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An ecosystematic investigation of two graminoids (*Digitaria eriantha* and *Setaria sphacelata* var. *torta*) in the semi-arid grasslands of southern Africa

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Abstract. Comparing the response of two grass species (*Digitaria eriantha* Steud. and *Setaria sphacelata* (Schmach.) Moss. var. *torta*) to the grazing impact revealed various dissimilarities between the high and low rainfall regions and different edaphic conditions in the semi-arid grasslands of southern Africa. The same species often reacts differently to grazing in different topographical positions, as well as between habitats of the same topographical unit. This gave cause for assuming that different ecotypes within these species are involved. A study aimed at the delimitation of ecotypes within important pasture grasses of southern Africa was initiated, whereby 42 morphological and 5 chemical characters and productivity of each species were studied and included in a principle component analysis. The ultimate grouping of these ecotypes into a functional special purpose classification system can provide rangeland ecologists with lists of ecotypes, to be used when interpreting ecological data and describing vegetation dynamic processes in the semi-arid grasslands of southern Africa.

Key words: *Digitaria eriantha*; Ecological status; Ecotypic variation; Poaceae; Semi-arid grasslands; *Setaria sphacelata* var. *torta*; Vegetation dynamics.

Introduction

Ecological research by Bosch and Janse Van Rensburg (1987) and Janse Van Rensburg and Bosch (1990) have revealed that *Digitaria eriantha* Steud. and *Setaria sphacelata* (Schumach.) Moss. var. *torta* are important pasture grass species in the semi-arid grasslands of southern Africa. Both species have a widespread distribution in southern Africa, Zimbabwe and Angola, occurring in most vegetation types, including grassland, savanna and woodland and extending into marshes and along riverbanks (Chippindall, 1955; Chippindall and Crook, 1976; Tainton *et al.*, 1985). These species show extreme morphological, cytological and reproductive variation (Gibbs Russell and Spies, 1988; Spies and Gibbs Russell, 1988). Most of the morphological variation within *D. eriantha* and *S. sphacelata* var. *torta* exists throughout the geographical distribution of the taxa.

Vegetation dynamic studies on species response on the degradation gradient have indicated that certain strains of *D. eriantha* and *S. sphacelata* var. *torta* react differently to defoliation and grazing (Bosch, 1989; Bosch and Janse Van Rensburg, 1987; Janse Van Rensburg and Bosch, 1990). *D. eriantha* has previously been classified as a Decreaser species (i. e. species which decrease when vegetation is under- or overutilized) on the shallow soils in both high and low rainfall areas (Fig. 1A), whereas the same species also reacts as an Increaser species (i. e. species which increase when vegetation is moderately severely overutilized) on the deeper soils of these areas and pediments of the high rainfall area (Fig. 1A). *S. sphacelata* var. *torta* can also be

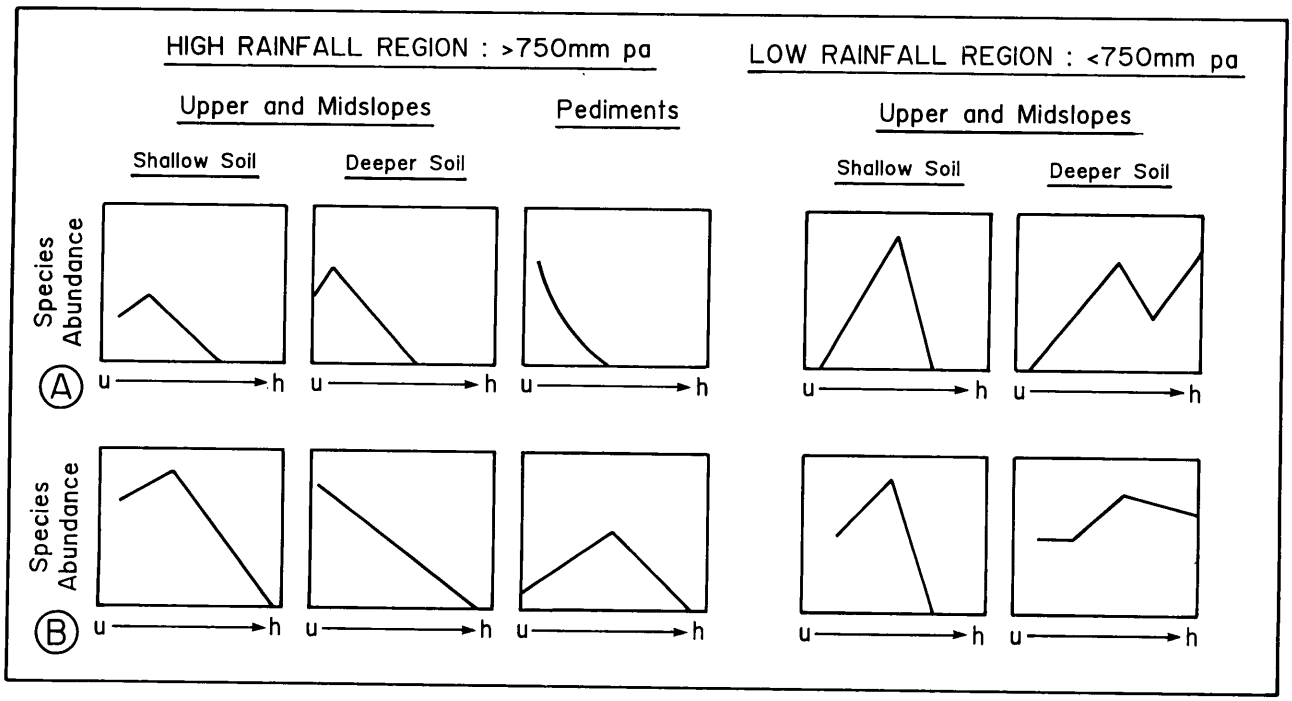

Fig. 1. Changes in abundance of two species on the grazing gradient on the shallow and relatively deeper soils of the upper and midslopes in the high and low rainfall regions, and the pediments in the high rainfall region. A, *D. eriantha*; B, *S. sphacelata* var. *torta*. (The grazing gradient, which is represented by the x-axis, ranges from ungrazed (u) to heavily-grazed (h).)

classified as an Increaser species on the pediments of the high rainfall region (Fig. 1B), whereas this species reacts as a Decreaser species on the deeper and shallow soils of both rainfall areas (Bosch and Janse Van Rensburg, 1987; Janse Van Rensburg and Bosch, 1990). Pronounced differences in ecological status and the high degree of morphological variation within these species, gave reasons for assuming that different ecotypes of *D. eriantha* and *S. sphacelata* var. *torta* are involved (Bosch, 1988).

The above mentioned ecological research in the semi-arid grasslands of southern Africa has therefore shown, that the present taxonomic classification of important grass species is unsuitable for use by ecologists. This hampers the understanding and interpretation of vegetation dynamic models, rangeland condition assessments, the reaction of grass species to a variety of environmental gradients, and the functional contribution of grass species in vegetation dynamic processes. This consequently hinders the development of sound strategies to improve the rangelands through species management. This paper reports on a study that was subsequently undertaken to investigate the presence of ecotypic variation within important pasture grasses of the semi-arid regions of southern Africa.

Materials and Methods

The study was conducted in the semi-arid grassland region of southern Africa which is situated 24° 30′ and 30° 20′ S and 25° 30′ and 33° 20′ E. The long term average rainfall varies from 400-800 mm per annum. However, rainfall is erratic and seasonal droughts may occur. Specimens of *D. eriantha* and *S. sphacelata* var. *torta* were obtained from four different collection locations at three possible habitats along a rainfall gradient (Table 1).

Five specimens were collected at each habitat and cultivated under uniform environmental conditions. Plants were grown in polyethylene bags (200 mm, diameter) in a glasshouse maintained at 27/22°C day/night temperature and watered every third day. The five individuals from each habitat will henceforth be collectively referred to as a habitat group.

The morphological (including vegetative morphol-

Table 1. *Information on the* ***D. eriantha*** *and* ***S. sphacelata*** *var.* ***torta*** *plant material used*

Collection site number	Collection location	Long term average rainfall (mm)	Habitat*
1	Golden Gate	800-700	shallow soil (D, S) deep soil (D, S) water course (S)
2	Willem Pretorius	700-600	shallow soil (D, S) deep soil (D, S) water course (D, S)
3	Ventersdorp	600-500	shallow soil (D, S) deep soil (D, S)
4	Faan Meintjes	500-400	shallow soil (D, S) deep soil (D) water course (D)

*Plant material of each species used is indicated by a letter following the habitat [*D. eriantha* (D); *S. sphacelata* var. *torta* (S)]

ogy and epidermis characters) and chemical characters studied, are given in Table 2. For a detailed discussion on the methods used for studying the characters involved and determining production, phenolic containing cells, and trichome index, refer to Theunissen *et al.* (1991). The methods used in the chemical analysis will henceforth be discussed as this section was not included in the above-mentioned reference.

Oven dried (38°C for 72 h) leaf material was used for determining the amount of total phenolics, lignin, cellulose and anthocyanins present in the leaves of *D. eriantha* and *S. sphacelata* var. *torta*. For determining total phenolics the method as suggested by Julkunen-Tiitto (1985) was employed. The methods of Moon and Abou-Raya (1952) and Crampton and Maynard (1937) were used to determine the amount of lignin and cellulose, respectively. Anthocyanins were extracted with a methanol and HCl solution (97:3 v/v) and the differences in concentration amongst the habitat groups of *D. eriantha* and *S. sphacelata* var. *torta* were determined by measuring the absorbance at 510 nm on a Bausch and Lomb spectronic colorimeter (Theron and Booysen, 1966). All chemical determinations were made in triplicate for each individual, resulting in a total of 15 determinations for each habitat group.

The initial morphological descriptions, measurements and countings, chemical analysis, production and trichome index determinations were made immediately after the specimens were collected from the field in February 1988. After this had been completed the specimens were defoliated every sixty days for a period of seven months to enhance vegetative growth among all plants simultaneously. With the exception of defoliation, all the above-mentioned procedures were repeated on the same individuals in March 1989. A comparison was drawn between the first (1988) and second (1989) data sets, in order to determine whether the variation within *D. eriantha* and *S. sphacelata* var. *torta*, had a genetic basis, and not merely the result of phenotypic plasticity.

Numerical Analysis

The five individuals from each habitat were investigated separately and the raw data were processed as a mean for the habitat group. The final data for each species were standardized using the method of Sneath and Sokal (1973) and analyzed by means of a principal component analysis (PCA). The principal components were calculated by the PRINCOMP-program. The principal components are sorted by descending order of the eigenvalues, which are equal to the variance of the components (SAS Institute Statistical Analysis System, 1985).

Results

Digitaria eriantha

The first component of the PCA accounts for 23% of variation in the analysis. The ordination graph of components 1 and 2 of the PCA differentiates habitat

Table 2. *Characters of* ***D. eriantha*** *and* ***S. sphacelata*** *var.* ***torta*** *studied*

Number	Character	Unit
	MORPHOLOGY	
	A. Vegetative morphology	
1	Culm length	mm
2	Mean internode length	mm
3	Leaf blade length	mm
4	Leaf blade width	mm
5	Ligule length	mm
6	Ligule width	mm
7	Number of internodes	-
8	Number of nodes	-
9	Culm branching	-
10	Leaf blade hairiness	-
11	Position of hair on leaf blade	-
12	Leaf blade position (flat or folded)	-
13	Leaf blade colour	-
14	Ligule membranous or fringe of hairs	-
15	Ligule colour	-
16	Basal leaf sheath (flattend/not flattend)	-
17	Leaf sheath hairiness	-
18	Position of hair on the leaf sheath	-
19	Leaf sheath colour	-
20	Tuft density	-
21	Habit	-
	B. Epidermis	
22	Prickle hairs (present/absent)	-
23	Intercostal distribution of prickles	-
24	Costal distribution of prickles	-
25	Angular prickles (present/absent)	-
26	Micro-hairs (present/absent)	-
27	Relative length of basal cells	-
28	Relative length of distal cells	-
29	Shape of distal cell	-
30	Apex of distal cell	-
31	Shape of basal cell	-
32	Intercostal distribution of micro-hairs	-
33	Macro-hairs (present/absent)	-
34	Number of cells comprising macro-hair	-
35	Epidermis cells associated with base of macro-hair	-
36	Nature of base of hair	-
37	Macro-hair length	-
38	Distribution of macro-hairs	-
39	Frequency of prickles	-
40	Frequency of micro-hairs	-
41	Frequency of macro-hairs	-
42	Trichome index	%
	CHEMICAL COMPOSITION	
43	Lignin	%
44	Total phenolics	%
45	Cellulose	%
46	Anthocyanins	%
47	Phenolic containing cells	%
	DRYMASS PRODUCTION	
48	Production	g/cm^2

groups 1, 2, 3, 4, and 5 form the remaining habitat groups on the positive side of the first component (Fig. 2A). Characters with strong loadings (absolute value ≧ 0.6) at component 1 include ligule colour and width, anthocyanin and lignin content and leaf blade width (Table 3). Habitat groups 6 to 10, which are placed on the positive side of the horisontal axis (Fig. 2A) have broad, light brown or dark brown ligules, relatively high levels of lignin and anthocyanin and broad leaf blades (Table 3). The remaining habitat groups, which are situated on the negative side of the horisontal axis have narrow, cream-white ligules, lower levels of lignin and anthocyanin and narrow leaf blades (Table 3).

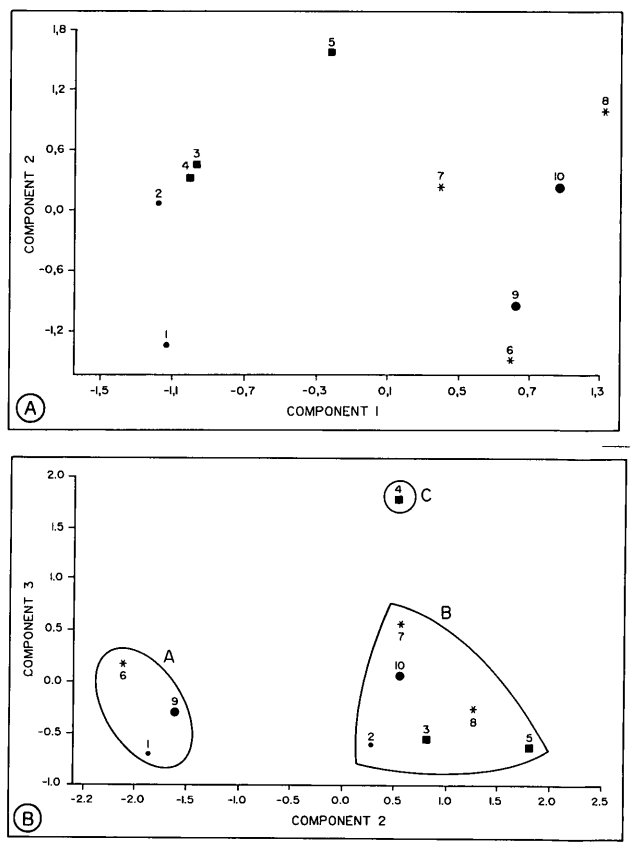

Fig. 2. Ordination diagrams of the three components of a principle component analysis on 10 habitat groups of *D. eriantha*. A, First and second components of the principle component analises. Variance accounted for: Component 1 - 23%. B, Second and third components of the principle component analysis. Variance accounted for: Component 2 - 20%; component 3 - 17%. (●, Golden Gate; ■, Willem Pretorius; ∗, Faan Meintjes; ●, Ventersdorp)

Components 2 and 3 of the PCA account for 20 and 17% of variation in the analysis, respectively. The ordination graph of components 2 and 3 of the PCA (Fig. 2B) indicate that the habitat groups of *D. eriantha* can be grouped into two major groups (groups A and B) situated on the positive and negative side along the horisontal axis (component 2). Character loadings on the second component indicate that these groups are distinguished by two main characters (absolute value ≧ 0.6), namely, growth form and culm position (Table 3). Group A has a stoloniferous growth form and geniculate culms, whereas groups B and C are characterized by a tuftlike growth form and erect culms (Table 3).

The separation of group C, as effected by the third component (Fig. 2B), can be attributed to three main characters (absolute value ≧ 0.6), namely, presence/absence and frequency of macro-hairs, leaf sheath colour and ligule length (Table 3). Group C is characterized by green yellow leaf sheaths, short ligules and the presence of large numbers of macro-hairs, whereas groups A and B both have longer ligules, greyish yellow green leaf sheaths and no or a relatively small number of macro-hairs (Table 3).

Setaria sphacelata var. *torta*

The first and second components of the PCA account for 24 and 21% of variation in the analysis, respectively. The ordination graph of components 1 and 2 of the PCA differentiates habitat groups 6 (group B) and 9 (group A) from the remaining habitat groups on the negative side of the horisontal axis (Fig. 3A). An examination of the character makeup of component 1 indicates that characters with strong loadings (absolute value ≧ 0.6) include culm length, trichome index, anthocyanin content, distribution of prickles, and number of prickles and micro-hairs (Table 4). Groups A and B differ from the rest of the habitat groups along component 1 (Fig. 3A), mainly on the basis of longer culms, a higher trichome index, low levels of anthocyanin, prickles with a costal and intercostal distribution, and an abundance of prickles and micro-hairs (Table 4). The remaining habitat groups on the other hand have shorter culms, a low trichome index, lower levels of anthocyanin, prickles with a costal distribution, and a small number of micro-hairs and prickles (Table 4).

Characters exhibiting strong loadings (absolute value ≧ 0.6) on the second component include leaf blade length, leaf sheath colour and hairiness, ligule length, width and colour (Table 4). Group B which is placed on the negative side of the vertical axis (Fig. 3A) has shorter leaf blades, greyish yellow green, glabrous leaf sheaths and short, broad, cream white ligules (Table 4). The remaining habitat groups and group A which are placed on an intermediate position and positive side along the vertical axis, respectively (Fig. 3A), are characterized by longer leaf blades, yellow green or greyish yellow green leaf sheaths with a purple base (with the exception of habitat group 5), hairy leaf sheaths and long, narrow, white ligules (Table 4).

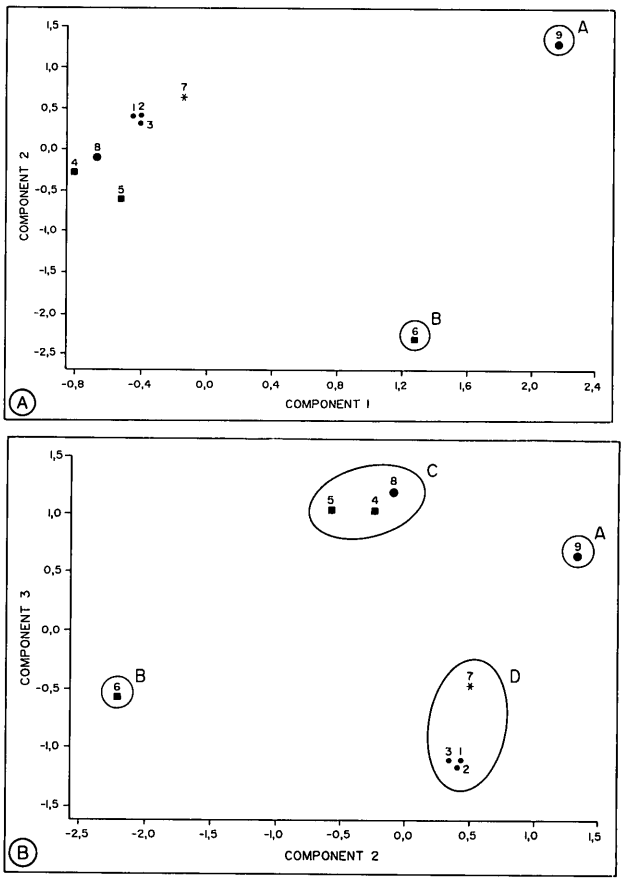

Fig. 3. Ordination diagrams of the three components of a principle component analysis on 9 habitat groups of *S. sphacelata* var. *torta*. A, First and second components of the principle component analises. Variance accounted for: Component 1 - 24%. B, Second and third components of the principle component analysis. Variance accounted for: Component 2 - 21%; component 3 - 15%. (●, Golden Gate; ■, Willem Pretorius; ∗, Faan Meintjes; ●, Ventersdorp)

The third component of the PCA accounts for 15%

Table 3. *Ten characters exhibit strong loadings (absolute value ≧ 0.6) on components 1, 2 and 3 of the principle component analysis and are responsible for the grouping of* ***Digitaria eriantha*** *into three ecotypes*

Habitat	Group	Component 1					Component 2		Component 3		
		*Ligule colour	Ligule width (mm)	Anthocyanin content (%)	Lignin content (%)	Leaf blade width (mm)	Growth form	Culm position	Macro-hairs	*Leaf sheath colour	Ligule length (mm)
A	1	Cream white	2.6	0.27	9.3	3.3	Stoloniferous	Geniculate	Scarce/ absent	Greyish yellow green	3.65
	6	Light brown	4.0	0.30	9.8	4.0	Stoloniferous	Geniculate	Scarce/ absent	Greyish yellow green	2.70
	9	Light brown	3.5	0.66	9.3	3.6	Stoloniferous	Geniculate	Scarce/ absent	Greyish yellow green	2.60
B	2	Cream white	2.8	0.12	9.2	3.1	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	3.60
	3	Cream white	2.9	0.38	9.4	2.9	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	3.41
	5	Cream white	3.6	0.37	9.1	2.8	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	2.84
	7	Drak brown	4.7	0.58	9.9	4.8	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	2.41
	8	Light brown	4.8	0.66	10.0	4.9	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	2.93
	10	Light brown	3.4	0.72	10.2	3.6	Tuftlike	Erect	Scarce/ absent	Greyish yellow green	2.44
C	4	Cream white	2.1	0.30	9.0	1.6	Tuftlike	Erect	Abundant	Green yellow	1.23

*Colour identification made by colour chart prepared by Rayner (1970).

Table 4. *Fifteen characters exhibit strong loadings (absolute value ≧ 0.6) on components 1, 2 and 3 of the principle component analysis and are responsible for the grouping of* ***Setaria sphacelata*** *var.* ***torta*** *into four groups*

Habitat	Group	Component 1					Component 2						Component 3			
		Culm length (mm)	Trichome index (%)	Antho-cyanin content (%)	Distri-bution of prickles	Number of prickles and Micro-hairs	Leaf sheath hairi-ness	*Leaf sheath colour	Ligule length (mm)	Leaf blade length (mm)	Ligule width (mm)	*Ligule colour	Leaf blade hairi-ness	Cellu-lose content (%)	Total phenolic content (%)	Culm position
A	9	630	10.9	0.28	costal & inter-costal	abundant	entire surface hairy	greyish yellow green & purple base	2.5	35	0.48	white	adaxial	47	0.34	geniculate
B	6	317	14.0	0.30	costal & inter-costal	abundant	glabrous	greyish yellow green	0.5	20	0.70	cream white	abaxial & adaxial	40	0.41	erect
C	4	308	6.3	0.41	costal	scarce	entire surface hairy	yellow green	2.3	20	0.48	white	adaxial	42	0.43	erect
	5	420	4.7	0.31	costal	scarce	entire surface hairy	greyish yellow green	2.4	22	0.50	white	adaxial	46	0.40	erect
	8	410	3.7	0.49	costal	scarce	entire surface hairy	yellow green	2.3	31	0.46	white	adaxial	42	0.31	erect
D	1	270	9.8	0.31	costal	scarce	entire surface hairy	greyish yellow green & purple base	2.8	28	0.51	white	abaxial & adaxial	34	0.63	geniculate
	2	273	7.0	0.41	costal	scarce	entire surface hairy	greyish yellow green & purple base	2.7	33	0.52	white	abaxial & adaxial	36	0.65	geniculate
	3	260	6.3	0.40	costal	scarce	entire surface hairy	greyish yellow green & purple base	2.7	31	0.50	white	abaxial & adaxial	36	0.61	geniculate
	7	470	5.9	0.40	costal	scarce	entire surface hairy	greyish yellow green & purple base	3.2	44	0.51	white	abaxial & adaxial	43	0.34	geniculate

*Colour identification made by colour chart prepared by Rayner (1970).

of variation in the analysis. An examination of component 3 (Fig. 3B) indicates that characters exhibiting strong loadings (absolute value ≧ 0.6) include leaf blade hairiness, cellulose and total phenolic content and culm position (Table 4). The habitat groups (1, 2, 3, 4, 5, 7 and 8) situated on an intermediate position along the horisontal axis are divided into two groups (groups C and D) by the third component of the PCA (Fig. 3B). Character loadings on the this component indicate that habitat groups 4, 5 and 8 (group C) have erect culms, relatively high levels of cellulose, low levels of total phenolics and an adaxial distribution of hair on the leaf blades (Table 4). Group D (habitat groups 1, 2, 3 and 7) is characterized by geniculate culms, lower levels of cellulose, higher levels of total phenolics and an ab- and adaxial distribution of hair on the leaf blades (Table 4).

Discussion

Results obtained from this investigation clearly indicate that distinct morphological and chemical composition differences exist between different habitat groups of *D. eriantha* and *S. sphacelata* var. *torta*, respectively. It appears however, that these differences are genetically controlled, as specimens from each collection locality and habitat within the species, retained their original morphological and chemical characters after having been cultivated under uniform environmental conditions for a period of 14 months.

This study shows, however, that in the semi-arid grasslands of southern Africa, both *D. eriantha* and *S. sphacelata* var. *torta* exhibit a considerable degree of variation with regard to morphology, production, chemical composition and trichome index. The habitat groups of *D. eriantha* can be divided into three main groups each representing a different, morphologically distinct ecotype, associated with a particular habitat. Representatives from group A are adapted to disturbed areas in both low and high rainfall regions, whereas habitat groups represented by group B are associated with undisturbed areas in these rainfall regions. Group C represents the only habitat group favouring water courses.

Although *D. eriantha* is associated with well managed vegetation (Decreser species), this species also becomes abundant in moderately severely overgrazed vegetation in the low rainfall region (Increaser species) (Fig. 1A). This is probadly due to the stoloniferous growth form of the species through which open bare patches in over-utilized vegetation become colonized (Bosch and Janse Van Rensburg, 1987). Indications are that certain strains of *D. eriantha* react as a typical pioneer species. Results from this study have revealed that growth form (showing strong loadings on component 2 of the PCA) has in fact played a major role in distinguishing between ecotypes within the species. The stoloniferous type, previously known as *D. pentzii* Stent. and later as *D. eriantha* subp. *pentzii*, was placed in the synonymy of *D. eriantha* by Kok (1984). Bosch and Janse Van Rensburg (1987) mention that a separation between the two growth forms is important from an ecological point of view, especially considering that the two growth forms have different ecological functions.

The habitat groups of *S. sphacelata* var. *torta* are grouped into four morphologically distinct groups. In contrast to *Themeda triandra* Forssk. (Theunissen, 1991), *Eragrostis racemosa* (Thunb.) Steud. (Theunissen *et al.*, 1991) and *D. eriantha* where habitat groups are divided into ecotypes which are associated with a particular environmental factor, the circumscribed groups of *S. sphacelata* var. *torta* do not relate to any environmental condition. Consequently the groups identified within *S. sphacelata* var. *torta*, will at this stage not be given ecotypic recognition. Further transplant experiments and cytogenetic studies are however, necessary to determine whether or not the grouping of habitat groups within *S. sphacelata* var. *torta* is possibly related to environmental factors or even different polyploid forms.

This investigation and previous studies by Theunissen (1991), Theunissen *et al.* (1991) and Bosch and Theunissen (1992) suggest that ecotypic variation is a common phenomenon in grasses. This is reflected by the presence of morphological distinct ecotypes, exhibiting spesific topographical and habitat preferences within the species involved. This phenomenon becomes more pronounced if one takes into account that these species have a widespread distribution and that each one can be classified into more than one ecological status group (Gibbs Russell, 1983).

Ecotypes within a species should, without altering the present taxonomic classification, eventually be included in a functional special purpose classification system. This merely implies that ecotypes of a given

species can be classified into a classification system devised to meet spesific demands made by rangeland scientists (Bosch and Theunissen, 1992). Furthermore, this classification system will not entail a revision of the present taxonomic delimitation of the species. The aim of the functional special purpose classification system is to assist rangeland ecologists in identifying functional ecotypes within grass species, thus facilitating the interpretation and understanding of ecological data and plant community dynamics in the semi-arid grasslands of southern Africa. The inclusion of ecotypes into a classification system also became a prerequisite for rangeland managers. Management strategies are defined on the basis of ecological, morphological and physiological characteristics of individual species. These characteristics are often studied in a particular area, involving therefore a given ecotype within a species. Should a management strategy be required to promote this species in another area, common practice would be a direct extrapolation of the principles to that area. However, as a different ecotype within the same species could be involved, such practice would lead to inefficient management decisions.

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南非半乾旱草原上兩種禾草(*Digitaria eriantha* 和 *Setaria sphacelata* var. *torta*)的生態分類調查

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本實驗以 42 種形態特徵，5 種化學特性和生產力，經由主成份分析法，以區別南非重要牧草的生態型。這些生態型可經由主成份分析的結果，依其功能上的相似度而劃分成不同的組別。這種依功能來區分生態型的方法，可提供農場生態學者來鑑定各種不同的生態型，並以解釋和描述南非半乾旱草原上的生態資料和植被更替的過程。