

Multivariate analysis of coastal grasslands at Mkambati Game Reserve, north-eastern Pondoland, Transkei

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ABSTRACT

The grassland vegetation on the coast of north-eastern Pondoland was analysed after sampling of 113 quadrats in Mkambati Game Reserve. Data were summarised using TWINSpan and DECORANA multivariate procedures. Several communities and subcommunities are recognized and described in relation to measured abiotic variables. A primary gradient from the shore inland is evident, corresponding with changes in altitude, soil conductivity, soil organic matter and soil texture. Time since the last fire influences the invasion of shrubland species.

UITTREKSEL

Die grasveld aan die kus van noordoostelike Pondoland is ontleed nadat monsters van 113 monsterpersele in die Mkambati-wildtuin geneem is. Data is d.m.v. TWINSpan- en DECORANA-veelvoudige prosedures opgesom. Verskeie gemeenskappe en subgemeenskappe word erken en met betrekking tot gemete abiotiese veranderlikes beskryf. Daar is 'n primêre gradiënt vanaf die kuslyn na die binneland wat ooreenkom met verskille in hoogte bo seevlak, grondgeleidsvermoë, organiese inhoud en tekstuur van die grond. Tydsverloop sedert die laaste veldbrand beïnvloed die indringing van struikspesies.

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INTRODUCTION

Areas of uniform species composition and structure commonly reflect a particular range of uniform environmental variables (Mueller-Dombois & Ellenberg 1974). Delineation of such homogeneous areas is desirable since it is assumed that they would require the same management intervention throughout the total uniform area to achieve specified management goals (Edwards 1972). Thus, description and classification of homogeneous vegetation units forms the primary basis for delineation of homogeneous physiographic units for management purposes.

The main aim of the present contribution towards a larger study at Mkambati Game Reserve (MGR), was to describe and map the vegetation of the reserve in order to assess the primary productivity of coastal grasslands (Shackleton 1989), and to delineate management units. As more than 80% of the reserve is grassland and this was the most intensively exploited vegetation type, quantitative sampling was restricted to this formation. Specific aims of this paper were to determine the range in physiognomy, species composition and spatial distribution

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of the various grassland communities at MGR; and to correlate these with selected biotic and/or abiotic factors.

STUDY AREA

Location

Mkambati Game Reserve (7 720 ha) is situated on the coast of north-eastern Pondoland, Transkei ($31^{\circ} 13' - 20'S$ and $29^{\circ} 55' - 30^{\circ} 04'E$) (Figure 1). It is bounded by the Mtentu River to the north and the Msikaba River in the south, with approximately 12 km of coastline forming the eastern boundary. The only non-natural boundary is the inland fence in the west (± 300 m a.s.l.). MGR is characterized by a combination of geomorphic, edaphic and phytogeographic factors that are not found elsewhere along the coast of southern Africa (Feely 1986).

Geology and geomorphology

The reserve is underlain by Palaeozoic pre-Karoo sediments of the Natal Group sandstone (Johnson & Meyboom 1976). Although doleritic intrusions are common in Transkei, very few are present in this area (Du Toit 1912; McKenzie 1984), but several small localized outcrops were noted at MGR during the course of this study. A small outcrop of Upper Cretaceous deposits is present at the coast between the Mtentu River (northern boundary) and the Mgwetyana stream within the reserve to the south (Du Toit 1912; Geological Survey 1976). Between the rivers and streams the land-sea interface is marked by generally horizontal, abrupt rock outcrops of the Msikaba Formation which is relatively resistant to weathering except along lines of weakness (Feely 1986). Consequently, both the

shore and foreland are homeostatic, i.e. neither prograding nor degrading (Tinley 1985).

Situated at the southern end of the Natal monocline, the terrain at MGR is a typical example of the tableland topography described by Kruger (1983). Land facets are orientated parallel to the coast except where drainage systems have cut across them at right angles. Most of the slopes are less than 5.0%, except on scarp surfaces, so that the average gradient from the sea (the eastern boundary) to the inland boundary (300 m a.s.l.) is 3.8%.

This gentle topography is the result of intense planation since the Tertiary. It is interrupted by two steps parallel to the coast that indicate surf-scars during intervals of past geologic uplift (Du Toit 1912; King 1963; Tinley 1978). These steps are evident at 85 m and 190 m and are characterized by steeper surface gradients ranging between 10% and 15%. They mark the position of past shorelines.

Soils

Being derived from Natal Group sandstones under a high rainfall regime, the soils of MGR are acidic, dystrophic, and sandy (Tinley 1978; Shackleton 1989). They are also characterized by a weak structure, high permeability and low available moisture capacity (Maud 1966).

Shackleton (1989) determined that the soil forms covering the largest areas were Mispah (64.7%), Clovelly (15.9%), Champagne (6.8%) and Pinedene (2.2%) [nomenclature follows MacVicar *et al.* (1977)]. Other forms encountered included Glenrosa, Hutton, Katspruit and Kroonstad. Berea Formation sands form an irregular belt across the reserve close to the shoreline.

Other than those forms characterized by shallow sub-soil horizons (e.g. Mispah and Glenrosa), the soils at MGR are, on average, deep (>1.2 m). Ferricrete is not prevalent and the primary limitation to rooting depth is saprolite and wet season waterlogging. In some areas the saprolite itself forms a deep, highly decomposed horizon (>1.0 m). Signs of gleying and gley horizons are common in profiles in the vicinity of the base of the slope (Shackleton 1989).

Climate

Mkambati Game Reserve has a humid, temperate climate according to the Köppen classification (Schulze 1947). On a local scale, details of the major climatic variables are given below.

Rainfall

The average annual rainfall is 1 200 mm (56 years data), of which 61% is received during spring and summer (September to February). A minimum of 50 mm is expected every month. The monthly distribution of the annual rainfall is illustrated in Figure 2. The nature of the rain is usually cyclonic but more convectional during summer. Thunderstorms occur, on average, twenty days per annum, generally restricted to early spring (Tyson 1986).

Analysis of the distribution of annual rainfall revealed that the median is close to the mean, reflecting a relatively even distribution (Figure 3).

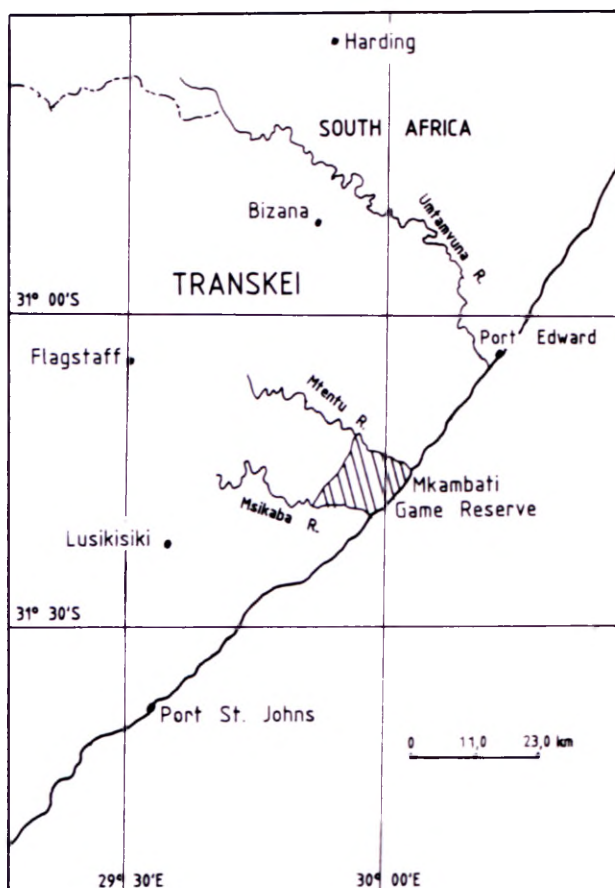


FIGURE 1.—Location map of Mkambati Game Reserve.

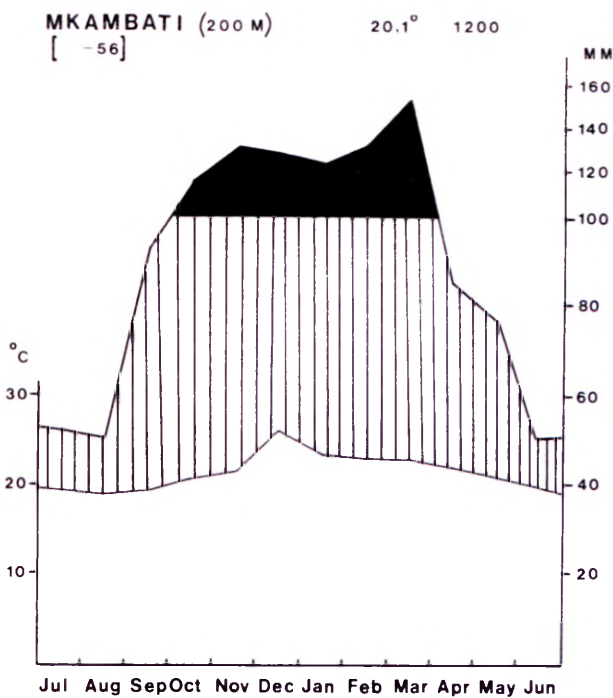


FIGURE 2.—Walter-Lieth diagram for Mkambati Game Reserve.

Temperature

Characteristic of its coastal location, MGR has a relatively equable temperature regime with respect to both diurnal and seasonal variations. Data for Port St Johns (50 km to the south) indicate that the warmest months are January and February (see Figure 2). Minimum temperatures are recorded during July and August. Frost is absent. Diurnal temperature variations are relatively small, even in winter. Differences in the mean temperature at 08h00 and 12h00 are less than 6°C for all months of the year (Weather Bureau 1986).

Vegetation

Biogeographically MGR is situated in the Indian Ocean Coastal Belt (Werger 1978), which extends along the eastern seaboard of Africa from south-eastern Somalia to Port Elizabeth (RSA). Due to abrupt small-scale changes in climate and soils within this belt, it is divided into a mosaic of various vegetation types ranging from edaphic grasslands to tall forest (White & Moll 1978). The southern portion, referred to as the Tongoland-Pondoland Regional Mosaic, extends from the Limpopo River (25°S) to Port Elizabeth.

The vegetation of MGR is a typical example of the edaphic grasslands that constitute part of the Tongoland-Pondoland Mosaic. Recent work by Feely (1986) indicated that significant portions of the coastal belt (including north-eastern Pondoland) have been dominated by grasslands for at least the last 2 000 years, but more probably throughout the Holocene. Consequently, by implication, the present disjunct, small patches of forest were not significantly more extensive than at present for at least 10 000 years, contrary to general belief.

Productivity is high, permitting a high burning frequency of two or three times per annum (White & Moll

1978; pers. obs.). This high burning frequency has promoted the dominance of fire-tolerant species such as *Tristachya leucothrix*, *Trachypogon spicatus* and *Themeda triandra* and, according to White & Moll (1978), it also promotes invasion and dominance by *Aristida junciformis*, if coupled with selective grazing.

On a finer scale the Tongoland-Pondoland Mosaic includes Acocks's (1988) veld type nos 1, 2, 3, 5, 6, 10, 23 and 24. By location, MGR should be classified as veld type no. 1, Coastal Forest and Thornveld. However, Shackleton (1989) argues that the predominance of grassland and its species composition make it more akin to Pondoland Coastal Plateau Sourveld (veld type no. 3).

Six major physiognomically different vegetation types are clearly discernible at MGR. Most of these can be subdivided into several communities on the basis of physiognomy and species composition (Table 1).

The MGR lies in the sandstone region of southern Natal/Pondoland which is significant in terms of its conservation status through the presence of a relatively large number of endemic angiosperms (Wildlife Society of southern Africa 1977; Van Wyk & Schrire 1986) and outlying taxa that exhibit no contiguity with the rest of the taxon's distribution. To date, one family (Rhyncho-calyceae), six genera (e.g. *Jubaeopsis*, *Pseudoscolopia*) and more than 50 species have been listed as endemic to the region, 40 or more of which have been noted in the reserve (A.E. van Wyk pers. comm.).

Fauna

The reserve supports approximately 1 600 introduced wild ungulates, mostly concentrate grazers (Shackleton 1989). The most abundant species are blesbok (*Damaliscus dorcas phillipsii*), blue wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*) and red hartebeest (*Alcelaphus buselaphus*). Non-introduced species such as reedbuck (*Redunca arundinum*), bushbuck (*Tragelaphus scriptus*) and duiker (*Sylvicapra grimmia*) exist in small numbers.

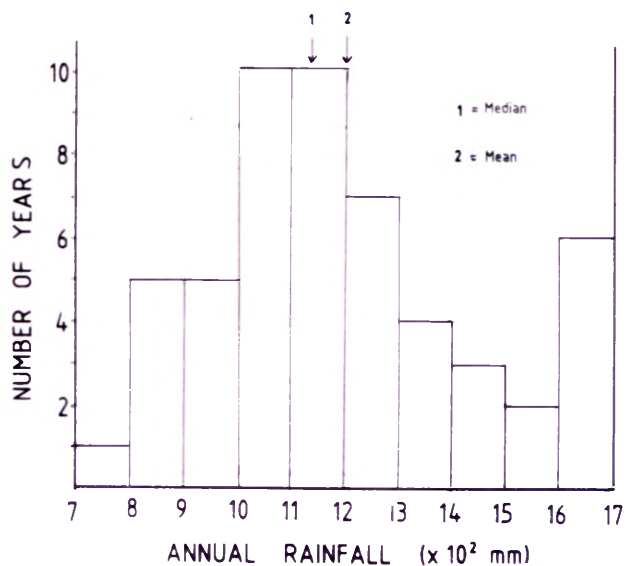


FIGURE 3.—Frequency histogram of annual rainfall.

TABLE 1.—Major communities at Mkambati Game Reserve (areas are approximate)

Vegetation type	Communities	Dominant genera/species
Forest (662 ha)	Dune	<i>Mimusops</i> , <i>Brachylaena</i> , <i>Psychotria</i>
	Swamp	<i>Syzygium</i> , <i>Voacanga</i> , <i>Rauvolfia</i>
	Undifferentiated	<i>Schefflera</i> , <i>Milletia</i> , <i>Trichilia</i>
	Mangrove	<i>Bruguiera gymnorrhiza</i>
	Exotic	<i>Eucalyptus</i> spp.
Scrub (40 ha)	<i>Stoebe</i> — <i>Athanasia</i>	<i>Stoebe vulgaris</i> , <i>Athanasia calva</i>
	<i>Protea</i>	<i>Protea caffra</i>
	Exotic	various (e.g. <i>Lantana</i> sp., <i>Hakea sericea</i> , <i>Acacia saligna</i>)
Grassland (6 250 ha)	Short	<i>Themeda triandra</i> , <i>Stenotaphrum secundatum</i> , <i>Ruellia cordata</i>
	Medium	<i>Tristachya leucothrix</i> , <i>Loudetia simplex</i> , <i>Elionurus muticus</i>
	Tall	<i>Cymbopogon validus</i> , <i>Digitaria natalensis</i>
	<i>Aristida</i>	<i>Aristida junciformis</i>
Terrace	<i>Strelitzia</i>	<i>Strelitzia</i> , <i>Gnidia</i> , <i>Rhoicissus</i>
Wetland (490 ha)	Perennial	various
	Seasonal	<i>Eragrostis inamoena</i> , <i>Scleria</i> spp.
	Reed	<i>Phragmites australis</i>
	<i>Prionium</i>	<i>Prionium serratum</i>
	Streambank	various
Beach pioneer		<i>Ipomoea brasiliensis</i> , <i>Scaevola</i> , <i>Sporobolus virginicus</i>

Human impact

Historical

One of the factors contributing to the proclamation of Mkambati as a conservation area was its low settlement density which minimised translocation of rural people to alternative sites. The low density settlement of this entire tableland region had certainly prevailed for the last 2 000 years (Feely 1986) and it is unlikely that it was any higher before that. Possible reasons for this feature were discussed by Bigalke (1979), Hall (1981) and Feely (1986). The occurrence of marine shell-middens along the coast and in several rock shelters further inland indicates exploitation of intertidal resources since at least the Middle Stone Age (Feely 1986; Prins & Strever 1987). It is also likely that these hunters fired these grasslands on a frequent basis (Hall 1984; McKenzie 1984), thereby maintaining a long period of fire occurrence.

Present management (1978 to date)

The present area was stocked with wild herbivores in 1979 to be managed as a hunting concern. This was dissolved in 1983 and a Board of Directors was appointed by the Government of Transkei. This body is presently responsible for management policy and decisions.

The reserve is divided into six management 'blocks' of approximately equal size (A–F). Prescriptions are that each block is burnt on a biennial basis so that 50% (three blocks) of the reserve is burnt each year. Due to poor fire control *Prionium serratum* wetlands, swamp forests and coastal forests are frequently burnt.

The provision of concentrated supplementary feeds during the winter ceased in the early 1980's. However,

localized patches characterized by a different species composition persist at these sites.

METHODS

Data were collected in the field using the Braun-Blanquet approach (see Mueller-Dombois & Ellenberg 1974; Werger 1974). This was adopted in preference to a more quantitative sampling method (such as the wheel-point) as it provides a more comprehensive list of species (Novellie & Strydom 1987), an important consideration since the flora of MGR had been poorly collected before this study was begun.

One hundred and thirteen quadrats (5 m × 5 m) were distributed judgementsly throughout the reserve. The distribution of quadrats in each vegetation unit, provisionally recognized during reconnaissance visits (on the basis of physiognomy, dominant species composition and abundance), was in approximate agreement with the contribution of that community to the total area, but with bias towards the smaller units (a minimum of three quadrats per unit as far as possible). The following provisional units were identified: (i) *Tristachya leucothrix*–*Loudetia simplex* unit (assigned the prefix of 'L'—78 quadrats), (ii) *Cymbopogon validus*–*Digitaria natalensis* unit ('C'—15 quadrats), (iii) *Themeda triandra*–*Centella asiatica* unit ('T'—8 quadrats), (iv) unburnt moribund areas dominated by *Stoebe vulgaris* and *Athanasia calva* ('S'—4 quadrats), (v) several small areas dominated by *Aristida junciformis* ('A'—3 quadrats) or (vi) by *Festuca costata* ('F'—2 quadrats), and a (vii) *Watsonia* sp. (*Shackleton 426*) unit ('W'—3 quadrats). Sampling was carried out between November and February in areas burnt in the previous winter (except the *Themeda triandra*–*Centella asiatica* unit which failed to burn). This period coincided with the flowering period for most

species which greatly aided identification. As only 50% of the reserve is burnt each year, field sampling was spread over two growing seasons (1985/1986 and 1986/1987).

The following variables were recorded for each quadrat: (i) all species observed and an estimate of their cover-abundance on the Braun-Blanquet scale as modified by Werger (1973), (ii) gradient (Abney level), (iii) altitude (from 1:10 000 ortho-photographs), (iv) aspect (compass), (v) rockiness (estimated as a percentage of the ground cover), (vi) soil form according to the Binomial Classification of southern Africa (MacVicar *et al.* 1977) (auger sample), (vii) soil depth (auger sample). A soil sample from the A-horizon was taken at the centre of each quadrat. These were analysed in the laboratory for pH (in KCl), texture (Andressian pipette method), conductivity (conductivity cell) and organic carbon (Walkley-Black method) according to the methods given by the Fertilizer Society of South Africa (1980).

Species data were subjected to analysis via TWINSpan and DECORANA (Hill 1979a, b) after conversion of the cover-abundance values to a scale of 1–9. For descriptions and summaries of the basic algorithms, see Hill & Gauch (1980); Gauch (1982); Scotcher (1982) and Conlong (1986). In each case default values of the programmes yielded the most satisfactory results, after several iterations with altered pseudospecies cutoff levels and/or unequal weightings for species of differing abundance.

The ordination score of each quadrat on the first two axes was correlated (product-moment correlation coefficient) with each of the measured environmental variables. To permit correlation of aspect with the ordination scores, aspects greater than 180° were converted to the mirror-image of aspects less than 180° as described by Wikum & Wali (1974). This was done after correction of the compass readings for the magnetic declination. For quadrats with a recorded soil depth greater than 1.2 m, a value of 1.8 m was used in the calculation of correlation coefficients and mean depths per community.

It was probable that there would be non-linear associations between vegetation types and site characteristics which would not be evident from the linear correlation of axis score and environmental variables. This was checked by means of Correspondence Analysis (CA) described by Greenacre (1986). Organic matter was not included in the CA because of missing values.

Final description of the grassland communities and sub-communities was drawn from the interpretation of the results of TWINSpan and DECORANA and field notes. Physiognomic nomenclature followed that of Phillips (1971) rather than Edwards (1983), as the height divisions suggested by Phillips (1971) resulted in a more meaningful physiognomic differentiation of the various grassland communities at MGR. Edwards' limits resulted in most of the vegetation units being classified into the same category and there was, therefore, no distinction between units except on floristics. To facilitate identification of communities by management personnel, usually unfamiliar with species identification, it was considered important to be able to differentiate the vegetation units at MGR on the basis of physiognomy, where possible. Phillips (1971) classified grasslands as dwarf (<150 mm), short (150–

450 mm), medium (460–1 000 mm), tall (1.0–2.0 m) and high (>2.0 m).

The vegetation map (Figure 8) was drawn from ground survey using 1:30 000 aerial photographs and 1:10 000 ortho-photographs and results obtained from the multivariate analyses.

To provide more detailed data on species composition to act as a baseline for further studies, sixteen wheel-point samples (Tidmarsh & Havenga 1955) were divided between the two most extensive grassland communities. Each sample consisted of 200 points.

The plant names used are according to Gibbs Russell *et al.* (1985, 1987). Specimens were identified by staff at the University of Transkei Herbarium, the National Botanical Institute (Pretoria), Mr B.D. Schrire, the SALO at Kew and Dr O.M. Hilliard at the University of Natal, Pietermaritzburg.

As a consequence of the inability to distinguish with certainty between vegetative material of *Rendlia altera*, *Diheteropogon filifolius*, *Elionurus muticus*, *Koeleria capensis* and *Bulbostylis schoenoides* in all quadrats, they were collectively recorded as 'wire grasses'. Specimens were housed at the National Botanical Institute, Pretoria, and the Herbarium, University of Transkei.

RESULTS

Classification of the grasslands

The resultant hierarchical division of the sample plots from the TWINSpan analysis is given in Figure 4.

The short grassland immediately adjacent to the coast was recognized as being very different from the remainder of the reserve, with all eight quadrats (plus one from the provisional *Watsonia* sp. vegetation unit) being separated from the rest of the data set at the first level of division. Indicator species were *Centella asiatica* and *Ruellia cordata*. At the second level of division the included *Watsonia* sp. quadrat was split from the eight *Themeda triandra*–*Centella asiatica* quadrats. Further divisions of this community were not recognizable in the field and were therefore ignored in the final dendrogram.

The main group of 104 quadrats on the positive side of the first division was divided into two groups of almost equal size at the second level. Each consisted of quadrats differing widely in floristics, physiognomy and habitat. Thus, this level did not yield meaningful results for classification.

On the other hand, the third level of division succeeded in reducing each of these groups to recognizable units. In the first instance, three quadrats that represented unburnt grasslands invaded by woody species, primarily *Stoebe vulgaris* and *Athanasia calva*, were separated as a unit. These two species acted as indicators for the positive side of the division. The fourth quadrat dominated by these two species was not included in this group, probably because it had a greater number of species (50 as opposed to 34, 27 and 17 for the other three quadrats), giving it more

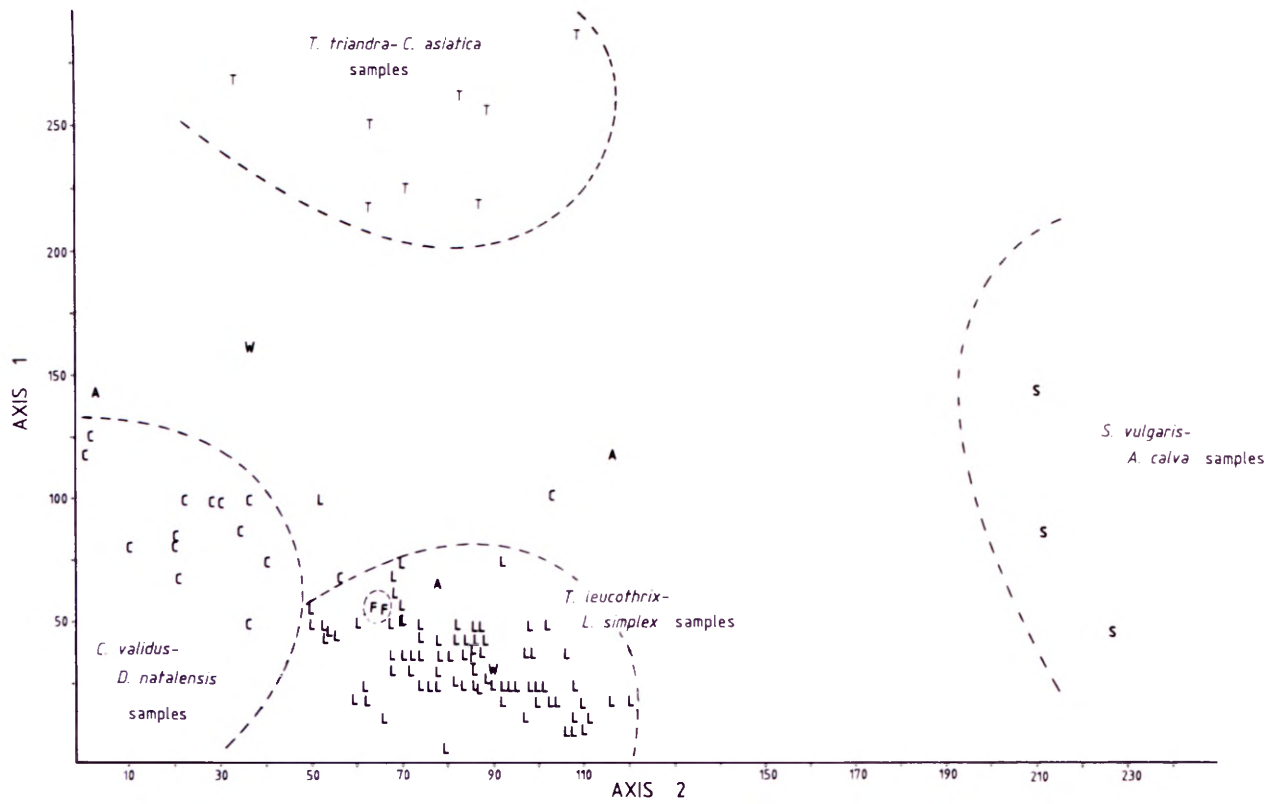


FIGURE 5.—DECORANA ordination of the coastal grassland communities of Mkambati Game Reserve (all samples): T, *Themeda triandra*—*Centella asiatica* samples; C, *Cymbopogon validus*—*Digitaria natalensis* samples; L, *Tristachya leucothrix*—*Loudetia simplex* samples; S, *Stoebe vulgaris*—*Athanasia calva* samples; F, *Festuca costata*—*Albuca setosa* samples; A, *Aristida junciformis*—*Helichrysum mixtum* samples; W, *Watsonia* sp. samples.

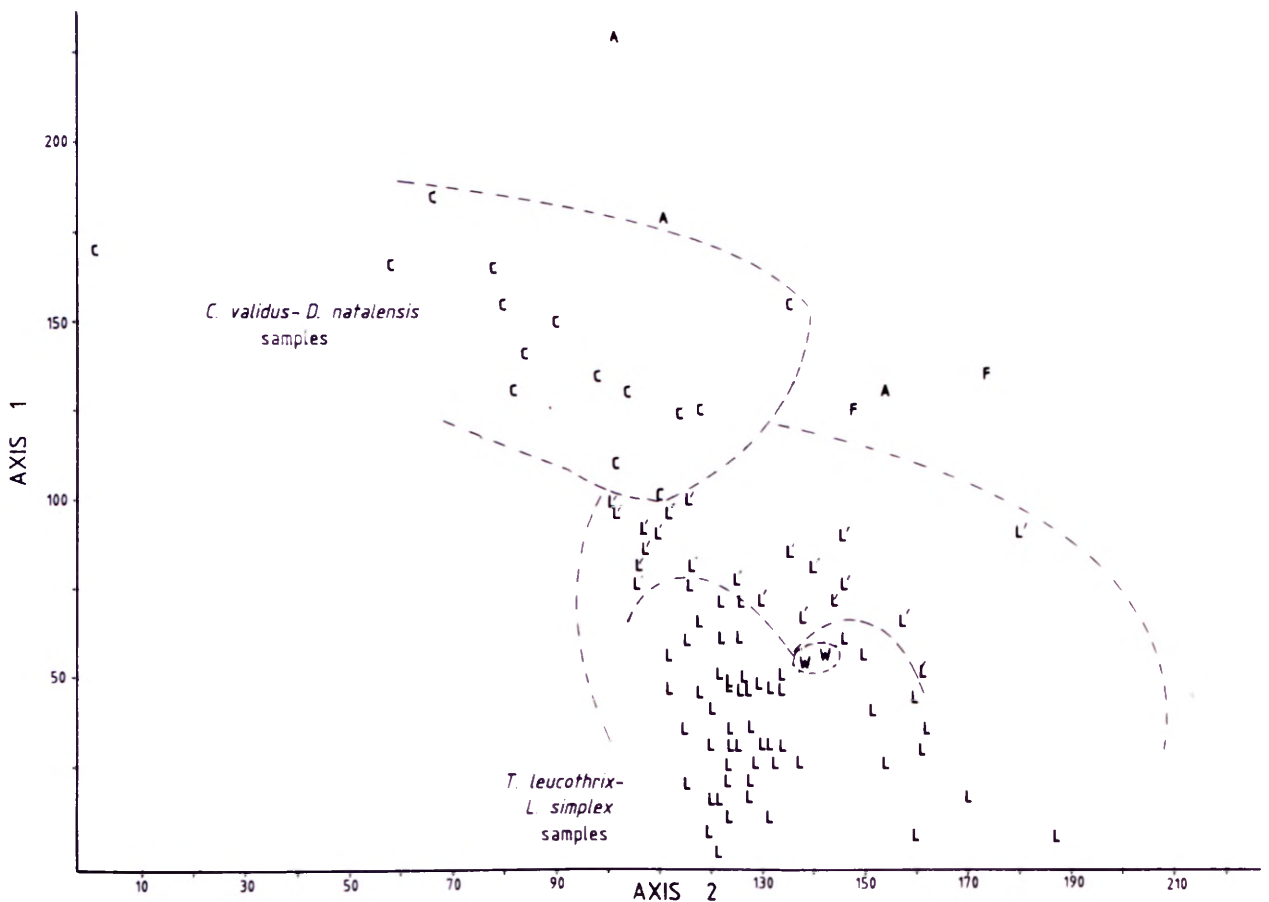


FIGURE 6.—DECORANA ordination omitting samples from the *Themeda triandra*—*Centella asiatica* and *Stoebe vulgaris*—*Athanasia calva* samples (compare to Figure 5).

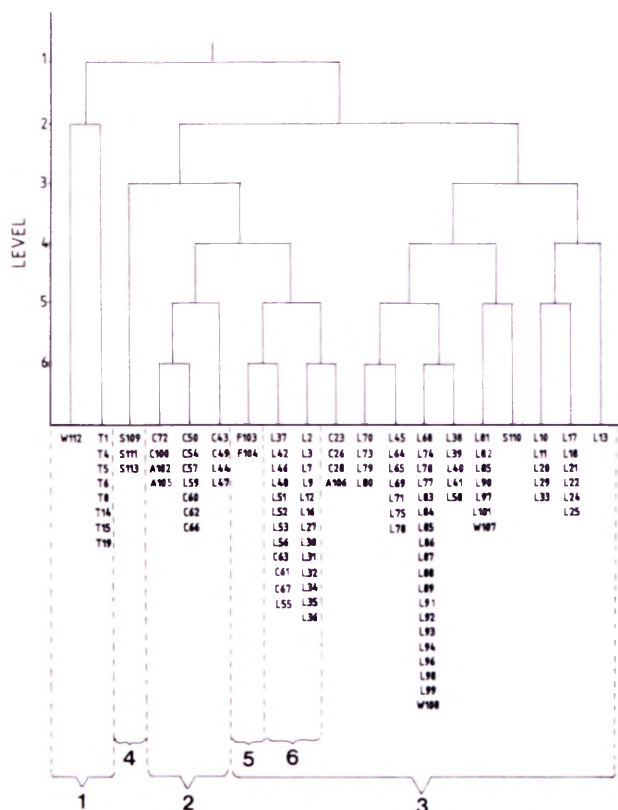


FIGURE 4.—Dendrogram of TWINSpan classification: 1, *Themeda triandra*–*Centella asiatica* community; 2, *Cymbopogon validus*–*Digitaria natalensis* community; 3, *Tristachya leucothrix*–*Loudetia simplex* community; 4, *Stoebe vulgaris*–*Athanasia calva* subcommunity; 5, *Festuca costata*–*Albucca setosa* subcommunity; 6, *Tristachya leucothrix*–*Athrixia phyllicoides* subcommunity.

species in common with the *Tristachya leucothrix*–*Loudetia simplex* community on the other side of the division at level two. From the field situation this is a 'mis-classification' as these four quadrats were the only ones characterized by woody species (shrubs) and were therefore very distinct from the rest of the data set.

The 45 quadrats on the negative side of this division included samples from four of the provisional vegetation units identified during reconnaissance visits. Successive divisions of this group, at the fourth, fifth and sixth levels, isolated the two quadrats dominated largely by *Festuca costata*, although it was not selected as an indicator species in the TWINSpan analysis.

Most of the *Cymbopogon validus*–*Digitaria natalensis* quadrats were subsequently separated from the *Tristachya leucothrix*–*Loudetia simplex* quadrats at level four. Divisions within the *Cymbopogon validus*–*Digitaria natalensis* quadrats appeared to have few practical implications beyond level four. The exception to this were quadrats C23, C26 and C28 which were all situated in management block A. This was of interest considering that the *T. leucothrix*–*L. simplex* quadrats of this block were also recognized as distinct from others of this community at level six. Similarly, soils of areas in this block dominated by *C. validus* and *D. natalensis* are different to other areas of the reserve also dominated by these two species (S.E. Shackleton 1989). The TWINSpan results, therefore, indicate that the same holds true for the areas not

dominated by *C. validus* and *D. natalensis*. The lower level divisions also separated quadrats of this community situated on Hutton (form) soils, but included these with quadrats intended to characterize areas dominated by *Aristida junciformis*.

The partitioning of the *A. junciformis* quadrats between two groups at the fourth level, and the failure to isolate them by the sixth level, leads us to the conclusion that these areas of the reserve do not merit recognition as a separate community for management purposes. These areas obviously share a large number of species with other communities, and are therefore not floristically distinct.

More difficult to interpret was the major division of the *Tristachya leucothrix*–*Loudetia simplex* quadrats at the second level. The majority of quadrats (55) form a major group that is successively divided into smaller groups at the lower levels. The remaining 23 quadrats were included on the positive side at level two, along with the *Cymbopogon validus*–*Digitaria natalensis* and *Festuca costata* quadrats. Several of the measured environmental variables associated with this group of quadrats were intermediate between those of the pre-recognized *C. validus*–*D. natalensis* and *T. leucothrix*–*L. simplex* communities (see Table 5).

Ordination of the grasslands

From Figure 5 it is evident that the quadrats of both the *Themeda triandra*–*Centella asiatica* and *Stoebe vulgaris*–*Athanasia calva* samples form distinct units at the ends of the first and second ordination axes, respectively. To assist in the interpretation of these axes, three additional iterations were performed successively: 1, omitting the *T. triandra*–*C. asiatica* quadrats only; 2, omitting the *S. vulgaris*–*A. calva* quadrats only; and 3, omitting quadrats from both these two communities. The last case is presented in Figure 6.

The clusters obtained for the first and second axes tended to substantiate the groups identified in the TWINSpan classification. The *Cymbopogon validus*–*Digitaria natalensis* quadrats were grouped together in both ordination diagrams. Furthermore, the *Tristachya leucothrix*–*Loudetia simplex* quadrats that were included on the same side of the TWINSpan dichotomy at level 3, along with the *C. validus*–*D. natalensis* quadrats, are in an intermediate position between the two major communities. During field sampling these quadrats were not recognized as having close affinities with the *C. validus*–*D. natalensis* community because they lacked these two physiognomically distinctive species.

Interpretation of the first two ordination axes was assisted through linear correlation of the ordination scores with each of the measured environmental variables. These have been summarized in Table 2.

These results indicated that there was a complex of interrelated environmental variables (see Table 3) correlated with the pattern illustrated in the ordination diagram. The primary axis, with an eigenvalue of 0.409, was highly correlated with soil conductivity, altitude (negative) and organic matter, and marginally correlated with the amounts of sand (negative) and clay (all quadrats

TABLE 2.—Correlation coefficients between the ordination scores and measured environmental variables

Variable	All samples (Figure 5)		Excluding extreme samples (Figure 6)	
	Axis 1	Axis 2	Axis 1	Axis 2
Conductivity	0,50 p < 0,001	0,23 p < 0,05	0,41 p < 0,001	0,40 p < 0,001
Altitude	-0,34 p < 0,001	-0,34 p < 0,001	0,37 p < 0,001	-0,36 p < 0,001
% Sand	-0,24 p < 0,05	0,44 p < 0,001	-0,59 p < 0,001	0,40 p < 0,001
% Clay	0,21 p < 0,05	-0,38 p < 0,001	0,58 p < 0,001	-0,47 p < 0,001
Organic matter	0,49 p < 0,001	-0,54 p < 0,001	0,58 p < 0,001	-0,04 p > 0,05
pH	0,18 p > 0,05	0,34 p < 0,001	0,11 p > 0,05	-0,27 p < 0,01
Slope	0,18 p > 0,05	0,14 p > 0,05	-0,01 p > 0,05	0,20 p < 0,05
Aspect	0,16 p > 0,05	-0,05 p > 0,05	0,13 p > 0,05	0,10 p > 0,05
Soil depth	0,05 p > 0,05	-0,01 p > 0,05	0,04 p > 0,05	0,06 p > 0,05

considered). The first two were to be expected, as there was an increase in altitude and distance from the sea across the whole reserve. Such correlations have been shown elsewhere for coastal regions (e.g. Westman 1981) and are associated with the concomitant reduction in sodium chloride input. The second axis (eigenvalue = 0,233) showed correlation with the same variables and pH. However, the degree of correlation was less for soil conductivity, but greater for the amounts of sand and clay (negative). This indicates some degree of interaction between the two axes. There was a strong degree of interaction between altitude and both soil texture and conductivity. The third and fourth axes had eigenvalues of 0,150 and 0,107 respectively, and were not considered further. Omission of the *Themeda triandra*-*Centella asiatica* and *Stoebe vulgaris*-*Athanasia calva* quadrats did not alter the correlations except to strengthen the degree of correlation with soil texture along the primary axis.

The results from Correspondence Analysis (CA) were in agreement with those obtained above. They are presented in Figure 7 and the breakdown of row and column contributions are provided in Table 4.

Axes one and two accounted for 69,2% and 27,7% of the inertia respectively. The greatest correlations with axis one were soil conductivity and altitude (negative). Thus, one extreme was characterized by the *Themeda triandra*-*Centella asiatica* quadrats associated with sandy soils, high soil conductivity, high slope and low altitude. At the opposing extreme were the *Cymbopogon validus*-*Digitaria natalensis* quadrats at higher altitudes, with clay soils and low soil conductivity. The *Tristachya leucothrix*-*Athrixia phylicoides* quadrats were intermediate between the *Tristachya leucothrix*-*Loudetia simplex* and *Cymbopogon validus*-*Digitaria natalensis* quadrats.

Environmental variables most closely associated with the second axis were altitude and soil depth. The *Stoebe vulgaris*-*Athanasia calva* quadrats were strongly associated with pH and soil depth. This was the only feature highlighted by CA not evident from the previous analyses.

Grassland communities at MGR

It was evident from synthesis of the above results that several distinct grassland units were present in MGR.

TABLE 3.—Correlation coefficients between the measured environmental variables

	Organic matter	pH	% Sand	% Clay	Soil depth	Altitude	Slope	Aspect
Conductivity	-0,42 p < 0,001	-0,30 p < 0,01	0,04 p > 0,05	0,03 p > 0,05	0,04 p > 0,05	-0,24 p < 0,05	0,28 p < 0,001	0,16 p > 0,05
Organic matter		0,05 p > 0,05	-0,74 p < 0,001	0,70 p < 0,001	-0,31 p < 0,01	0,28 p < 0,01	0,06 p > 0,05	0,04 p > 0,05
pH			0,14 p > 0,05	0,15 p > 0,05	0,20 p < 0,05	0,15 p > 0,05	0,03 p > 0,05	-0,05 p > 0,05
% Sand				-0,96 p < 0,001	0,25 p < 0,05	-0,49 p < 0,001	-0,10 p > 0,05	0,10 p > 0,05
% Clay					-0,30 p < 0,01	0,50 p < 0,001	0,13 p > 0,05	-0,03 p > 0,05
Soil depth						-0,20 p < 0,05	-0,08 p > 0,05	0,11 p > 0,05
Altitude							-0,11 p > 0,05	-0,21 p < 0,01
Slope								0,18 p > 0,05

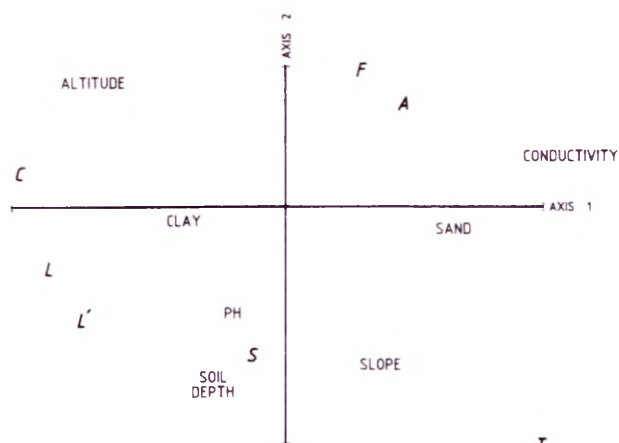


FIGURE 7.—Correspondence analysis scatterplot of coastal grassland communities and subcommunities and associated abiotic variables at Mkambati Game Reserve.

Small areas within the major communities differing with respect to only the dominant species, or their 'invasion' by other species, were designated as subcommunities. The following descriptions of each community deal with the floristically dominant and more easily identified species. The spatial distribution of these communities is depicted in Figure 8. The name assigned to each community was drawn from two species, the first being the physiognomic dominant which was usually abundant, and the second being an indicator species identified by the TWINSPAN analysis.

Each of the grassland communities was associated with particular ranges of environmental variables (overlapping in some cases) which are summarized in Table 5.

Themeda triandra–*Centella asiatica* Dwarf Grassland Community (8 quadrats)

This was an easily identified dwarf grassland community (mean height was 131 ± 5.8 mm) adjacent to the sea shore. Indicator species were *Centella asiatica* and

Ruellia cordata. This community had many preferential species, the most easily identifiable in the field being *Euryops leiocarpus*, *Stenotaphrum secundatum*, *Geranium ornithopodum*, *Moraea spathulata* and a short, slender form (ecotype?) of *Themeda triandra*. The last three were faithful to this community. Other faithful, but less abundant species included *Ehrharta calycina*, *Polygala fruticosa*, and *Crassula pellucida*. Total cover was usually 100%, with forbs contributing a large proportion, especially *R. cordata*, *Isoglossa ovata* and *Tephrosia grandiflora*. In localized areas forbs were dominant and the sward appeared more as a herbland (sensu Edwards 1983). Moist areas were indicated by the presence of *Juncus kraussii* and smaller sedges, as well as an abundance of *Gazania rigens*. Where the sward had been opened up (along roads, dung middens, etc.) *Stenotaphrum secundatum* often became dominant, forming a dense mat/lawn in which little else grew.

The total number of species per quadrat ($\bar{x} = 34.4 \pm 1.93$) was less than recorded in the other grassland communities at MGR. This was probably a reflection of the strong dominance of *Themeda triandra*, which always had a high cover-abundance rating. The inland boundary of this community was not distinct (nor discernible on aerial photographs), with a gradual transition into the *Tristachya leucothrix*–*Loudetia simplex* community inland. The boundary was mapped where the slender ecotype of *T. triandra* ceased to be a conspicuous member of the sward. The maximum width was 450 m, and the total area was 219 ha.

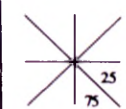
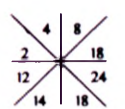
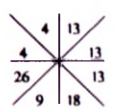
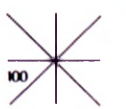
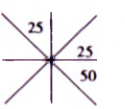
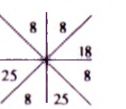
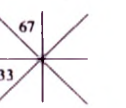
This community was associated with deep sandy soils of which the Champagne and Mispah Forms and coastal sands were the most frequently encountered. Soil conductivity was very high, probably due to the high input of sodium chloride from the sea-spray as a result of the proximity of the surf zone. Wind and salt-spray pruning of the few woody species associated with rock outcrops, especially *Carissa macrocarpa*, indicated that wind and salt-spray were important factors here, and it seems probable that they were also responsible for the shortness

TABLE 4.—Row and column contributions from the Correspondence Analysis

Row contributions	Variable	QLT	MAS	INR	k=1	COR	CTR	k=2	COR	CTR
1	Altitude (al)	999	297	342	-351	748	369	203	251	310
2	Slope (sl)	605	5	5	128	112	1	-269	493	10
3	Soil depth (sd)	976	188	139	-130	158	32	-295	818	411
4	Conductivity (co)	1000	349	420	406	958	582	85	42	63
5	pH	924	7	2	-93	175	1	-191	748	1
6	Sand (sa)	873	120	67	-61	47	4	-257	826	199
7	Clay (ca)	317	34	25	-179	306	11	-33	11	1
Column contributions	Community									
1	<i>Themeda triandra</i> – <i>Centella asiatica</i> (TC)	986	110	264	423	519	198	-401	468	447
2	<i>Tristachya leucothrix</i> – <i>Loudetia simplex</i> (TL)	922	104	121	-345	714	125	-186	207	91
3	<i>Tristachya leucothrix</i> – <i>Athrixia phylloides</i> (TA)	980	128	158	-401	912	208	-110	68	39
4	<i>Festuca costata</i> – <i>Albucca setosa</i> (FA)	982	181	91	116	186	24	239	796	261
5	<i>Stoebe vulgaris</i> – <i>Athanasia calva</i> (SA)	982	156	78	262	958	108	-41	23	7
6	<i>Cymbopogon validus</i> – <i>Digitaria natalensis</i> (CD)	946	128	196	-452	931	264	59	16	11
7	<i>Aristida junceiformis</i> – <i>Helichrysum mixtum</i> (AH)	982	192	92	193	543	72	173	438	145

QLT, the quality of representation of the element in K dimensional subspace; MAS, the proportion of observations of the element concerned scaled to 1000; INR, inertia of the element concerned relative to the total inertia, scaled to 1000; k=n, the co-ordinate of the element on the nth axis scaled to 1000; COR, the relative contribution of the axis to the inertia of the element scaled to 1000; CTR, the absolute contribution that the element makes to the inertia of the axis.

TABLE 5.—Selected characteristics of the grassland communities at Mkambati Game Reserve (values in parentheses are ranges)

Variable	Community / subcommunity						
	<i>T. triandra— C. asiatica</i>	<i>T. leucothrix— L. simplex</i>	<i>T. leucothrix— A. phylicoides</i>	<i>F. costata— A. setosa</i>	<i>S. vulgaris— A. calva</i>	<i>C. validus— D. natalensis</i>	<i>A. junciformis— H. mixtum</i>
No. of samples	8	53	23	2	4	16	3
Altitude (m)	13,0 ± 2,1 (0–22)	148,5 ± 10,6 (30–330)	201,8 ± 17,8 (45–305)	235,0 ± 20,0 (215–255)	123,3 ± 45,5 (60–258)	230,4 ± 45,4 (0–330)	217,3 ± 31,4 (155–255)
Slope (°)	3,8 ± 0,4 (2–5)	2,6 ± 0,3 (0–7)	2,3 ± 0,3 (0–6)	4,0 ± 2,0 (2–6)	3,8 ± 0,6 (2–5)	2,3 ± 0,5 (0–7)	2,0 ± 1,0 (0–3)
Aspect (% of samples)							
Organic matter (%)	5,0 ± 0,5 (3,5–8,3)	3,0 ± 0,1 (1,1–4,8)	3,4 ± 0,2 (2,2–4,8)	—	—	5,0 ± 0,4 (2,3–8,1)	—
Soil depth (cm)	117,5 ± 14,6 (70–120+)	99,9 ± 8,2 (10–120+)	131,3 ± 12,8 (20–120+)	75,0 ± 25,0 (50–100)	110,0 ± 36,1 (60–120+)	108,1 ± 17,5 (20–120+)	96,7 ± 41,7 (50–120+)
Conductivity (s)	208,0 ± 23,7 (79–280)	66,6 ± 2,3 (43–120)	77,7 ± 3,5 (57–130)	310,0 ± 10,0 (300–320)	283,3 ± 16,7 (250–300)	78,2 ± 4,9 (54–135)	350,0 ± 28,9 (300–400)
pH	4,1 ± 0,1 (3,9–4,3)	4,0 ± 0,1 (3,8–4,4)	4,0 ± 0,1 (3,8–4,3)	3,8 ± 0,1 (3,7–3,8)	3,7 ± 0,1 (3,5–3,7)	4,1 ± 0,1 (3,9–4,5)	3,8 ± 0,1 (3,7–3,8)
Sand (%)	70,4 ± 1,7 (62–77)	75,9 ± 0,8 (63–89)	70,5 ± 1,6 (61–86)	59,0 ± 6,0 (53–65)	75,0 ± 4,0 (70–83)	52,1 ± 4,8 (21–79)	66,6 ± 6,0 (55–76)
Clay (%)	17,1 ± 1,6 (11–23)	13,0 ± 0,6 (4–22)	17,4 ± 1,5 (3–27)	24,0 ± 5,0 (19–29)	14,3 ± 2,3 (9–18)	30,1 ± 4,1 (8–60)	19,2 ± 4,6 (12–28)
Height of sward (cm)	13,1 ± 0,6 (11–15)	31,0 ± 1,0 (22–50)	35,0 ± 2,0 (22–55)	48,5 ± 1,5 (47–50)	35,0 ± 3,0 (30–42)	64,3 ± 3,2 (47–100)	35,3 ± 4,4 (28–43)
No. of species:							
Total	35,4 ± 1,9 (26–43)	56,3 ± 0,1 (44–72)	53,7 ± 1,9 (38–73)	56,0 ± 2,0 (54–58)	32,0 ± 7,0 (17–50)	53,2 ± 2,2 (38–67)	39,3 ± 2,8 (36–45)
Graminoids	9,4 ± 0,6 (7–11)	13,9 ± 0,4 (8–20)	13,0 ± 0,5 (8–17)	12,0 ± 1,0 (11–13)	12,3 ± 1,4 (10–16)	13,3 ± 0,7 (7–17)	13,0 ± 1,0 (11–14)
Forbs	26,0 ± 1,9 (18–33)	41,9 ± 0,8 (30–57)	40,7 ± 1,6 (27–59)	44,0 ± 1,0 (43–45)	19,8 ± 6,3 (7–37)	39,9 ± 1,9 (25–51)	26,3 ± 2,4 (23–31)
Cover (%)	94,5 ± 2,4 (80–100)	67,3 ± 1,7 (40–93)	71,4 ± 1,8 (60–90)	65,0 ± 15,0 (50–80)	51,3 ± 18,0 (15–95)	59,1 ± 2,6 (40–80)	61,7 ± 11,7 (40–80)

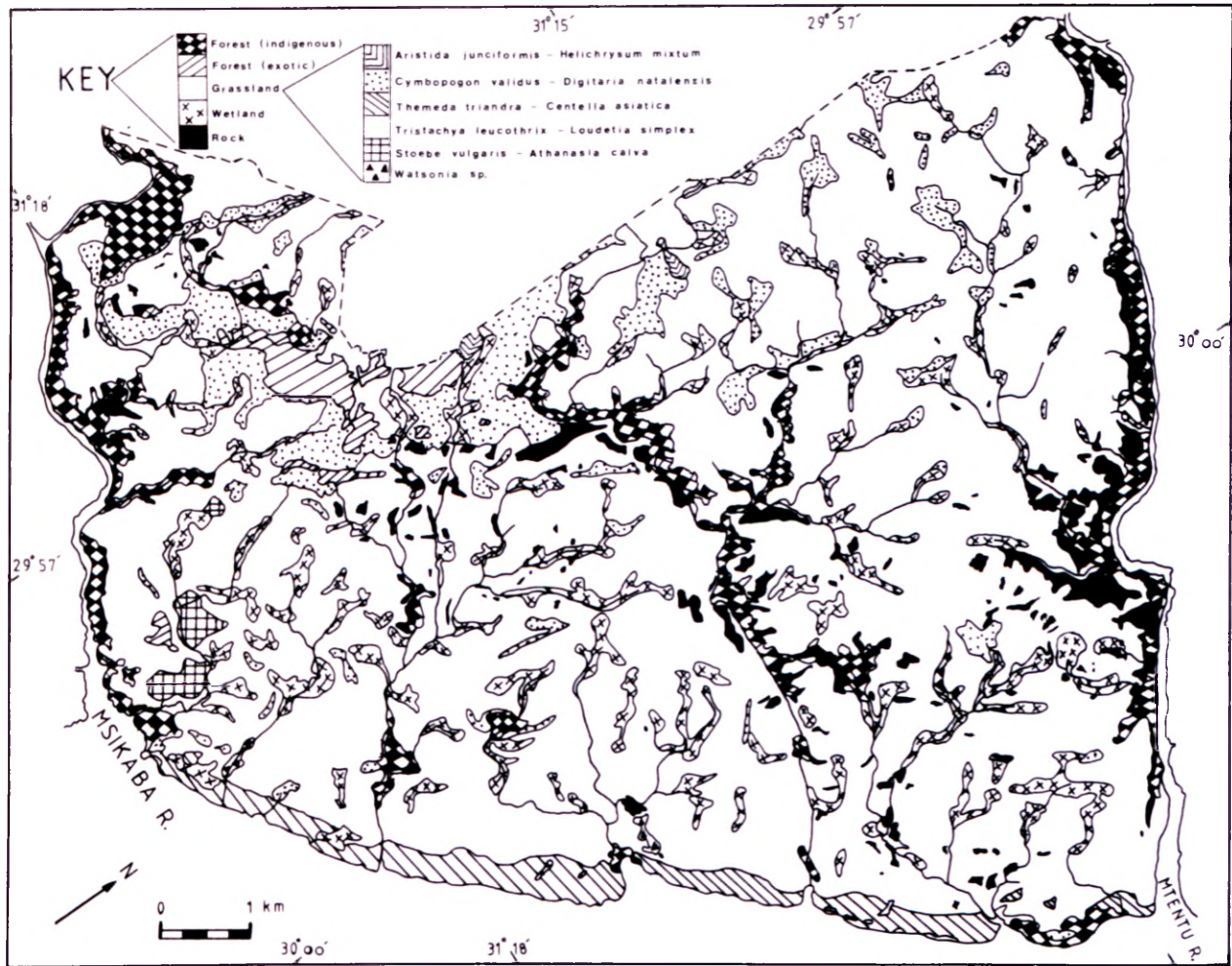


FIGURE 8.—Vegetation map of Mkambati Game Reserve.

of this grassland, as was also suggested by Edwards (1967) when describing the coastal grasslands of the lower Tugela basin.

Tristachya leucothrix–*Loudetia simplex* Short Grassland Community (53 quadrats)

This was the most extensive grassland in MGR, which, together with the *Tristachya leucothrix*–*Athrixia phyllioides* Subcommunity, contributed 71,1% (5 487,3 ha) to the total area. Together with the various subcommunities it was the most species-rich community of the reserve ($\bar{x} = 56,3 \pm 0,11$ species per quadrat), with a high cover-abundance of graminoids. Graminoids contributed approximately 70% of the relative basal cover (Table 6). Dominant grasses included *Tristachya leucothrix*, *Alloteropsis semialata*, *Trachypogon spicatus*, *Loudetia simplex* and *Diheteropogon amplexens* and wire grasses. Common forbs were *Gnidia kraussiana*, *Osteospermum imbricatum*, *Helichrysum adenocarpum*, *Senecio erubescens*, *S. bupleuroides*, and *Acalypha punctata*, amongst others. Indicator species included *Syncolostemon parviflorus*, *Heteropogon contortus*, *Urelytrum agropyroides*, *Relhania pungens* and *Asclepias praemorsa*.

Faithful species did not have much meaning for such a widespread community, where they may be locally absent. Recognition of faithful species for other communities and subcommunities was useful because of their limited distribution. Therefore preferential species were

TABLE 6.—Relative basal cover of species with a cover of 1.0% and more in the *Tristachya leucothrix*–*Loudetia simplex* community (n = 13)

Species	Relative basal cover (Mean + SE)
Grasses	
<i>Alloteropsis semialata</i>	69,2 + 6,20
<i>Ctenium concinnum</i>	4,9 + 1,35
<i>Deheteropogon amplexens</i>	1,4 + 0,96
<i>Eulalia villosa</i>	3,7 + 2,34
<i>Heteropogon contortus</i>	1,6 + 0,96
<i>Loudetia simplex</i>	3,6 + 3,48
<i>Panicum ecklonii</i>	5,6 + 3,04
<i>Themeda triandra</i>	2,9 + 2,34
<i>Trachypogon spicatus</i>	1,5 + 1,80
<i>Tristachya leucothrix</i>	9,9 + 5,57
<i>Urelytrum agropyroides</i>	12,2 + 4,72
wire grasses	2,2 + 1,18
	15,6 + 4,92
Sedges	
<i>Cyperus obtusiflorus</i>	13,8 + 4,83
<i>Scleria bulbifera</i>	3,0 + 1,51
<i>Bulbostylis</i> sp.	2,8 + 1,94
	7,7 + 3,33
Forbs	
<i>Becium obovatum</i>	17,0 + 5,33
<i>Cyanotis speciosa</i>	1,2 + 0,81
<i>Hybanthus enneaspermus</i>	1,5 + 1,33
	1,3 + 0,93
Absolute basal cover	
Basal cover	24,2 + 2,63
Bare ground	68,9 + 3,37
Litter	5,9 + 1,56
Rock	0,7 + 1,41
Total number of species	36,5 + 3,62

better indicators of this community. Easily identified preferential species included *Callilepis laureola*, *Pentania prunelloides*, *Clusia hirsuta*, *Muraltia lancifolia*, *Gnidia myrtifolia*, *Thunbergia atriplicifolia* and *Syncolostemon parviflorus*. As this community covered such a wide area, recognition of dominants was influenced by the patchy nature of some of the more conspicuous species and/or those in flower. Less abundant grasses included *Eulalia villosa*, *Heteropogon contortus*, *Urelytrum agropyroides*, *Ctenium concinnum*, *Panicum ecklonii* and *Themeda triandra*. Where present, the *T. triandra* in this community was of a more robust form than that of the *Themeda triandra*–*Centella asiatica* community adjacent to the shoreline and they were easily differentiated. Species with a relative basal cover of 1.0% or greater are listed in Table 6.

The mean height was 310 mm three to five months after burning. This community was found on all aspects and gradients throughout the reserve. However, it did occupy areas of different soil structure and chemistry to some of the other communities. The soils were sandy loams (mean % sand = 75.9 ± 0.82) with a maximum recorded clay content of 22%. Soil conductivity and organic matter were lower than that of the other grassland communities in the reserve, with means of 66.6 ± 2.28 ohms ($p < 0.005$) and $3.0 \pm 0.1\%$ ($p < 0.01$), respectively. pH was also marginally lower. This community was recorded growing on all soil forms encountered in the reserve, except for Champagne. Total cover-abundance was often lower on shallow soils.

Tristachya leucothrix–*Athrixia phyllicoides* Short Grassland Subcommunity (23 quadrats)

Despite being separated from the rest of the quadrats dominated by *T. leucothrix* as high as the second level of the TWINSPAN classification, this unit was ranked only as a subcommunity since it was not readily discernible in the field, neither on the basis of floristics nor of physiognomy. This explains why it was not recognized during reconnaissance visits and why no quadrats were expressly apportioned to it with the aim of defining and delimiting it. However, the results of both the classification and ordination suggest the existence of such a unit. Subsequent field validation of these results was inconsistent, some areas being readily discernible as belonging to this vegetation unit, but others not, even upon revisiting the sites of the initial quadrats. Consequently, this subcommunity was not mapped (Figure 8), but is possibly worthy of further investigation. Field recognition failed in most areas because the defining species were both scarce and inconspicuous.

The dominants were the same as for the *Tristachya leucothrix*–*Loudetia simplex* community. Preferential species included *Panicum aequinerve*, *Oxalis* sp. (*Shackleton 120*), *Ajuga ophrydis* and *Ledebouria revoluta*. The total number of species was similar to the *T. leucothrix*–*L. simplex* community although the height (350 ± 19 mm) was slightly greater.

Despite the difficulties of recognizing this as a distinct subcommunity, its validity is supported by its clear association with different ranges of specific environmental

variables (Table 5). The mean altitude of 201.8 ± 17.8 m a.s.l. was intermediate between that of the *Tristachya leucothrix*–*Loudetia simplex* community and the *Cymbopogon validus*–*Digitaria natalensis* community, but the ranges overlapped and therefore this was a poor indicator. Soil conductivity was higher than in the *T. leucothrix*–*L. simplex* community ($p < 0.005$) and similar to that of the *C. validus*–*D. natalensis* community. Overall soil texture was similar to the *T. leucothrix*–*L. simplex* community although there was more clay ($p < 0.005$).

Festuca costata–*Albuca setosa* Medium Grassland Subcommunity (2 quadrats)

The species composition of this subcommunity did not differ greatly from the *Tristachya leucothrix*–*Loudetia simplex* community. The primary differences were the presence of *Vigna vexillata* and the high abundance of *Festuca costata*. However, the tall growth form of the latter species, and its dark green foliage were distinct as small patches within the *T. leucothrix*–*L. simplex* community, even though it covered only a very small area (2.8 ha — hence only two quadrats). The dark colour facilitates detection of these patches at long distances, which assists its collection by local weavers who use *F. costata* to make various household items. Other species present in abundance were *T. leucothrix*, *Alloteropsis semialata*, *Panicum aequinerve*, *Acalypha punctata* and wire grasses. The less abundant graminoids included *Themeda triandra*, *Trachypogon spicatus*, and *Eulalia villosa*. The total number of species was 54 and 58 in the two quadrats respectively. *L. simplex* was absent, which was also a characteristic of the *Cymbopogon validus*–*Digitaria natalensis* community. The mean height was 485 mm.

The two quadrats located in this subcommunity had a mean clay value of $24 \pm 5\%$, which was higher than that of all the other vegetation units except the *Cymbopogon validus*–*Digitaria natalensis* community. *Festuca costata* was also present in low abundance in the *C. validus*–*D. natalensis* community, indicating its preference for the more clayey soils of the reserve. It therefore seems reasonable to speculate that these areas could be invaded by *C. validus* and *D. natalensis*. The soil conductivity was significantly higher than that of the *C. validus*–*D. natalensis* community. However, with only two samples this can be considered only as a generalization. Both quadrats were on a WSW aspect. Hilliard & Burt (1987) noted that *F. costata* is often locally dominant in damp locations in the southern Natal Drakensberg.

Stoebe vulgaris–*Athanasia calva* Short Shrub Grassland (heathland) Subcommunity (4 quadrats)

This vegetation unit was ranked as a subcommunity and assumed to be merely an old, moribund phase of the main *Tristachya leucothrix* grasslands, despite being very distinct within both the TWINSPAN and DECORANA analyses (and some areas having a low abundance of *Cymbopogon validus*). The invasion by *Stoebe vulgaris* and *Athanasia calva* is presumably facilitated by the absence of fire. All the areas sampled in which these two woody species were dominant had not been burnt for at least five years (P. Ruddle pers. comm.). Exclosure plots erected in winter 1985 in a two year old sward of the *Tristachya leucothrix*–*Loudetia simplex* community had four

established *A. calva* plants by winter 1987 and two *Rhus* sp. (Shackleton 326) by April 1988, i.e. after three years of protection from fire. The first woody species was recorded in September 1986. Furthermore, extensive areas of A block, as well as a few areas of B block were dominated by these two species during several reconnaissance visits in late 1984 and early 1985. With the onset of a regular biennial burn cycle in winter 1985 this woody growth was removed. As yet there are no signs of any re-invasion under the biennial burning programme. Because the extent of this community is related to the period since the last burn, the total area varies, but at the time of mapping it covered 33.1 ha.

Stoebe vulgaris and *Athanasia calva* were the TWIN-SPAN indicator species as well as being the physiognomic dominants in the field for this subcommunity. *Gnidia myrtifolia* was the only other species in the shrub layer, which had a mean height ($n = 4$) of $1\ 185.0 \pm 274.9$ mm. The herb stratum was moribund, relative to the other grasslands of the reserve. Litter cover was high, relative to the other communities. Dominant species in the herb stratum were *Loudetia simplex*, *Trachypogon spicatus* and *Panicum deustum*. Preferential and faithful species were *Eriochrysis pallida* and *Erica cubica*. Other preferentials included *Leonotis leonurus*, *Aristea cognata*, *Helichrysum cymosum*, *Fimbristylis complanata*, *Xyris capensis* and *Dissotis canescens* amongst others. The mean height of the herb stratum was 350 ± 30 mm. The total number of species varied considerably from one quadrat to another (17 to 50) with a mean of 32.

As previously stated, this subcommunity was assumed to be merely a moribund phase of the *Tristachya leucothrix* grasslands of MGR. Yet it had a lower pH and higher soil conductivity ($p < 0.05$) than all the other communities save the *Festuca costata*–*Albucca setosa* subcommunity. This suggested two possible explanations. All grasslands in the reserve may be invaded by these shrub species in the relatively prolonged absence of fire. Following such invasion *Stoebe vulgaris* and *Athanasia calva* alter the physical environment, hence the increased soil conductivity and decreased pH (perhaps thereby promoting facilitative succession?). Alternatively, in the absence of fire, these species can only invade certain areas of the reserve that have particular physical and chemical characteristics. These two possibilities require further investigation and subsequent recognition in the fire plan for MGR.

Values for the other measured environmental variables were similar to those of other communities. Soils were generally sandy in the A horizon, becoming moister with depth. Three of the four quadrats occurred on a Katspruit Form. All the quadrats were situated on northerly and easterly facing slopes, but this preference needs to be verified through exclusion of fire from alternative aspects other than those measured.

Cymbopogon validus–*Digitaria natalensis* Medium Grassland Community (16 quadrats)

Scattered throughout the reserve were patches of various sizes of medium grassland dominated by *Cymbopogon validus* and *Digitaria natalensis*. The total area of these patches was 536.0 ha (6.9% of the reserve). This estimation excludes the numerous, very small patches that could

not be mapped at the scale of 1:10 000. The indicator species for this community were *C. validus*, *D. natalensis*, *Borreria natalensis*, *Eriosema salignum* and *Argyrolobium rupestre*. The more conspicuous preferentials included *Scleria melanomphala*, *Hypericum aethiopicum*, *Tritonia* sp. (Shackleton 124) and *Hypoxis argentea*. Small amounts of *Aristida junciformis* were not uncommon in this community. There was a marked absence of *Loudetia simplex* and a low abundance of wire grasses. Rare, but faithful graminoids included *Helictotrichon hirtulum* and *Harpechloa falx*. Invasives such as *Eragrostis curvula*, *E. plana* and *Sporobolus africanus* were found mostly in this community (although in relatively low abundance). The wheel-point data are summarized in Table 7.

The average height was 643.0 ± 31.5 mm three months after a fire, but heights of up to 850 mm were recorded in two-year-old enclosure plots. The maximum number of species recorded in a quadrat was 67, with a mean of 53.2 ± 2.2 . Besides forming independent patches within the *Tristachya leucothrix*–*Loudetia simplex* community, the dominant species of this community were also associated with forest margins, roadsides and disturbed sites, indicating characteristics of early successional species. In the larger patches of this community there were obvious signs that the soil had been ploughed some time

TABLE 7.—Relative basal cover of species with a cover of 1.0% and more in the *Cymbopogon validus*–*Digitaria natalensis* community ($n = 3$)

Species	Relative basal cover (Mean + SE)
Grasses	65.3 + 5.48
<i>Alloteropsis semialata</i>	2.2 + 3.33
<i>Ctenium concinnum</i>	2.3 + 4.04
<i>Cymbopogon validus</i>	20.0 + 7.05
<i>Digitaria natalensis</i>	2.8 + 9.30
<i>Eragrostis capensis</i>	2.0 + 1.32
<i>Eragrostis curvula</i>	2.0 + 3.04
<i>Eulalia villosa</i>	2.2 + 3.32
<i>Panicum aequinerve</i>	1.0 + 0.50
<i>Paspalum scrobiculatum</i>	3.7 + 1.61
<i>Themeda triandra</i>	6.5 + 7.09
<i>Tristachya leucothrix</i>	3.8 + 5.01
wire grasses	2.5 + 2.00
Sedges	4.8 + 3.18
<i>Schoenoxiphium lehmannii</i>	2.5 + 1.80
<i>Bulbostylis</i> sp.	1.5 + 0.87
Forbs	29.8 + 5.48
<i>Acalypha punctata</i>	3.5 + 3.28
<i>Borreria natalensis</i>	1.2 + 1.61
<i>Desmodium dregeanum</i>	1.2 + 1.26
<i>Gerbera ambigua</i>	1.0 + 1.32
<i>Hypoxis filiformis</i>	1.2 + 2.02
<i>Hypoxis</i> sp.	3.0 + 2.78
<i>Helichrysum pilosellum</i>	1.2 + 0.76
<i>Senecio glaberrimus</i>	1.0 + 1.32
<i>S. bupleuroides</i>	1.8 + 2.75
Absolute basal cover	
Basal cover	26.2 + 3.52
Bare ground	64.7 + 2.57
Litter	9.2 + 5.80
Rock	0.0
Total number of species	42.0 + 5.72

in the past. Fields were evident on the 1974 aerial photographs where the largest patches of *Cymbopogon validus* dominated areas are presently located.

This community was prevalent towards the western regions of the reserve. Nearer the seashore it occurred as small patches, usually associated with termite mounds. It was found on heavier textured soils of the reserve, with significantly higher levels of clay and less sand than in the widespread *Tristachya leucothrix*–*Loudetia simplex* grassland ($p < 0,0005$). Soil conductivity and organic matter were significantly higher than in the *T. leucothrix*–*L. simplex* community ($p < 0,005$), as was the nutrient status (S. E. Shackleton 1989). Wherever Hutton soils occurred in the reserve they invariably supported vegetation of this community. However, it was also found on most other soil forms recorded in the reserve, except Champagne. Its association with heavier textured soils, high levels of organic matter, termite mounds, roadsides, forest margins, and Hutton soils, indicated a preference for sites with a high nutrient status and with high capacity for moisture retention, but well drained. A tendency for *Cymbopogon validus* to follow drainage lines was noted by Hilliard & Burt (1987) in the Natal Drakensberg. Previously Killick (1963) had also noted its preference for moist areas.

Aristida junciformis–*Helichrysum mixtum* Short
Grassland Subcommunity (3 quadrats)

This was ranked as a subcommunity since the quadrats were not isolated from those of the *Cymbopogon validus*–*Digitaria natalensis* community in the TWINSPAN analysis. This indicates that areas dominated by *C. validus* had a considerable number of species in common with those dominated by *A. junciformis*. However, their separation in the ordination diagram, and physiognomic difference in the field promoted the recognition of these areas as a separate vegetation unit, despite their small contribution to the total area of the reserve (12,1 ha).

A. junciformis was the dominant species contributing more than 25% (up to 75%) to the cover-abundance. Other dominants differed between the three quadrats. The total number of species ranged from 36 to 45. The mean height was $363,0 \pm 44,1$ mm.

Each of the three plots was situated on a different soil form and thus the small sample size precludes anything but the broadest generalization about soil factors associated with this subcommunity.

DISCUSSION

Evaluation of the classification and ordination results

The TWINSPAN classification, in conjunction with the DECORANA ordination and field observations provided the basis for describing several grassland communities and subcommunities. These may now be used in the identification of management units. The 'validity' of the results of the multivariate analyses was assessed by division of the data set into subsets and re-running the programmes.

The initial division was based on the year of data collection (a 1985/86 subset and a 1986/87 subset), and a second division separated plots north of the Mkambati River from those to the south. In both instances the separation of communities was similar to that obtained using the whole data set.

The final units were recognized on the basis of a combination of these three approaches, on the assumption that one or another alone might well have yielded a different perspective of the vegetation units. For example, the *Watsonia* sp. areas were not differentiated as a unit by either TWINSPAN or DECORANA (although a larger number of samples may have overcome this), but they were obvious in the field on the basis of physiognomy and the dominance of *Watsonia* sp. The high abundance of this species in these localized areas implies its specialized environmental requirements which were not measured in the course of field sampling. This specialist requirement could mean that these areas should be managed differently to maintain them (if so desired). Hence, these areas were included in Figure 8, but not in the community descriptions.

A further example was that of the *Aristida junciformis*–*Helichrysum mixtum* quadrats. They were not 'isolated' at any level of the TWINSPAN analysis, but they were separated from all others in the ordination diagram, although not adjacent. Thus, one technique 'succeeded' where another 'failed', but coupled with field observations it was decided to accept this as a realistic vegetation unit. It could require different management to be maintained or eradicated as desired.

In general, the multivariate analyses appeared to corroborate the field observations, and extracted the vegetation units recognized after the reconnaissance visits prior to sampling. There were exceptions however. The *Tristachya leucothrix*–*Athrixia phylicoides* subcommunity was not recognized during the reconnaissance and sampling stages, and hence was not allocated quadrats nor mapped. However, the results from both the TWINSPAN and DECORANA analyses indicated the presence of a community intermediate between the *Tristachya leucothrix*–*Loudetia simplex* community and the *Cymbopogon validus*–*Digitaria natalensis* community which necessitated further visits for validation in the field.

The final step of field validation is often omitted by researchers (Mueller-Dombois & Ellenberg 1974). This is unfortunate as it may lead to the definition and description of vegetation units from tabulation and synthesis of field data, that are unrecognizable as separate entities in the field. This may be a result of the indicator and preferential species being small and difficult to detect, difficult to identify, or being present in very low abundances, thus precluding a different management regime for such an 'abstract' community.

Although the identification of environmental variables as the causal agents of gradients in species composition suffers from the problem of non-linear responses of most species to environmental variables (Austin 1976), DECORANA is influenced far less by non-linearities of ecological data than earlier ordination methods (Cowling

1982). Furthermore, the high degree of intercorrelation of the variables correlated with the gradients extracted by DECORANA in this study, permitted generalization about the most important factors governing species distributions. These were corroborated by the Correspondence Analysis. The first ordination axis accounted for a considerable amount of variation and appears to represent a reduction of salt-spray influence with increasing distance from the seashore. However, the possibility that the most important variables (those exerting the most influence) were not measured, must not be discounted.

Comparison with other coastal areas of Transkei

Some of the vegetation units described for MGR are common along the coastal region of Transkei. Immediately south of the Msikaba River (the southern boundary of MGR) Cawe *et al.* (1983) described widespread grasslands dominated by *Themeda triandra* and with *Tristachya leucothrix*, *Alloteropsis semialata*, *Diheteropogon amplexens*, *Eulalia villosa* and *Ctenium concinnum* in abundance. These authors also noted a thin strip along the coastal forelands dominated by *Stenotaphrum secundatum*, but this was not mapped as it was not visible on aerial photographs. McKenzie & Cowling (1979) and Hoffman (1983) recorded both a *Themeda triandra* dominated dwarf/short grassland adjacent to the coast (with differing abundances of *S. secundatum*), and a *Cymbopogon* spp.-dominated tall grassland in both the Dwesa and Hluleka Nature Reserves, respectively. A *Tristachya*–*Aristida* grassland also occurs in the Dwesa Nature Reserve. However, the *Tristachya leucothrix* dominated areas of MGR bear little resemblance to this community in that they possess many more species, especially forbs, and lack the relatively high abundance of *Themeda triandra* and *Aristida junciformis*. In general, the major difference between the grasslands of MGR and these reserves appears to be high species diversity at MGR.

Comparison with other sour grasslands

Considering coastal grasslands north of MGR, little comparative quantitative work has been done, due to the high human population and agricultural pressures, which have severely altered whatever coastal grasslands there once were. Edwards (1967) described *Stenotaphrum secundatum* grasslands immediately adjacent to the coast in the lower Tugela valley, as did Ward (1980) in the Isipingo Beach area in Natal. Edwards (1967) considered that these were located in areas of disturbance (grazing, trampling, or clearance of dune scrub), as noted at MGR.

Recently, quantitative data were analysed for the grasslands surrounding Lake St Lucia which are apparently similar to those at MGR in terms of rare species composition (R. Ellis pers. comm.) and structure. The results from Conlong's (1986) work indicate that there is strong similarity between the *Alloteropsis semialata*–*Diheteropogon filifolius* community on the eastern shores of Lake St Lucia, and the *Tristachya leucothrix*–*Loudetia simplex* community of MGR. Dominant grasses in both areas include *T. leucothrix*, *A. semialata*, *Trachypogon spicatus* and *D. filifolius* (a constituent of the wire grass component at MGR). Abundant forbs common to both areas include *Callilepis lauroleola*, *Pentanisia prunelloides*, *Acalypha punctata*, *Thunbergia atriplicifolia*, *Tephrosia* spp. and *Commelina* spp. However, the other communities

described by Conlong (1986) do not have equals at MGR; those at Lake St Lucia appear to be dominated by species characteristic of wetter areas than MGR. Quantitative analysis of the wetlands at MGR may well reveal floristic similarities with the Lake St Lucia system.

A noteworthy feature of the MGR grasslands is the relative scarcity of *Themeda triandra* considered in the light of the results of both Acocks (1988) and Cawe *et al.* (1983) for the same and adjacent grasslands, respectively. Furthermore, the major difference between the grasslands of MGR and those of the Natal Drakensberg appears to be the dominance of *T. triandra* in the Drakensberg as recorded by Killick (1963) and Scotcher (1982). Such a shift in dominance from *T. triandra* in favour of *Tristachya leucothrix*, species of wire grasses, *Loudetia simplex* and *Alloteropsis semialata* may be interpreted as a replacement of decreaser species by increaser I and III species through under- and selective utilization of the grasslands of MGR (Tainton 1981). However, this presupposes that these grasslands were once dominated by *Themeda triandra*.

Fire and 'invasion' of fynbos species

The incidence of a large number of species of fynbos affinity is also noteworthy. The most abundant fynbos species were *Stoebe vulgaris*, *Athanasia calva*, *Erica cubica*, *E. natalensis*, *E. natalitia*, *Calopsis paniculata*, *Protea caffra*, *P. simplex*, *P. roupelliae*, *Leucodendron spissifolium*, *Leucospermum innovans*, *Agathosma ovata*, and *Muraltia lancifolia*. Most of these species, although not all, were confined to unburnt grasslands or rock outcrops and terraces where they were, presumably, protected from fire. The present record of fire control is poor. Management should therefore decide whether these species are important, and if so, alter and implement the fire policy accordingly.

The invasion of woody species into unburnt areas of MGR indicates that these grasslands can support limited woody vegetation. However, the fact that forest and woodland require well drained sites (Tinley 1982) and the predominance of grassland vegetation on old plantation surfaces and hydromorphic soils (Tinley 1982; McKenzie 1984; Feely 1986) indicates that it is unlikely that the whole of MGR would develop into forest in the absence of fire. There is strong inferential evidence that this region (Feely 1986), as well as most of the grassland-dominated eastern seaboard of Natal (Mentis & Huntley 1982), has been grassland for millennia. However, it is quite probable that the area of forest could increase to a limited extent if protected from fire, especially along the well developed terrace areas. An alternative to the extensive development of forest might be the expansion of the *Stoebe vulgaris*–*Athanasia calva* shrubland to cover the whole reserve. However, it appears unlikely that such vegetation could cope with the wind and spray of the coastal forelands. If large areas of the reserve were dominated by *S. vulgaris*–*A. calva* shrubland, its development would depend on management aims and practices.

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