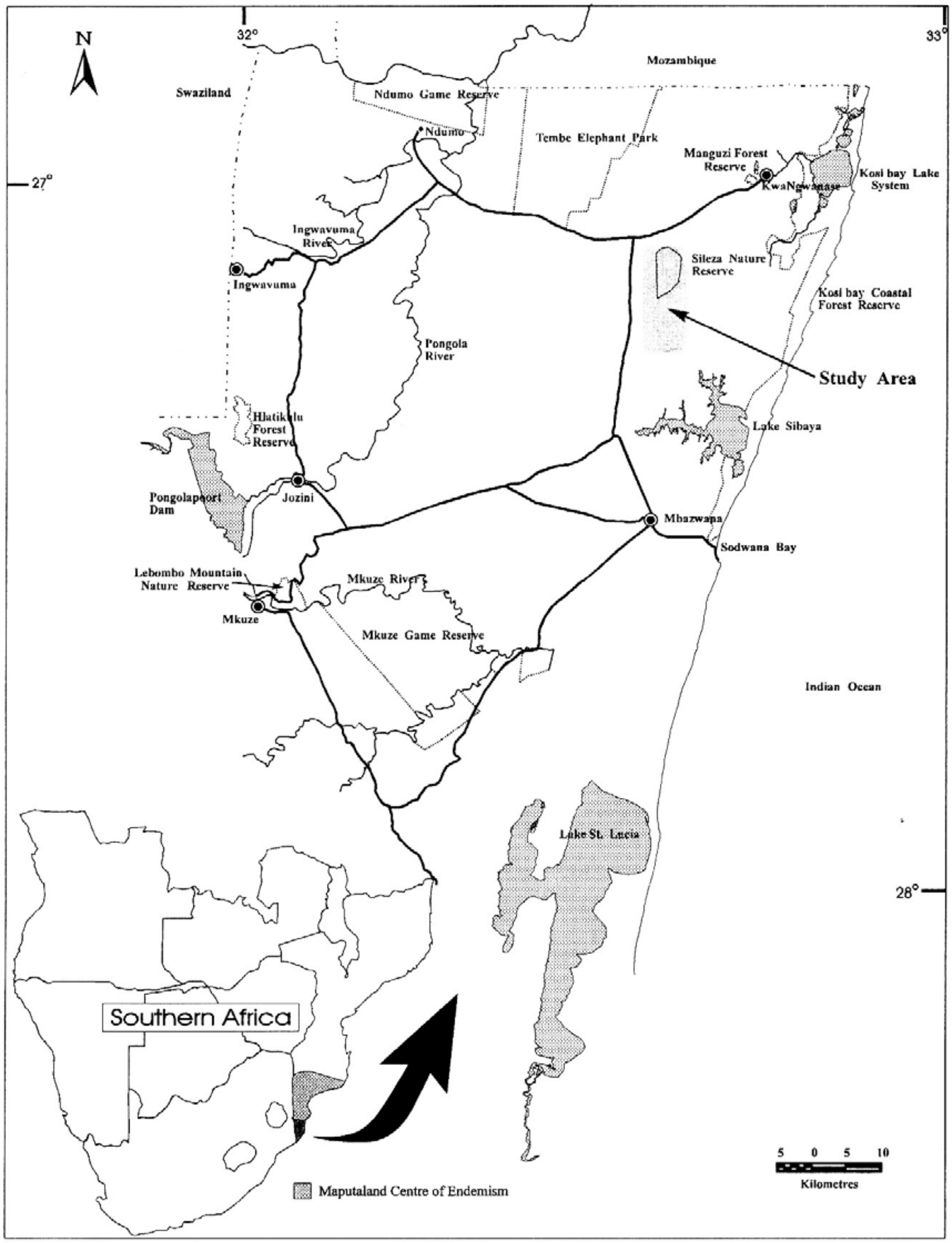

FIGURE 1.—Map showing the Maputaland Centre of Endemism and the location of the study area.

short or tall forest, usually bordered by woodland. Moll & White (1978) have categorised this area as Coastal Grassland, although in many ways this is a mosaic of Moll & White's (1978) Coastal Grassland and Palm Veld. Most of the area is undeveloped and is utilised as grazing land for cattle. An important local industry is the making of palm wine from the sap of *Hyphaene coriacea* and *Phoenix reclinata* (Cunningham & Wehmeyer 1988; Cunningham 1990a, b).

Geology

Geologically the study area is very similar to the rest of the Maputaland and southern Mozambican coastal plain. The principal stratigraphic units are unconsolidated Quaternary grey aeolian sands and Quaternary yellowish redistributed sands, underlain by a multi-layered sedimentary sequence of Quaternary, more clayey consolidated sands (Port Durnford Formation) and Tertiary white sandy limestone with basal conglomerate, all resting unconformably on an undulating impermeable Cretaceous siltstone floor which slopes downwards to the east (Hobday 1979; Maud 1980; South African Committee for Stratigraphy 1980).

Topography and climate

The study area is characterised by undulating sand ridges (linear north-south-trending dunes) interspersed with depressions which may form pans or swamps due to the poor drainage and high water table of the region. The highest dune in the study area reaches 98 m asl. The lowest point lies at ± 76 m asl—a difference of only 22 m. Of the few pans to be found in the study area, Gondetembe (± 50 ha^2) is the largest.

Maputaland has a warm to hot, humid, subtropical climate (Schultze 1982). Average annual humidity is high, even in the drier inland parts of the region. Winters are drier than the summers, although rain is received throughout the year. Rainfall data are given in Table 1, with Phelendaba being the weather station nearest to the study area (± 2.5 km). This station is compared to Sihangwana and Ndumo (both from drier inland areas) as well as the much wetter Kosi Bay on the coast. Owing to the undeveloped nature of much of Maputaland, there is a shortage of certain environmental data, such as temperature.

Hydrology

A shallow water table (ground level to a depth of 7–15 m) exists within the aeolian sands and its level varies according to ground water movements, topography and rainfall. The exact ground water levels (more specifically, the deeper ones), are difficult to determine and fluctuate greatly over time. Values deeper than 2 m are, therefore, approximate. Ground water is almost exclusively replenished by rainwater. This shallow water table feeds all the marshes and pans in the study area. After rains, quick fluctuations in local water table levels can be experienced, with an estimated vertical seepage rate in the order of 0.1 m/day (Kruger 1986). Fluctuations unrelated to the season's rains are ascribed to water movements through the sands, with Kruger (1986) reporting an average transmissivity of 20 m^2/day and a co-efficient of storativity of 1×10^{-3}. The general flow direction is from west to east, away from the watershed which lies more centrally in Maputaland.

Soils

Soils are developed from the relatively homogeneous, grey, siliceous, aeolian sands. Soil types are limited, but soil patterns are intricate, though predictable, as a result of the relationship between topography and water table levels (areas subjected to periods of inundation). Soil nomenclature follows the FAO soil classification system (FAO-UNESCO 1974) and Soil Classification Working Group (1991). Most of the soils show signs of high levels of leaching (dystrophic) as well as being relatively acidic [approximate pH (water) 6.1]. An unusual feature is the presence of above average levels of the micronutrient Boron (G. Mann pers. comm.).

Three main soil types (forms) are present in the study area, namely dystric regosols (SA-Namib), histosols (SA-Champagne) and humic gleysols. Dystric regosols are moderate to well-drained acidic sands found in elevated places such as dune crests and slopes. Histosols are sour organic soils with an organic rich A horizon thicker than 400 mm and are found in swampy areas and pans. Humic gleysols are wet acidic sands with an abnormal accumulation of organic matter and are found in depressions (areas with a high water table). The regosols cover most of Maputaland and are Quaternary sand deposits of generally low fertility (Watkeys *et al.* 1993).

METHODS

Fifty 100 m^2 sample plots (10 × 10 m) were distributed in a stratified manner throughout the study area. As far as was possible, plots were equally distributed in the different physiographical-physiognomically homogeneous units, distinguished on the basis of physical environment, physiognomy, as well as dominant plant species composition and abundance. Sampling was carried out from January to May 1993. Scientific names of plant taxa follow Arnold & De Wet (1993). The following information was recorded for each plot: 1, total floristic composition and cover-abundance value for each species, according to the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois & Ellenberg (1974); 2, water table depth/level at the time of sampling, using a 2 m soil auger; 3, signs of grazing pressure, mainly by cattle; 4, soil type/form (FAO-UNESCO 1974; Soil Classification Working Group 1991) and basic colour; 5, amount of organic material

TABLE 1.—Mean annual and absolute maximum and minimum rainfall for four weather stations in the region (based on Weather Bureau records)

Station	Period (yrs)	Annual rainfall (mm)		
		Mean	Absolute max. (year)	Absolute min. (year)
Kosi Bay	42	944	1 552 (1985)	506 (1959)
Sihangwana	28	726	2 105 (1975)	245 (1960)
Phelendaba	5	699	958 (1991)	449 (1992)
Ndumo	71	614	1 160 (1938)	276 (1931)

ranked as distinct or indistinct and its depth of occurrence; 6, herbaceous biomass estimates by means of a disc pasture meter (Trollope & Potgieter 1986), following calibration as explained by these authors; 7, topographical position based on terrain types (Land Type Survey Staff 1986), namely (a) crests, (b) scarp, (c) midslope, (d) footslope and (e) valley bottom or floodplain; 8, geology, according to 1:250 000 geological survey maps (Geological Survey 1986) and locally at a larger scale through personal observations in the field; 9, land type according to 1:250 000 land type map (Land Type Survey Staff 1986); 10, a 50 point species count using the step-point method (Mentis 1981).

Two-way indicator species analysis (TWINSPAN) was applied to the basic floristic data set to derive a first approximation of the possible plant communities (Hill 1979a). Refinement of this classification was done by the application of Braun-Blanquet procedures (Behr & Bredenkamp 1988; Bredenkamp *et al.* 1989).

Major vegetation and associated habitat gradients, as well as the floristic relationships among the plant communities were explained by subjecting the floristic data to Detrended Correspondence Analysis (DECORANA) (Hill 1979b).

Maputaland Centre endemics and near-endemics mentioned in the text are based mainly on the work of Van Wyk (1996). The term 'endemic' refers to a taxon limited in its range to a restricted geographical area, or a particular substrate; when a taxon is also marginally present elsewhere (sometimes in the form of distant satellite populations), it is referred to as a 'near-endemic' (Matthews *et al.* 1993).

RESULTS

Classification of vegetation

A classification of the vegetation is presented in a phytosociological table (Table 2). Five major plant communities were identified. These communities closely reflect differences in water table depth (soil moisture) which is directly correlated with the regional topography (Figure 2). Soil type also plays an important role, particularly in the case of hygrophilous communities. The number of species per plot (= species richness) ranges from a minimum of seven to a maximum of 60, with an average of 25. Hierarchical classification of the vegetation reinforces the correlation between habitat and communities (Figures 2 & 3). The distribution among plant communities of MC endemic/near-endemic taxa, is listed in Table 3. A summary of selected community attributes is supplied in Table 5.

Plant communities recognised in the study area are classified as follows:

1. *Artabotrys monteiroae–Dialium schlechteri* forest of deep water table areas (relatively dry sands).
2. *Themedeto–Salacietum* M. Myre (1964); woody grasslands of relatively dry sandy areas.
2.1. *Catunaregam spinosa–Acacia burkei* woodland and woodland areas of forest edges.
2.2. *Themedo–Salacietum Parinarietosum* M. Myre (1964); woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes.
2.2.1. *Eugenia capensis–Mundulea sericea* woody grassland of relatively deep water table areas.

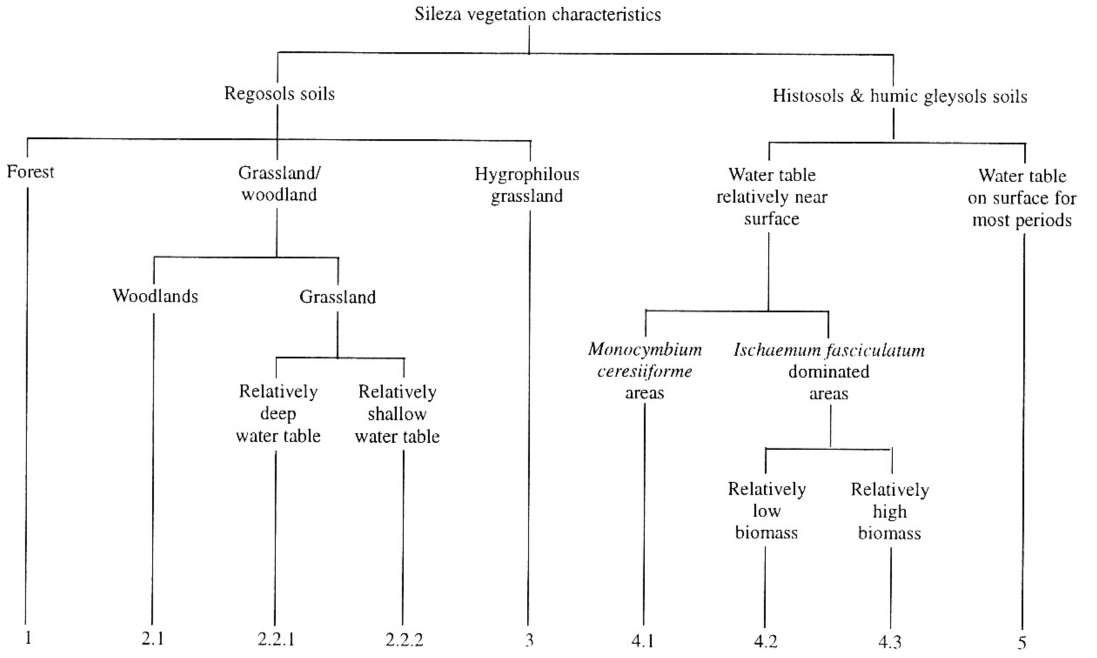

FIGURE 2.—Dendrogram illustrating the habitat relationships of the different communities. Community numbers correspond with descriptions in the text.

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted)

COMMUNITY NUMBER	1					2																		3							4														5					
						2.1					2.2																				4.1						4.2					4.3								
											2.2.1							2.2.2																																
RELEVÉ No.	033	041	039	027	036	046	043	038	042	006	025	012	011	007	003	045	049	013	018	050	040	044	017	037	026	001	016	022	048	010	029	031	032	021	014	020	047	015	034	024	035	009	002	028	004	019	023	008	030	005
SPECIES PER RELEVÉ	33	47	38	48	34	60	49	48	43	45	46	46	33	16	38	46	28	39	41	24	30	22	34	21	20	20	14	20	22	14	14	12	16	14	10	15	17	15	15	13	17	11	07	10	12	13	12	16	11	12
SPECIES GROUP A																																																		
Artabotrys monteiroae	+	+	+	+	+																																													
Commiphora neglecta	+	+	+	+	+	+																																												
Dialium schlechteri	+	+	+	+	+			+		+		+																																						
Acacia kraussiana	+	+	+	+	+	1	+																																											
Tricalysia lanceolata	+	+	+	+	+	+		+																																										
Achyranthes cf. *aspera*		+	+	+	+																																													
Diospyros natalensis	+	+		+	+																																													
Mimusops caffra	+	+	+		+					+																																								
Strychnos henningsii	+	+	+	+																																														
Albertisia delagoense	+	+	+	+							+		+					+																																
Albizia anthelmintica	+		+	+	+	+				+																																								
Asparagus falcatus	+	+	+		+	+				+																																								
Grewia occidentalis	+	+		+																																														
Cyperus albostriatus	+	+	+																																															
Erythroxylum emarginatum	1	+	+																																															
Pteleopsis myrtifolia	+	1	+					+																																										
Deinbollia oblongifolia	+	+		+						+																																								
Sansevieria concinna	+	+	+																																															
Sarcostemma viminale	+	+	+																																															
Ochna barbosae			+	+																																														
Ptaeroxylon obliquum		+	+																																															
Dovyalis caffra	+		+																																															
Pyrenacantha scandens	+			+																																														
Maytenus undata	+	+																																																
Tarenna junodii			+	+																																														
Eragrostis moggii				+	1																																													
Croton pseudopulchellus		+	+																																															
Ficus natalensis	+		+																																															
Isoglossa woodii	+			+																																														
Carissa tetramera	+	+									+																																							
SPECIES GROUP B																																																		
Catunaregam spinosa		+		1		1	+	+	+	1									1				+					+																						
Panicum maximum				+		+	1	+	+	+		+							+																															
Corchorus junodii				+	+	+	+	+	+	+		+		+			+																																	
Sapium integerrimum					+	+	+	+	+	+																																								
Acacia burkei	+					+	+	+	+	+					R																																			
Vangueria infausta						+	+	+	+	+									+																															
Indigofera vicioides						+	+	+	+																																									
Antidesma venosum					+		+	+	+	+									+																															
Limeum cf. *viscosum*						+	+	+	+		+																																							
Phyllanthus sp.					+	1	+	+																																										
Asystasia gangetica						+	+	+																																										
Canthium inerme					+	+	+	+																																										

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted) (cont.)

COMMUNITY NUMBER	1					2																		3							4														5					
						2.1					2.2																				4.1						4.2					4.3								
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SPECIES GROUP B (cont.)																																																		
Strychnos spinosa							+		+	+	+																																							
Ozoroa obovata							+	+		+																																								
Garcinia livingstonei						+		+		+	+																																							
Andropogon gayanus						+			+	+	+					+																																		
Cryptolepis delagoensis						+	+																																											
Annona senegalensis						+	+																																											
Hermbstaedtia cf. *odorata*								+	+																																									
Lippia javanica						+	+																																											
Ocimum urticifolium							+	+																																										
Landolphia kirkii				+		+				+	1																																							
Vernonia natalensis						+	+																																											
Galopina circaeoides						+		+																																										
Abrus precatorius ssp. *africanus*						+			+																																									
Cymbopogon plurinodis									+	+									+																															
SPECIES GROUP C																																																		
Synaptolepis kirkii		+	+	+	+	+		+		+																																								
Zanthoxylum capense		+		+	+	+	+			+																																								
Rhoicissus revoilii		1	+	+		+				+	+	+																																						
Brachylaena discolor		+	+					+		+		+																																						
Dalbergia obovata		1				+	+									+																																		
Crotalaria monteiroi				+		+				+																																								
Clausena anisata	+	+				+																																												
Gardenia volkensii		+		+		+																																												
SPECIES GROUP D																																																		
Eugenia mossambicensis									+		+	+	+	+	+	+							+																											
Mundulea sericea								+			+	+	+	+			+				R																													
Dicerocaryum eriocarpum									+			+	+	+	+		+					+																												
Stylosanthes fruticosa									+		+	+		+	+	+					+		+					R	+	+																				
Indigofera williamsonii											+				+	+	1									R																								
Setaria sphacelata							+				+	+	+			+		+								R																								
Combretum molle				+		+					+	+				+			+																															
Gymnosporia markwardii ms.									+		+		+	+						R	+																													
Bewsia biflora											+	R	R																																					
Raphionacme galpinii														+	+																																			
Tephrosia longipes											+				+																																			
SPECIES GROUP E																																																		
Strychnos madagascariensis		+						+	A	+	+	+	+	1																																				
Pogonarthria squarrosa							+		+	+	+		+	+	+																																			
Eustachys paspaloides								R		+		+	+		+	+																																		
Digitaria natalensis						+	+				1		+		+		+				+										+																			
Digitaria eriantha									+	+		+	1	+				1																																

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted) (cont.)

COMMUNITY NUMBER	1					2																		3							4														5					
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SPECIES GROUP E (cont.)																																																		
Rhynchosia confusa									+	+		+			+		+	+																																
Cissampelos hirta								+	+		+		+			+																																		
Ochna natalitia	+	+				+		+				+	+	+				+																																
Sporobolus fimbriatus							A	+				+		+					+																															
Xylotheca kraussiana						+			+							+																																		
SPECIES GROUP F																																																		
Parinari capensis ssp. *incohata*									+		1	+	1	A	A	A	+	+	+	A	1	A	A	+				+																						
Diheteropogon amplectens							+			+	+	+	+	1	+	A	+	+	+	1	1	B	+					+			1	1	A		1															
Oxygonum robustum									+		+	+	+	+	+	+	+	+	+	+	+	+	+																											
Vernonia oligocephala											+	+	+	+	+	+	+	+	+	+			+																											
Eugenia albanensis									+	+	+		+	+	+	+	+	+	+	+	+	+																												
Urelytrum agropyroides								+		+	+	+	+			+		1	+	+	+	+	+																											
Trichoneura grandiglumis									+		+			+	+	+		+	+	+	+	+	+																											
Elionurus muticus							+				+		+	+	R	+		+	+		+		+																											
Dichrostachys cinerea		+		+						+		+	+	+	R		+	+	+			+	+																											
Ancylobotrys petersiana									1	A		1	1	+		1	3	+		+		+																												
Salacia kraussii							+					+		+	+	+		+	+	+		+																												
Sporobolus mauritianus								+					+	+	R	+		+	+		+	+																												
Eragrostis sclerantha											+	+			1	1		+		A	A																													
Diospyros lyciodes											+	+				+	+			+	+																													
Tricliceras mossambicensis									+			+	+			+		+	+																															
SPECIES GROUP G																																																		
Themeda triandra							+	+	A	+	A	A	B	+	A	B	+	A	+	B	A	1	+										+																	
Aristida stipitata							+	+	+	+	+	+	1	+	+	+	+	+	1	+		+	+																											
Abildgaardia hygrophila						+	+	1	+		+	+	+	+	+	+		+	+	+	+	+	+	+		1				+		+			+			+										+		
Hyphaene coriacea				+			+	+	+	+	+	+			+	+	+	+	1	+	R		+	+				+																						
Perotis patens						+	+		+	+	+	R		+	+	+	+		+	+			+																											
Helichrysum kraussii					+		+	+	1		+	+		+	+	+		+	+		+		+																											
Agathisanthemum bojeri						1	1	+			+	+		+	+	+	+		+	+			+		1	+		1		+													+							
Terminalia sericea					1	1	A	A	1	1	1	1				+		+	+				+																											
Phoenix reclinata					+	A	+	+		+	+	+			R	+			+		R							R																						
Diospyros galpinii									+	+		+	+		+	+	+				+	+																												
Mariscus albomarginatus							+	+	+			+	+				+	+			+																													
Syzygium cordatum					A	A	+	+							R	+			+				+																											
Commelina africana				+		+		+							+					+	+		+																											
SPECIES GROUP H																																																		
Chamaecrista plumosa							+					+	+		+	+	+	+		1	+	+	+	+	+	+		+	+	R																				
Cyperus tenax						+	+					+	1		1	+		+	+		1		A	B	+	+	+	A		+																				
Bulbostylis contexta																	+					+	+				A	+								+														
SPECIES GROUP I																																																		
Helichrysopsis septentrionale																							+	+	+	+	+	+	+																					
Wahlenbergia abyssinica																			+					+	+	+	+	+	1					+						+										
Vahlia capensis																							+	+	+	+		R																						

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted) (cont.)

COMMUNITY NUMBER	1					2																		3							4														5					
						2.1					2.2																					4.1						4.2					4.3								
											2.2.1							2.2.2																																
RELEVÉ No.	033	041	039	027	036	046	043	038	042	006	025	012	011	007	003	045	049	013	018	050	040	044	017	037	026	001	016	022	048	010	029	031	032	021	014	020	047	015	034	024	035	009	002	028	004	019	023	008	030	005
SPECIES PER RELEVÉ	33	47	38	48	34	60	49	48	43	45	46	46	33	16	38	46	28	39	41	24	30	22	34	21	20	20	14	20	22	14	14	12	16	14	10	15	17	15	15	13	17	11	07	10	12	13	12	16	11	12
SPECIES GROUP I (cont.)																																																			
Hypericum lalandii																								+		+	+	+																							
Striga junodii																								+	+		+		+					+																	
Helichrysum sp.																					+		+	+																													
SPECIES GROUP J																																																			
Eragrostis lappula								R													1				1	+	3	B	3	B	+	3	+	+	A	+	+	+			+											
Sporobolus subtilis																			+		+				+	+				1	1	+	+	+	1		+														
SPECIES GROUP K																																																			
Monocymbium ceresiiforme																															3	3	A	R	3																
Panicum genuflexum																										+					+	+		+											+						
Pycreus atribulbus						+																											+		+																		
SPECIES GROUP L																																																			
Sorghastrum stipoides																									R								+					1	B	+	A											
Fuirena pubescens																													+							+		+	A	+	1												
Lobelia erinus																														+									+	+	+	+		+							+	+	+
Polygala capillaris																																							+	+			+										+
Andropogon eucomus																																							+	+			+			+						
SPECIES GROUP M																																																			
Ischaemum fasciculatum																									+	1				1	+	+	+	4	+	+	B	4	A	A	B	1	4	4						A
Eragrostis inamoena																									+	+				+	+	+	+	+	+	+	1	+	+	1	+		1	+				+	+	+
SPECIES GROUP N																																																			
Cyperus sphaerospermus								+												+				+	+	+	+	+		+	+	+	+	+		1	1	+	+	+	+	+	+	+			+		+	1	+
Desmodium dregeanum																							+	+	+	+	+	+	A			+	+	+		+		+	+		+	+	+							
Centella asiatica																								+	+				B		+		+				+		+	+	+								
SPECIES GROUP O																																																			
Leersia hexandra																																													A	+	1	+	+	+
Hemarthria altissima																																					1	+				B		R	+	+	1	+	+	A
Pycreus polystachyos																																									+				+	+	A	1		+
Acroceras macrum																														+									+				+	+		R	A	A	B	1	3	
Fuirena obcordata																																		+				A	+						+	A			1	+	3
Oldenlandia cephalotes																																		+			+				+	+				+	+	1	+	
Hydrocotyle bonariensis																											+		+							1		+				1			+	+	1			R
Eleocharis dulcis																																													+		1	1		
Cyperus sp.																																								+						+	+				
Cyperus fastigiatus																																														+	1			
Nymphaea capensis																																													+				+	
SPECIES GROUP P																																																			
Cyperus obtusiflorus											+	+	+	+		+		+	+		+	+		+	+	R	+	+		+	1	+	+	+	+	+		+												
Cyperus natalensis						+	+				+				+		+		+	+				+	+	+		+		+		+					+	1				+	A	+	+	+	+	+	+	+	

2.2.2. *Urelytrum agropyroides–Trichoneura grandiglumis* woody grassland of relatively shallower water table areas.

3. *Eragrostis lappula–Helichrysopsis septentrionale* hygrophilous grassland on humic gleysols (inter-dune depressions).

4. *Ischaemum fasciculatum–Eragrostis inamoena* hygrophilous grasslands on Champagne soils.

4.1. *Monocymbium ceresiiforme–Eragrostis lappula* grassland of areas not as regularly inundated by water as 4.2.

4.2. *Ischaemum fasciculatum–Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans.

4.3. *Ischaemum fasciculatum* grassland representing low species diversity but relatively high biomass, dominated by *Ischaemum fasciculatum*.

5. *Leersia hexandra–Hemarthria altissima* grassland of marsh/pan areas (water-table on surface during most years).

Description of plant communities

1. *Artabotrys monteiroae–Dialium schlechteri* forest of deep water table areas (relatively dry sands)

Found on dune crests and slopes, this community is associated with grey dystric regosols in places with the deepest water table. In four of the five investigated plots the water table could not be reached with the soil auger (>2 m deep). Biomass measurements were not undertaken in this community as the field layer in most instances was mainly short shrubs with very few grasses and forbs.

Characterised by species group A (Table 2), diagnostic species include the trees *Dialium schlechteri* and *Commiphora neglecta*, understorey shrub *Tricalysia lanceolata* and the lianas *Artabotrys monteiroae* and *Acacia kraussiana*. Prominent species (>50% constancy) include the trees *Mimusops caffra*, *Albizia anthelmintica*, *Strychnos henningsii* and *Erythroxylum emarginatum*, shrubs *Diospyros natalensis*, *Grewia occidentalis*, *Pteleopsis myrtifolia* and *Deinbollia oblongifolia*, understorey perennial *Achyranthes* cf. *aspera*, rhizomatous succulent *Sansevieria concinna*, sedge *Cyperus albostriatus* and lianas *Albertisia delagoense*, *Asparagus falcatus* and *Sarcostemma viminale*. *Synaptolepis kirki*, with a high constancy in this community, is a character taxon of species group C. Species group C links the present community with the woodland community (2.1). On average 40 species per plot were recorded. No less than 12 MC endemic/near-endemic species were found in these forests, thus making this one of the richest communities for such taxa (Table 3).

TABLE 3.—Maputaland Centre endemic or near-endemic plant species (according to Van Wyk 1996), and the plant communities with which they are associated (* = diagnostic species for community)

Endemic/near-endemic taxon	Family	Plant community number 1	2.1	2.2.1	2.2.2	3	4.1	4.2	4.3	5
Acacia kraussiana	Mimosaceae	×*	×							
Acridocarpus natalitius var. *linearifolius*	Malpighiaceae			×						
Albertisia delagoensis	Menispermaceae	×*		×	×					
Brachystelma tenue	Asclepiadaceae			×						
Cissampelos hirta	Menispermaceae		×	×						
Corchorus junodii	Tiliaceae	×	×*	×						
Crotalaria monteiroi var. *monteiroi*	Fabaceae	×	×							
Dialium schlechteri	Caesalpiniaceae	×*	×							
Dovyalis longispina	Flacourtiaceae	×								
Encephalartos ferox	Zamiaceae	×								
Eragrostis moggii	Poaceae	×								
Erythroxylon delagoense	Erythroxylaceae	×								
Eugenia capensis ('*mossambicensis*' form)	Myrtaceae		×	×*	×					
Grewia microthyrsa	Tiliaceae	×	×							
Gymnosporia markwardii ms.	Celastraceae		×	×	×					
Helichrysopsis septentrionale	Asteraceae				×	×*				
Helichrysum adenocarpum subsp. *ammophilum*	Asteraceae					×				
Helichrysum tongense	Asteraceae					×				
Indigofera inhambanensis	Fabaceae				×					
Ochna barbosae	Ochnaceae	×								
Ochna natalitia (suffruticose form)	Ochnaceae			×	×					
Oxygonum robustum	Polygonaceae		×	×*	×*					
Ozoroa engleri	Anacardiaceae		×		×					
Parinari capensis subsp. *incohata*	Chrysobalanaceae		×	×*	×*	×				
Podocarpus falcatus (sand/swamp forest form)	Podocarpaceae	×								
Restio zuluensis	Restionaceae						×		×	×
Salacia kraussii	Celastraceae		×	×*	×*					
Sansevieria concinna	Dracaenaceae	×								
Striga junodii	Scrophulariaceae					×*	×			
Syzygium cordatum (suffruticose form)	Myrtaceae			×	×					
Tarenna junodii	Rubiaceae	×								
Tricliceras mossambicensis	Turneraceae		×	×	×					
Vahlia capensis subsp. *vulgaris* var. *longifolia*	Vahliaceae				×	×*				
Vernonia centaurioides	Asteraceae				×					
TOTAL NUMBER OF TAXA	34	14	13	13	14	6	2	0	1	1

This community is structurally a forest, the canopy varying from as low as 5 m up to about 20 m. The species composition is unique and other authors have referred to this community as Sand Forest (e.g. Moll 1977, 1980; Moll & White 1978; Ward 1981), typical elements of which include *Dialium schlechteri*, *Pteleopsis myrtifolia*, *Ptaeroxylon obliquum*, *Croton pseudopulchellus* and *Ochna barbosae*. Pendulous lichens (*Usnea* spp.) are particularly abundant in the protruding crowns of many of the trees. Sand forests in the study area lie at the eastern limits of their distribution and are floristically notably impoverished compared with their inland counterparts (unpublished data). Because of their proximity to the coast, they also contain species more characteristic of coastal dune forest, such as *Mimusops caffra*, *Acacia kraussiana* and the understorey herb *Isoglossa woodii*.

2. *Themedeto–Salacietum* M. Myre (1964); woody grasslands of relatively dry sandy areas

An association restricted to grey dystric regosols on dune crests, slopes and relative high-lying level plains. Average water table depth was ± 1.8 m, whereas in many of the other sampling sites it could not be reached by the soil auger (>2 m). Average biomass was 2091.1 kg.ha^{-1}.

Characterised by species group G (Table 2), diagnostic species include the grasses *Themeda triandra* and *Aristida stipitata*, sedge *Abildgaardia hygrophila* and the palm *Hyphaene coriacea*. Prominent species (>50% constancy) include the palm *Phoenix reclinata*, geoxylic suffrutex *Diospyros galpinii*, grass *Perotis patens*, woody forb *Helichrysum kraussii*, rhizomatous forb *Agathisanthemum bojeri* and *Terminalia sericea*, which varies from a dwarf shrub to a large tree. On average 39 species per plot were recorded.

This association is subdivided into two subassociations on the basis of structure and floristic composition, thus indicating a strong correlation between the tall woodlands and the woody (suffrutex-rich) grasslands.

2.1. *Catunaregam spinosa–Acacia burkei* woodland and woodland areas of forest edges

A subassociation of grey dystric regosols on crests and slopes of dunes. Average water table depth was ± 1.8 m, with two samples deeper than the soil auger length (>2 m). Average biomass was 2291.5 kg.ha^{-1}, a value slightly higher than those of related grassland communities and attributable to a slightly higher woody component.

Characterised by species group B (Table 2), prominent diagnostic species include the shrubs *Catunaregam spinosa* and *Vangueria infausta*, shrubs/trees *Acacia burkei* and *Sapium integerrimum*, grass *Panicum maximum* and the forb *Corchorus junodii*. *Terminalia sericea* is consistent as well as achieving its highest abundance. Other prominent species (>50% constancy) are the shrubs/trees *Antidesma venosum*, *Canthium inerme*, *Strychnos spinosa*, *Ozoroa obovata* and *Garcinia livingstonei*, forbs *Indigofera vicioides*, *Limeum* cf. *viscosum*, *Phyllanthus* sp. and *Asystasia gangetica* and the grass *Andropogon gayanus*. On average 49 species per plot were recorded, the highest average number of species among all the communities, with 11 MC endemic or near-endemic species (Table 3).

2.2 *Themedo–Salacietum Parinarietosum* M. Myre (1964); woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes

A subassociation of grey dystric regosols on dune crests, slopes and low-relief plains. Average water table depth was ± 1.9 m, with the depth in many samples extending further than the soil auger length (>2 m). Average biomass was 1990.9 kg.ha^{-1}.

Characterised by species group F (Table 2), diagnostic species include the geoxylic rhizomatous suffrutex *Parinari capensis* subsp. *incohata*, which in places can attain a high canopy cover, the grass *Diheteropogon amplectens* and forb *Oxygonum robustum*. Other prominent species (>50% constancy) include the forb *Vernonia oligocephala*, rhizomatous suffrutices *Eugenia albanensis*, *Ancylobotrys petersiana* and *Salacia kraussii*, a dwarf shrubby form of *Dichrostachys cinerea*, as well as the grasses *Urelytrum agropyroides*, *Trichoneura grandiglumis*, *Elionurus muticus*, *Sporobolus mauritianus* and *Eragrostis sclerantha*. *Themeda triandra* attains its highest cover values. On average 34 species per plot were recorded.

This subassociation is subdivided into two variants determined by differences in water table depth.

2.2.1. *Eugenia capensis–Mundulea sericea* woody grassland of relatively deep water table areas

A variant associated with grey dystric regosols on dune crests, slopes and sandy plains. Average water table depth nearly always exceeded 2 m. Only one of the water table samples did not extend deeper than the soil auger length (>2 m). Average biomass for this subcommunity was 1995.9 kg.ha^{-1}.

Characterised by species group D (Table 2), the geoxylic rhizomatous suffrutex *Eugenia capensis* (also referred to as *E. mossambicensis*) is one of the diagnostic species. Other prominent species (>50% constancy) are a dwarf shrub form of *Mundulea sericea*, the forbs *Stylosanthes fruticosa* and *Indigofera williamsonii*, prostrate creeper *Dicerocaryum eriocarpum* and the grass *Setaria sphacelata*. *Themeda triandra* attains its highest cover values in this variant. Other species showing a strong affinity to this variant (usually >50% constancy) are the forb *Vernonia oligocephala*, shrub *Strychnos madagascariensis* and grasses *Pogonarthria squarrosa*, *Eustachys paspaloides* and *Digitaria natalensis*. The last four species belong to group E, which represents the species shared between this and the woodland community (2.1). This again underscores the relationship between the woodlands and the woody grasslands. On average 36 species per plot were recorded, with 12 MC endemic or near-endemic species (Table 3).

2.2.2. *Urelytrum agropyroides–Trichoneura grandiglumis* woody grassland of relative shallower water table areas

A variant associated with grey dystric regosols on dune crests, slopes and sandy plains. Average water table depth was ± 1.8 m, with only one sample extending deeper than the soil auger length (>2 m). Average biomass for this subcommunity was 1985.8 kg.ha^{-1}.

Although lacking a characteristic species group, this subcommunity is characterised by the absence of species group D (Table 2). Consistent species include the grasses *Urelytrum agropyroides* and *Trichoneura grandiglumis*. Other species which show a strong affinity to this community are the grasses *Themeda triandra* and *Aristida stipitata*, sedge *Abildgaardia hygrophila*, geoxylic rhizomatous suffrutex *Eugenia albanensis*, palm *Hyphaene coriacea* and the forb *Chamaecrista plumosa*. This forb comes from species group H, a group representing the species shared between the woody grassland communities (2.2) and the hygrophilous grasslands (4). This connection signifies a floristic relationship between the 'wetter' woody grasslands on dystric regosols (this variant) and the truly hygrophilous grasslands on Champagne soils. On average 32 species per plot were recorded, with 13 MC endemic or near-endemic species (Table 3), the highest number for all the investigated plant communities.

3. *Eragrostis lappula–Helichrysopsis septentrionale* hygrophilous grassland on humic gleysols (inter-dune depressions)

This plant community is found in interdune depressions and other low-lying areas, and is associated with grey to dark grey sands (humic gleysols). These soils show signs of slightly higher organic matter accumulation than those of the preceding communities. Average water table depth was ± 1.2 m. Average biomass was 1758.3 kg.ha^{-1}, the lowest value of all the plant communities and quite obvious to the naked eye in the field.

Characterised by species group I (Table 2), diagnostic species include the forbs *Helichrysopsis septentrionale*, *Wahlenbergia abyssinica*, *Vahlia capensis*, *Hypericum lalandii* and the hemi-parasite *Striga junodii*. Species showing a strong affinity to this community are the sedges *Cyperus tenax* and *Cyperus obtusiflorus* and the forb *Desmodium dregeanum*. The grass *Eragrostis lappula* attains high cover values. On average 19 species per plot were recorded, with six MC endemic or near-endemic species (Table 3).

This community shows relationships with drier grasslands (species group H) as well as with wetter (hygrophilous) communities (species group J) on histosols.

4. *Ischaemum fasciculatum–Eragrostis inamoena* hygrophilous grasslands on Champagne soils

Found on wet, seasonally waterlogged, bottom lands and associated with dark grey to black histosols, with high levels of organic matter composition compared to the substrates of the preceding communities. Average water table depth was ± 0.65 m. Average biomass was 3454.7 kg.ha^{-1}.

Characterised by species group M (Table 2), diagnostic species include the grasses *Ischaemum fasciculatum* and *Eragrostis inamoena*. The former species attains some of the highest cover values in places and is very prominent. On average, 13 species per plot were recorded.

This community shows relationships with the hygrophilous grassland community on Namib soils (species group N). It is subdivided into three subcommunities on the basis of the prominence of *Ischaemum fasciculatum*, a species reflecting periods of inundation.

4.1. *Monocymbium ceresiiforme–Eragrostis lappula* grassland of areas not being as regularly inundated by water as the *Ischaemum fasciculatum–Cyperus sphaerospermus* grassland

A plant subcommunity of bottom lands, associated with dark grey to black soils (mixture of histosol and humic gleysols very rich in organic matter) and usually bordering on communities 4.2 and 4.3 (Figure 3). Average water table depth was ± 0.7 m, with three samples lying at a depth of 1 m. Average biomass was 2419.5 kg.ha^{-1}.

Characterised by species group K (Table 2), the grass *Monocymbium ceresiiforme* is the most diagnostic species. Another diagnostic grass (>50% constancy) is the small-growing *Panicum genuflexum*. Other prominent species are the sedges *Cyperus obtusiflorus* and *C. sphaerospermus* and the grasses *Sporobolus subtilis* and *Eragrostis lappula*. The last two species are from group J and indicate a strong relationship between this subcommunity and the hygrophilous grasslands on humic gleysols (3). On average 14 species per plot were recorded, with two MC endemic or near-endemic species (Table 3).

4.2. *Ischaemum fasciculatum–Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans

A plant subcommunity of bottom lands, associated with dark grey to black histosols rich in organic matter and usually bordering on pans and marshes. Average water table depth was ± 0.5 m, with only one sample reaching a depth of 1 m. Average biomass was 2986.8 kg.ha^{-1}.

Characterised by species group L (Table 2), the most prominent diagnostic species is the tall grass *Sorghastrum stipoides*. Other diagnostic species (>50% constancy) include the sedge *Fuirena pubescens*, forbs *Lobelia flaccida* and *Polygala capillaris* and the grass *Andropogon eucomus* and, although of lesser constancy, the grasses *Ischaemum fasciculatum* and *Eragrostis inamoena*. Also characteristic are the sedge *Cyperus sphaerospermus* and the prostrate forbs *Centella asiatica* and *Desmodium dregeanum*. The latter three species are from group N, thus showing a relationship between this subcommunity and other hygrophilous grasslands (3 & 4.1). On average 15 species per plot were recorded, with no MC endemic/near-endemic species (Table 3).

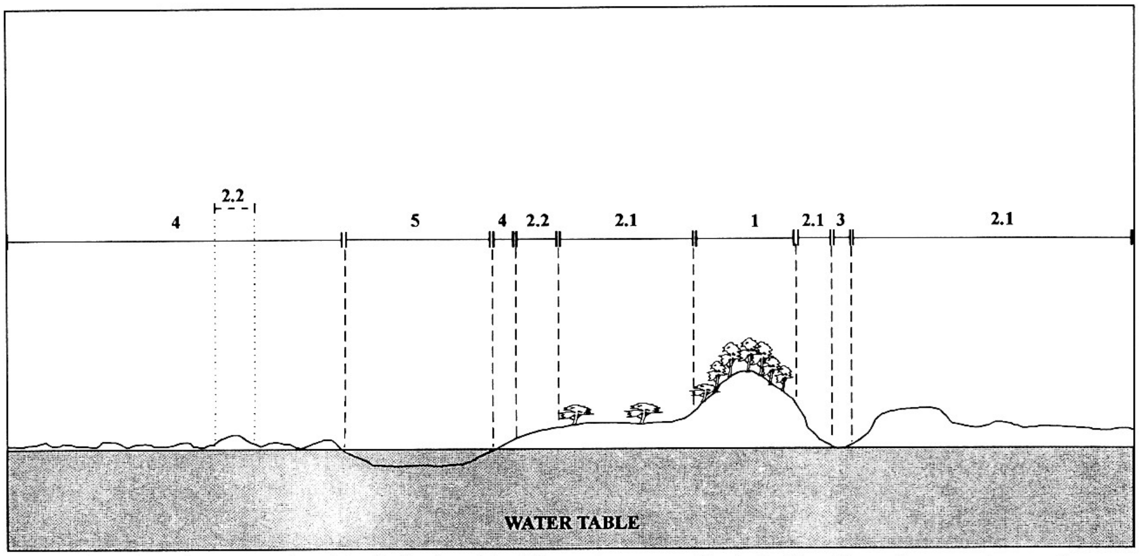

FIGURE 3.—Schematic representation of the distribution of the different plant communities in the Sileza Nature Reserve and surrounding community areas. Dotted lines indicate overlapping distributions. 1. *Artabotrys monteiroae–Dialium schlechteri* forest in deep water table areas (relatively dry sands). 2.1. *Catunaregam spinosa–Acacia burkei* woodland and woodland areas of forest edges. 2.2. *Themedo–Salacietum Parinarietosum*; woody grasslands in deep water table areas (relatively dry sands), e.g. dune crests and slopes. 3. *Eragrostis lappula–Helichrysopsis septentrionale* hygrophilous grasslands on humic gleysols (inter-dune depressions). 4. *Ischaemum fasciculatum–Eragrostis inamoena* hygrophilous grasslands of Champagne soils. 5. *Leersia hexandra–Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years).

4.3. *Ischaemum fasciculatum* grassland representing low species diversity but relatively high biomass, dominated by *Ischaemum fasciculatum*

Found in bottom lands on dark grey to black organic-rich soils (histosols). Average water table depth was ± 0.7 m (with one sample reaching 1 m), and is thus slightly deeper than that of the preceding two subcommunities. Average biomass was 4957.7 kg.ha^{-1}, the highest value of all plant communities in the study area, which is remarkable considering that none of the grasses making up the major proportion of the biomass are particularly tall plants. The dominant grass, *Ischaemum fasciculatum*, only reaches a height of ± 400 mm.

Characterised by the absence of species group L (Table 2), the most prominent taxon is the grass *Ischaemum fasciculatum*, a species which contributes significantly to the high average biomass. There are few other prominent species, the most consistent perhaps being *Cyperus natalensis*, a sedge from group P, which is common to all communities. Other species showing >50% constancy include the forb *Desmodium dregeanum* and the grasses *Hemarthria altissima* and *Acroceras macrum*. The last two species are diagnostic for community 5, the very wet one. On average nine species per plot were recorded, the lowest number among the studied plant communities, with only one MC endemic/near-endemic (Table 3).

5. *Leersia hexandra–Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years)

A plant community of bottom lands and associated with dark grey to black histosols very rich in organic matter. Average water table depth was ± 0.1 m with only two of the samples not having the water table present on the surface. Average biomass was 4584.4 kg.ha^{-1}, making this the community with the second highest biomass. Not all plots were sampled for biomass because of the presence of surface water.

Characterised by species group O (Table 2), diagnostic species include the grasses *Leersia hexandra*, *Hemarthria altissima* and *Acroceras macrum*, the latter attaining constantly relative high cover values. Other diagnostic members (>50% constancy) are the sedges *Pycreus polystachyos*, *Fuirena obcordata*, *Eleocharis dulcis* and *Cyperus natalensis*, the latter being common to all communities. Diagnostic forbs include *Oldenlandia cephalotes* and *Hydrocotyle bonariensis*. Many of these species are also sporadically present in other hygrophilous grasslands, notably in localised patches of wetter conditions. On average 13 species per plot were recorded, with only one MC endemic or near-endemic species (Table 3).

Ordination

Distribution of the sample plots (relevés) along the first and second axes of ordination is given in the form of a scatter diagram (Figure 4). A third axis of ordination contributes little to the interpretation of the communities and will therefore not be considered further.

Figure 4 illustrates a water table depth (moisture) gradient along the horizontal axis, with the wetter habitats to the right and the drier habitats to the left. There is only a slight discontinuity in the distribution of the sample plots representing the deep (community 1) and the shallow water table areas (community 2). However, all plant communities are more or less restricted to specific areas of the diagram.

A distinct discontinuity exists between the communities of the dystric regosols (Namib soil) and the histosols (Champagne soil), with the intermediate communities being placed centrally in the diagram. Subcommunities of the areas with a deep (1) and shallow (2) water table show no separation, thus supporting their treatment as closely related subcommunities. This pattern of one community merging with another along a water table depth gradient can be clearly seen in the field. There can be no doubt that the level of the water table, either directly, or indirectly through its role in soil formation, plays the deciding role in defining plant communities on the coastal plain of Maputaland.

DISCUSSION AND ADDITIONAL NOTES

Plant communities

Twelve ecologically interpretable plant communities have been distinguished and described. This information can be used in reserve and area management, land-use planning, extrapolation to other parts of Maputaland as well as in further ecological and floristic studies. The results of the ordination not only confirm the classification, but also give an indication of floristic and associated habitat gradients. Dynamics of water in the landscape, in this case the water table, clearly control the structure of the community at the first physiognomic level. This is a common phenomenon in savanna areas (Solbrig 1993).

All the communities are easily distinguishable in the field on the basis of growth form, general species composition and character species, despite the gradual environmental gradients. Variation in water table level, the overriding environmental factor, is much less easily distinguished and is best reflected by changes in plant community and the presence of different soil types. Water table levels fluctuate seasonally in accordance with rainfall as well as unseasonally because of non-rainfall related ground water movements (Kruger 1986). It is possible that water table levels rarely falls below 15 m.

With the exception of the excellent broad-scale classification of the coastal grasslands of southern Mozambique (Myre 1964, 1971), the present study is the first attempt at a more detailed, larger scale phytosociological classification of some of the Maputaland coastal plain grasslands. A correlation between the plant communities of the present study and the various syntaxa described by Myre (1964, 1971) has been attempted. Here we recognise his formally described *Themedeto–Salacietum* and

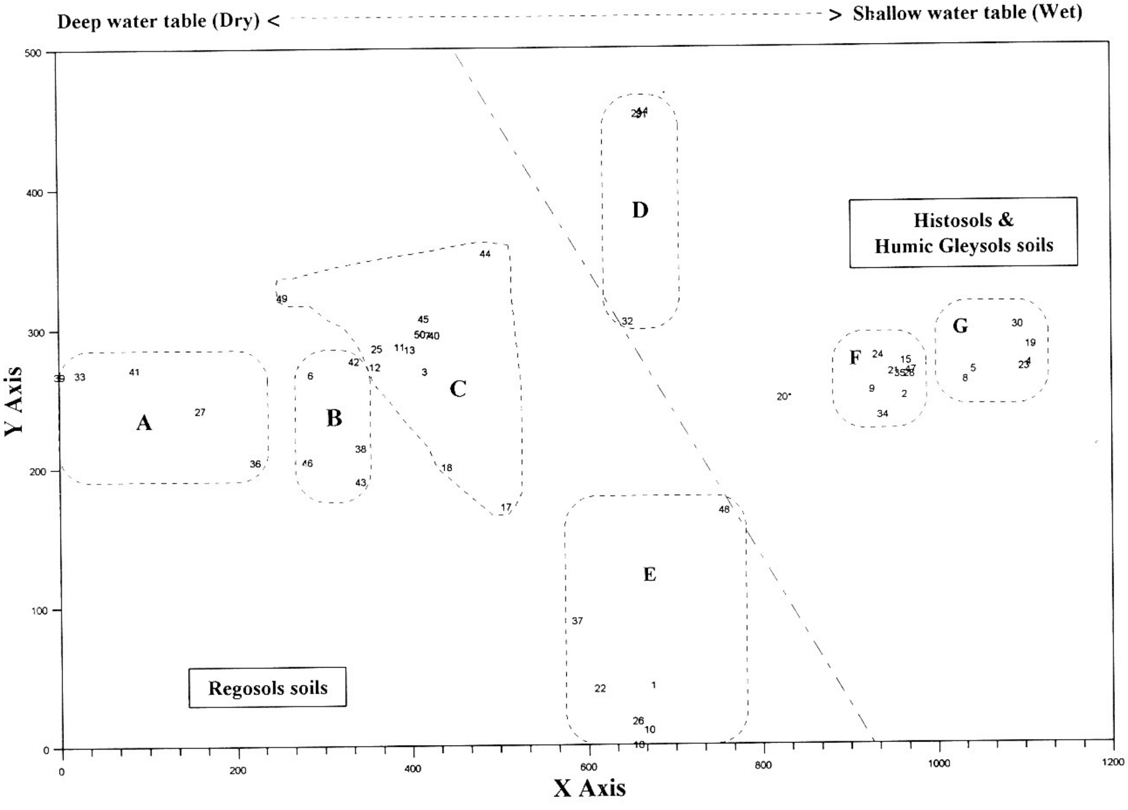

FIGURE 4.—Ordination of the vegetation of the Sileza Nature Reserve and surrounding community areas. A, *Artabotrys monteiroae–Dialium schlechteri* forest of deep water table areas (relatively dry sands). B, *Catunaregam spinosa–Acacia burkei* woodland and woodland areas on forest edges. C, *Themedo–Salacietum Parinarietosum*; woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes. D, *Monocymbium ceresiiforme–Eragrostis lappula* grassland of areas not as regularly inundated by water as F. E, *Eragrostis lappula–Helichrysopsis septentrionale* hygrophilous grasslands on humic gleysols (inter-dune depressions. F, *Ischaemum fasciculatum–Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans or/as well as the *Ischaenum fasciculatum* grassland subcommunity representing low species diversity but relatively high biomass. G, *Leersia hexandra–Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years).

TABLE 4.—Geoxylic suffrutices occurring in the study area, together with the plant communities with which they are associated

	Plant community number								
Taxon	1	2.1	2.2.1	2.2.2	3	4.1	4.2	4.3	5
Parinari capensis subsp. *incohata*		×	×××	×××	×				
Ancylobotrys petersiana		××	×××	××					
Eugenia albanensis		××	××	×××					
Eugenia capensis (dwarf form)		×	×××	×					
Diospyros galpinii		××	××	××					
Salacia kraussii		×	××	××					
Gymnosporia markwardii ms.		×	××	××					
Diospyros lycioides			××	××					
Terminalia sericea			××	×					
Syzygium cordatum			×	××					
Ochna natalitia			××						

× = rare; ×× = average; ××× = abundant; blank = absent.

Themedo–Salacietum Parinarietosum, two syntaxa which are easily recognisable throughout the MC. We have, however, considered it premature to formally describe the other syntaxa. More phytosociological studies in other areas of the Maputaland Coastal plain are needed to correlate results.

Geoxylic suffrutices

An outstanding feature of some of the Maputaland grasslands (e.g. the *Themedeto–Salacietum* woody grasslands of the present study) is the abundance of geoxylic (often rhizomatous) suffrutices (e.g. Henkel *et al.* 1936; Myre 1964, 1971; Moll & White 1978). These dwarf woody plants can be compared with extremely stunted trees, a fact which led White (1976) to refer to them as the 'underground forests of Africa'. Furthermore, in this type of grassland the phytomass of the suffrutices greatly exceeds that of the grasses (White 1976; unpublished data).

The geoxylic suffruticose habit is characterised by annual or short-lived woody shoots sprouting from massive or extensive woody, perennial, underground axes. This rather uncommon growth form appears to be best developed in Africa, with the greatest concentration in the Zambezian Region (White 1976, 1983). Despite White's (1976) statement that relatively few suffruticose species are confined to the Tongaland-Pondoland Regional Mosaic, plants with this growth form are abundant in the study area where they are almost exclusively confined to the *Themedeto–Salacietum* woody grasslands (Table 4).

White (1976) suggests that in Africa the geoxylic suffrutex probably originated as a response to unfavourable edaphic conditions, notably in strongly oligotrophic, seasonally waterlogged sandy soils in regions of extremely low relief. He argues that this habit is not primarily an adaptation to fire or frost, as has been supposed by Burtt Davy (1922), whilst acknowledging that for some species, at least occasionally, fire is necessary for vigorous growth.

The present study confirms the observation that geoxylic suffrutices are prevalent in areas of sandy soil and relatively low relief (Table 5). However, doubt is cast on the validity of White's perhaps too simplistic claim that seasonally waterlogged soil is the primary determinant for the presence of this growth form. In the study area the distribution of geoxylic suffrutices rather reflects the depth of the water table, with these plants being most abundant in sites where it is high, yet still below 1.8 m. These sites comprise mainly those relatively high-lying, well-drained areas such as dune crests and slopes, the surface soils of which are never waterlogged. In fact, geoxylic suffrutices are noticeably absent from inter-dune depressions, the only areas which are clearly seasonally waterlogged.

Fire might have played a more significant role in the evolution of the suffruticose habit than suggested by White (1976). In the absence of fire, the above-ground shoots of the suffrutices in frost-free areas (such as the study area) become less floriferous, moribund, and may even die back. Flowering and the sprouting of new shoots in suffrutices are considerably enhanced by the frequent annual burning of the Maputaland grasslands.

TABLE 5.—Environmental factors associated with the different plant communities. Other selected attributes are also presented

Plant community number	Average water table depth (m)	Predominant soil type	Average biomass (kg/ha)	Average number of plant species/ sample plot	Number of suffrutex taxa	Number of endemics	Size* (ha)	% in Sileza N.R.
1	>2	dystric regosols	–**	40	0	14	90	4.2
2.1	1.76	dystric regosols	2292	49	7	13	90	4.2
2.2.1	>2	dystric regosols	1996	36	11	13	1000	47.2
2.2.2	1.76	dystric regosols	1986	32	10	14	1000	47.2
3	1.32	humic gleysols	1758	19	1	6	500	23.5
4.1	0.725	histosols	2420	14	0	2	400	18.8
4.2	0.52	histosols	2987	15	0	0	400	18.8
4.3	0.7	histosols	4958	9	0	1	400	18.8
5	0.11	histosols	4584	13	0	1	44	2.1

* = estimates only; ** = not determined.

Grassland or savanna?

Physiognomically, typical grassland is characterised by strong dominance of hemicryptophytes of the Poaceae. Savanna, on the other hand, has been defined as a vegetation type comprising an herbaceous, usually graminoid, layer with an upper layer of woody plants of which the canopy cover does not exceed 75% (Edwards 1983). A non-quantitative, more functional savanna definition is that it is a tropical vegetation type in which ecological processes, such as primary production, hydrology and nutrient cycling, are strongly influenced by both woody plants and grasses, and only weakly influenced by plants of other growth forms (Scholes & Walker 1993).

Due to the abundance of geoxylic suffrutices, it is somewhat of a misnomer to refer to these communities merely as 'grassland'. We suggest 'woody grassland' as a more appropriate descriptive term. In a sense these woody grasslands imitate a savanna in which the tree stratum has been reduced to almost the same level as that of the graminoids and with many of the dwarf trees actually comparable to hemicryptophytes, particularly if fire is given its due recognition as a natural factor. Rutherford & Westfall's (1994) inclusion of the Maputaland grasslands under their Savanna Biome might therefore be more appropriate than would appear at first glance. Detailed comparative studies on the ecology of these unusual woody grasslands, in relation to conventional grassland and savanna, would be most instructive.

Fire

Growth in the coastal grasslands of Maputaland is not distinctly seasonal and herbage production is high, despite the infertile soils. Regular fires are a natural phenomenon in these grasslands, although today most are caused by humans. The same patch of grassland may be burned up to three times a year, with at least one fire a year being the norm. There can be no doubt that fire is an essential factor in maintaining the woody grasslands of coastal Maputaland. Margins of sand forest exposed to fire often acquire woodland elements and woodland character species. This, however, appears to be a temporary stage towards sand forest recovery.

An increase in burning frequency owing to an expanding human population over the last few decades has led to the commonsense assumption that tree-dominated vegetation types in the study area must be decreasing. However, a comparison of aerial photographs of the area taken in 1942, 1975 and 1991 indicates the contrary. In most cases the patches of woodland and sand forest have either increased in size (albeit slightly) or became more densely wooded. These forests and woodlands also turned out to be very stable features—all being strictly confined to the same sites over at least the past 50 years, although size and floristic composition might have changed.

It is hypothesised that the observed increase in size and the thickening-up of the forest/woodland patches could have been caused by changes in water table level. A drop in water table over the long term would be conducive towards the creation of habitats more suitable for the development of woodland, thicket and eventually forest. The continued afforestation of the woody grasslands with pines, eucalypts, cashew nuts and other alien trees will, almost certainly, bring about such a drop in the level of the water table. This could result in a dramatic increase in the woody component of the vegetation of the region. Woody grasslands might, in future, have to be increasingly maintained by fire in order to keep then in their current 'underground savanna/forest' state.

Primary or secondary grassland?

Are the extensive coastal grasslands of Maputaland primary or secondary? Rutherford & Westfall (1994) do not include them in their Grassland Biome, but consider them part of the Savanna Biome. They differentiate the true Grassland Biome climatically from the Savanna Biome in terms of minimum winter temperature in conjunction with moisture levels, thus restricting it mainly to the grasslands of the high central plateau and eastern parts of the Great Escarpment of South Africa.

Moll & White (1978) and White (1983) distinguish two broad types of grassland in the Tongaland-Pondoland Regional Mosaic, namely edaphically controlled grassland associated with scattered palms on badly drained sandy soils and secondary fire-maintained grassland that has replaced anthropogenically destroyed coastal forest. On deeper soils along the coast, grassland has been considered a phase in the primary succession to coastal dune forest, a fire-subclimax. In the absence of fire, succession quickly proceeds from grassland to dune scrub and forest (Weisser 1978). This trend towards forest development diminishes inland and in the study area, which falls within the edaphic grasslands of White (1983), grassland appears to be a more stable feature.

Although the frequency of fire in the coastal grasslands of Maputaland has obviously increased due to human activities, floristic and morphological evidence clearly indicate that they have been edaphically controlled and/or fire-maintained for a very long time. The high incidence of endemics, several of which developed an obligate geoxylic suffruticose habit (Tables 3 & 4), signifies a long evolutionary history for this particular vegetation type in the region.

As in the case of the Afromontane grasslands (Matthews *et al.* 1993), the presence of coastal grasslands in Maputaland is not the result of the relatively recent anthropogenic destruction of savanna or forest, although the presence of humans may have led to their expansion or contraction in certain parts. We contend rather that these grasslands are essentially primary in nature and not secondary in the sense of being 'unnaturally' degraded forest or savanna. In fact, the association between fire and these grasslands must be as old as the grasslands themselves, thus making fire a regular feature of the environment. Extensive afforestation with exotic trees, so-called conservation measures to curtail fire, woodcutting, grazing and shifting cultivation have already resulted in the all but total disappearance of grassland in many parts. Biodiversity has diminished accordingly, particularly in the southern coastal region of Maputaland (Weisser 1978).

Endemics

About 2 500 species (but probably more) of vascular plants occur in the MC. Of these at least 230 species or infraspecific taxa and three genera are endemic or near-endemic to the region (Van Wyk 1996; unpublished data). Thirty one of these MC endemics were recorded in the study area (Table 3), but the actual number present is expected to be slightly higher due to incomplete sampling. Most endemics were associated with only two of the five major plant communities. By far the majority of plant endemics are confined to non-hygrophilous grassland, a vegetation type hitherto usually considered secondary (anthropogenic) in origin (e.g. Henkel *et al.* 1936; Weisser 1978; White 1983). The observed low species diversity and paucity of regional endemics in hygrophilous grassland communities is a common phenomenon throughout southern Africa.

Four MC endemic/near-endemic bird species, Neergaard's sunbird (*Nectarinia neergaardi*), Rudd's apalis (*Apalis ruddi*), pinkthroated twinspot (*Hypargos margaritatus*) and Woodwards' batis (*Batis fratum*) are found mostly in sand forest. A subspecies of the pinkthroated longclaw (*Macronyx ameliae ameliae*), a rare MC endemic bird, is mainly associated with the *Ischaemum fasciculatum–Eragrostis inamoena* hygrophilous grasslands.

The present study enables comparison between the coastal plain grasslands of the MC and the high-altitude Afromontane grasslands of the Wolkberg Centre, a botanical centre of endemism along the northeastern Transvaal Escarpment (Matthews *et al.* 1993). Environmental factors associated with the montane plant communities are more diverse and include often complex interactions between lithology, soil type and depth, topography, precipitation (rain and mist), altitude, rockiness, slope and fire regime (Matthews *et al.* 1992a, b; 1994). A much simpler situation exists in the MC with the key determinants being the interconnected effects of water table, soil type and topography, upon which fire has been superimposed. The study on the Wolkberg Centre, however, covered a considerably greater area. Casual observations and comparison with other studies (notably Myre 1964, 1971) have nevertheless shown that the plant communities (and thus associated environmental factors) of the present study extend over most of the Maputaland coastal plain.

MC endemics recorded in the study area (and even more so for the centre as a whole) represent a wide spectrum of growth forms, including trees, shrubs, suffrutices, lianas, forbs, geophytes and annual herbs (Van Wyk 1996). Most noticeable among the more than 130 Wolkberg Centre endemics is the complete lack of annuals and large trees and the fact that nearly all these species are confined to grassland (Matthews *et al.* 1993; unpublished data). There is a conspicuous lack of local endemism in the associated patches of Afromontane forest. In contrast, MC endemics are well represented in both grassland and sand forest, with the latter, on a regional basis, being perhaps the single richest community in MC plant endemics. It is hypothesised that one of the reasons for this marked difference in growth form and for the vegetation-type partitioning of endemics between the two centres of endemism is the relative youthful age of the sandy Maputaland coastal plain (Quaternary) and its associated plant communities.

Threats and conservation

Conservation efforts in the MC have hitherto centred mainly around areas containing species of large game. The vegetation of nearly all existing nature reserves is dominated by various types of savanna. A notable exception is the Tembe Elephant Reserve which contains well-preserved stands of endemic-rich sand forest. The grasslands in the region are particularly poorly conserved and managed.

Afforestation is currently the most serious threat to biodiversity on the coastal plan of the MC. Uncontrolled cattle grazing and random, uncontrolled fire certainly effects species composition and diversity, but probably do not change the structure of the grasslands. The planting of alien trees over large tracts of grassland, on the other hand, not only destroys the grassland habitat but is also expected to affect the hydrology of the region negatively. Further afforestation by the timber industry and private individuals is expected. The establishment of other extensive monocultures, for example cashew nuts, sugar cane and coconut palms, also threatens the grasslands of this relatively unspoiled part of Africa. With so little grassland formally conserved, the SNR, despite its small size, fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC, one of the world's most unique centres of endemism.

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