

# Biogeographical patterns of grasses (Poaceae) indigenous to South Africa, Lesotho and Eswatini

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The ecological and economical importance of African grasses in sustaining animal production prompted studies to quantify the wealth of grass genetic resources indigenous to southern Africa. Plant collection and occurrence data were extracted from two southern African datasets, BODATSA and PHYTOBAS, and analysed to establish biogeographical patterns in the grass flora indigenous to South Africa, Lesotho and Eswatini. A total of 1 648 quarter degree grid cells, representing 674 grass species, were used in an agglomerative hierarchical clustering to determine biogeographical units being referred to as grasschoria. Six distinct groups formed, mainly following existing biome vegetation units, termed the Grassland, Indian Ocean Coastal Belt, Fynbos, Savanna, Central Arid Region and Succulent Karoo grasschoria. The description focuses on associated phytochoria, floristic links, key species, climate and soil properties. The main gradient distinguishing grasschoria was a rainfall-temperature gradient. The collection, conservation and breeding of pasture grass species adapted to especially arid and semi-arid environments, could be managed more efficiently by using these results, but also calling on the need to describe and label infraspecific genetic variants, including ecotypes.

**Keywords:** biomes, distribution, floristics, pastures, phytochoria

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## Introduction

The grass family, Poaceae (Gramineae) is considered the most valuable plant family in food production worldwide. In addition to its importance as a grain crop (e.g. maize, wheat and rice), its tolerance to grazing, fire and drought, makes grasses a significant component of livestock feed, mainly sourced from rangeland and/or planted pastures. Soreng et al. (2017) recognised at least 11 506 grass species worldwide of which approximately 685 species are indigenous to southern Africa (Trytsman et al. 2020). Considering that in southern Africa only eight indigenous grass species were extensively researched in the past century (Truter et al. 2015), the wealth of grass genetic resources, indigenous to the subcontinent, still needs to be prioritised, conserved and developed for forage production.

The classification and distribution of southern African grasses that included Botswana, Namibia, South Africa, Lesotho and Swaziland were described by Gibbs Russell et al. (1990) and was updated by Fish et al. (2015). Studies on the biogeographical patterns of grasses in relation to southern African vegetation types are, however, limited. Then again, there are numerous phytogeographical studies on the southern African flora, which include those by Acocks (1953, 1988), Goldblatt (1978), Clayton (1983), White (1983), Rutherford and Westfall (1986), Low and Rebelo (1996), Jürgens (1997), Cowling et al. (1998), Van

Wyk and Smith (2001), Bredenkamp et al. (2002), Linder et al. (2005), Steenkamp et al. (2005), Mucina and Rutherford (2006), Daru et al. (2016) and Trytsman et al. (2016). These studies mainly used criteria, such as species distribution, floristic composition, physiognomy, growth form, endemism or phylogeny. The well recognised study of White (1983) delineated three Regional Centres of Endemism for southern Africa, as well as a Centre, a Transitional Zone and a Regional Mosaic. The Regional Centres of Endemism include the Zambezian, Cape and Karoo-Namib, the lower ranked Afromontane Archipelago-like Centre and lastly the Kalahari-Highveld Transitional Zone and the Tongaland-Pondoland Mosaic. Linder et al. (2005) distinguished six narrow phytochoria within a broad southern African phytochorion, namely the Cape, Natal, Namib-Karoo, eastern Karoo, Kalahari and Karoo transition (listed here as highest to lowest in species richness), using more than 5 000 sub-Saharan species and infra-specific taxa. The phytochoria defined by mainly these two aforementioned studies will be used to interpret the main clusters resulting from the current study.

The use of the biome and bioregion maps of Mucina and Rutherford (2006), to identify biogeographical areas of the leguminochoria of southern Africa, formed distinctive patterns, as described by Trytsman et al. (2016). Rutherford et al. (2006) also stated that the biomes of South Africa,

Lesotho and Eswatini ‘...are partly derived from a bottom up approach that accounts for the perfect match between biome boundaries and floristically determined boundaries’. These authors presented evidence that the degree of correspondence between biomes and phytochoria delineated by White (1983) and Linder et al. (2005) were high for the Desert, Fynbos, Indian Ocean Coastal Belt, Nama-Karoo and Succulent Karoo biomes. In an earlier study Gibbs Russell (1987) found that, of the seven southern African plant families with more than 1% of taxa in all biomes, Poaceae has the highest number of taxa in the Savanna and Desert biomes, and second most in the Grassland and Nama-Karoo biomes. It was concluded that at family level, the winter and the summer rainfall biomes form two separate groups, the former include the Fynbos and Succulent Karoo and the latter the Savanna, Grassland, Nama-Karoo and Desert biomes. Gibbs Russell (1987) also confirmed that the Nama-Karoo Biome is floristically strongly linked (species, genus and family level) to the Savanna and Desert biomes.

Biodiversity loss in the Forest and Grassland biomes is predicted to be the most dramatic, compared with other biomes (Biggs et al. 2008). Grasslands contain a large grass genetic reservoir and, more important, many grasses contain ecotypes with a range of physiological and ecological adaptations for various conditions (Gibbs Russell 1983; Theunissen 1997; Mannetje et al. 2007). *Eragrostis curvula*, described by Dawson (1987) as a ‘complex of different genotypes’ resulting from the hybridisation between its ancestors and other species of *Eragrostis*, is such an example. Dawson (1987) presented evidence that rainfall is a major driver for the distribution patterns of *E. curvula* ecotypes, for example, the ‘curvula’ type is found mainly in the Savanna and Grassland and the ‘conferta’ group in the Karoo. Van Wyk (1995) pointed out that the widely employed biological species concept in plant taxonomy does not reflect the full extent of genetic diversity contained within such demarcated species. As had also been shown by others (Casetta et al. 2019, and references therein), reliance on the traditional species-based approach to assess genetic resources may result in failure to conserve and/or exploit the full spectrum of diversity present within organisms; this evidently also applies to the grasses. Although the bulk of grass diversity is to be found at the infraspecific level, taxonomists rarely name infraspecific variants, other than subspecies and varieties. This, however, has a financial implication for germplasm collection excursions by forage genebanks when addressing the gaps in existing collections (Parra-Quijano et al. 2012) in that a broader geographical scale should be adopted. However, these authors affirmed that tools, such as eco-geographical land characterization maps, distribution models and gap analysis could locate potential collecting sites and therefore reduce costs.

Evidence presented by Cang et al. (2016) suggested that habitat shifts of grasses as a result of climate change would most probably be too slow to save local populations and subsequently lead to local extinction, consequently placing an increased pressure on seed genebanks to ensure more comprehensive collections (Jarvis et al. 2010). Considering these findings, the principle aim of the current study was to analyse the biogeographical patterns

displayed by Poaceae, indigenous to South Africa, Lesotho and Eswatini and to determine how the resultant broad scale floristic units compare with other such units, i.e. to distinguish ecologically interpretable phytochoria (referred to as grasschoria). Furthermore, the biogeographical significance of both the grasschoria (from this study) and leguminochoria (from Trytsman et al. 2016), in terms of their adaptation to environmental factors, will be used in formulating a collection, conservation, screening and characterization strategy for indigenous genetic resources with pasture and or soil conservation potential for the South African National Forage Genebank (SA-NFG). For the purpose of the current study, ‘southern Africa’ is defined as the Republic of South Africa, Lesotho and Eswatini (formerly Swaziland). The same definition was followed in an earlier study on the distribution of legumes in the subcontinent (Trytsman et al. 2016).

## Materials and methods

### Distribution data

The occurrence records for Poaceae, indigenous to southern Africa, were extracted from two South African databases. The first one is the Botanical Database of Southern Africa (BODATSA), maintained by the South African National Biodiversity Institute (SANBI) and stored in the BRAHMS platform (Le Roux et al. 2017) and the second is PHYTOBAS, a National Vegetation Data Archive database containing botanical survey records for the period between 2003 and 2009 and maintained by the SA-NFG. As previously reported (Trytsman et al. 2020), the merging of the two datasets for the study area resulted in 1 803 quarter degree grid cell (QDGC) records and 685 species. There were eight grass species listed in Fish et al. (2015) that have no occurrence records in any of the two databases, as discussed in Trytsman et al. (2020). For the current study, further editing was done on the original dataset described by Trytsman et al. (2020). QDGCs with only one species were removed from the dataset (i.e. 150 QDGCs) and three species of *Pentaschistis* moved to *Pentameris*, resulting in 1 648 QDGCs and 674 species present within the borders of southern Africa and used in further statistical analyses. The recent taxonomic revision of *Helictotrichon* resulted in the reassignment of all members to *Trisetopsis* (Mashau et al. 2020). The decision to remove one-species QDGCs was based on the results of a previous study where a large non-specific group, termed the Generalist group, was formed by QDGCs containing only one legume species (Trytsman et al. 2016) and therefore treated as noise.

The Agricultural Research Council – Soil, Climate and Water (ARC–SCW 2009), supplied the maps that were used to generate data on climate (mean annual rainfall, mean annual minimum and maximum temperatures) and soil (phosphorus and pH) within each QDGC. The exchangeable sodium percentage (ESP) assigned to each bioregion was sourced from Nell (2010). The biomes map of Rutherford et al. (2006) was used as a base layer for plotting the different grasschoria using the QDGCs assigned to each unique grasschorion. ArcView GIS 3.2, ESRI Inc. 2002 was used to create the layers. For the bioregions, 32.7% of the QDGCs were classed as ecotones and for biomes 23.5%, resulting in a considerable loss of descriptive data. The

abiotic values, on the other hand, were described in real and transitional terms with no loss of QDGCs from the dataset. However, because of the large number of categories defined, especially for the rainfall and soil phosphorus variables, classes were formed by grouping categories together, as presented in Supplementary material 1.

Additional climatology and agrohydrology data (Schulze 2007) were used to describe grasschoria, based on data published in Trytsman (2013). These include notes on, for example, extreme maximum temperatures, net primary production, elevation, days of heavy frost per year, monthly solar radiation and extreme cold spells per year. The USDA Plant Hardiness Zones (PHZs) (Daly et al. 2012) will be cited, because extreme minimum winter temperatures are major contributing factors that determines perennial plant species distribution patterns, as had been confirmed as being a major driver for distinguishing between legume assemblages, indigenous to southern Africa (Trytsman et al. 2016). Glen and Van Wyk (2016) also used this concept within a southern African context and this map was used as reference in the current study to assign PHZs.

### Statistical analyses

A Multivariate Agglomerative Hierarchical Clustering (AHC) was applied to the presence or absence of grass species recorded in the dataset. The cluster analysis was performed using XLSTAT 01-Jun-2010 Software (Addinsoft to MS Excel) and PC-Ord (McCune and Mefford 2006) applying Euclidean distance for dissimilarity and the Ward's linkage method for agglomeration to establish and describe functional grass clusters. The use of both the Euclidean distance and Ward's method in geographical biodiversity studies were highlighted in Trytsman et al. (2016).

In a previous study, Trytsman (2013) concluded that the AHC results were similar, using either the XLStats or PC-Ord programs, but that XLStats groups formed sequentially whereas PC-Ord groups formed disjointedly. Table 1 shows the AHC results for the legume, as well as the grass studies, where the PC-Ord groups, even though similarly formed, were disjointed, more so for the grass than for the legume analyses. However, when comparing the percentage QDGC enclosed in the grasschoria because of using either these programs, it is clear from Table 1 that PC-Ord was more accurate in placing QDGC in defined grasschoria than XLStats. This resulted in less QDGC placed in the Generalist group using PC-Ord than XLStats (25% vs 34%, i.e. 157 QDGCs), therefore it was decided to use the PC-Ord outcome in terms of assigned QDGCs, but the dendrogram from XLStats for its simplicity.

A discriminant analysis (aka Canonical Variates Analysis) was performed on the grasschoria classes with records from the distribution data ( $n = 40\ 234$ ) using Canoco 5 (Ter Braak and Šmilauer 2012). The mean annual rainfall, mean annual maximum and minimum temperature, soil phosphorus and soil pH ( $H_2O$ ) (explanatory variables) expressed on an ordinal scale, with ranks based on classes were used to identify the possible drivers for discrimination between grasschoria (dependent variable). QDGCs assigned with a wide mean annual rainfall range, i.e. 200–1 000 mm (mainly recorded in the Fynbos) were removed from the dataset, given that they are an integral

part of each class. Some 514 records (1.17% of total records) were consequently removed. The significance of the discriminant function was tested using Monte Carlo permutations ( $n = 999$ ).

### Calculations

Where the distribution pattern of a grasschorion did not closely follow a biome border, i.e. where it either overlapped with a bordering biome or did not cover the biome in full, the percentage overlap of the bordering biomes was calculated, using designated degree squares (DS).

Species richness was calculated for each grasschorion by removing duplicate species and then dividing the resulting total number of species by the total number of QDGCs contained in the particular grasschorion. The total number of species occurrences (records) in a grasschorion was calculated and the first 20 species with the highest occurrence were selected as key species. These species are not indicator species, i.e. species whose abundance in a given area is believed to indicate certain environmental or ecological conditions or suitable conditions for a group of other species. Rather, from an agricultural viewpoint, a key species is one with potential as a pasture crop being more widely adapted than a rare species with most likely a narrow range of ecological tolerance. See Supplementary material 2 for a complete list of species recorded in each grasschorion. Species that are present as key species in one grasschorion only, are also noted.

### Terminology

In mapping the southern African flora, a distinction is made between biomes and bioregions. These two mapping units are frequently referred to in the current contribution and are not synonymous. The bioregions map is available in Rutherford et al. (2006), who defined these two concepts as follows:

Biome 'is viewed as a high-level hierarchical (hence simplified) unit having a similar vegetation structure exposed to similar macroclimatic patterns, often linked to characteristic levels of disturbance such as grazing and fire'.

Bioregion 'is a composite spatial terrestrial unit defined on the basis of similar biotic and physical features and processes at the regional scale'. Bioregions are 'subordinate units to a biome'.

## Results and discussion

### Grasschoria of southern Africa

Figure 1 shows the dendrogram of the three main clusters (A–C) and the subdivisions within each main cluster formed by the AHC analysis. Because the resultant grasschoria were largely congruent with the biomes described by Rutherford et al. (2006), the names we have assigned to them largely follow those of the corresponding biomes. Cluster A was subdivided into three grasschoria namely the Grassland (A1), the Indian Ocean Coastal Belt (A2) and the Fynbos (A3), Cluster B with one grasschorion, the Savanna and Cluster C into three grasschoria, namely the Central Arid Region (C1), the Generalist group (C2) and the Succulent Karoo (C3).

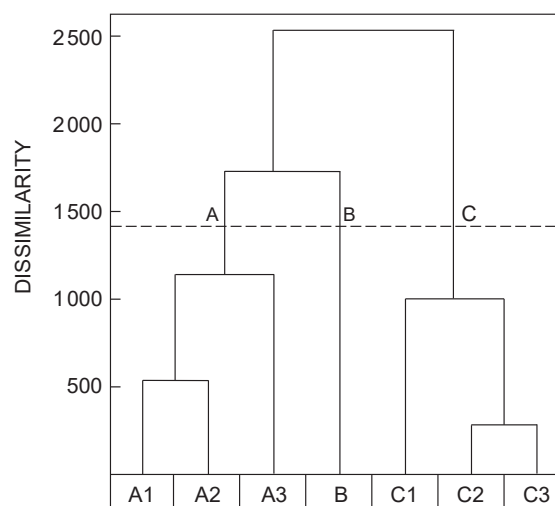
Cluster A is an amalgamation of the Cape Regional Centre of Endemism, the Afri-montane Archipelago-like

**Table 1:** Groups formed by Multivariate Agglomerative Hierarchical Clustering using two different statistical programs, XLStats and PC-Ord, for grass and legume species indigenous to southern Africa (South Africa, Lesotho and Eswatini) and the percentage quarter degree grid cells (QDGCs) enclosed in each of the grasschoria

Leguminochorion (Trytsman 2013)	XLStats group	PC-Ord group
Southern Afromontane	1	7
Albany Centre	2	8
Northern Highveld Region	3	7
Drakensberg Alpine Centre	4	8
Drakensberg Foothill and Coastal Region	5	12
Arid Western Region	6	5
Lower Rainfall Cape Floristic Region	7	6
Central Arid Region	8	3, 4
Generalist Group	9	1
Summer Rainfall Region	10	2
Northern and North-eastern Savanna Region	11	7
Kalahari Bushveld Region	12	7
Higher Rainfall Cape Floristic Region	13	9
Central Bushveld Region	14	10
Subtropical Lowveld and Mopane Region	15	10
Northern Mistbelt Forest	16	11
Grasschorion (Current study)		
Grassland	1	3, 11, 17
Indian Ocean Coastal Belt	2	4, 16
Fynbos	3	7, 13
Savanna	4	1, 8, 15
Central Arid Region	5	2, 5, 10, 14
Generalist	6	9
Succulent Karoo	7	6, 12
% QDGCs		
Grassland	17	18
Indian Ocean Coastal Belt	2	2
Fynbos	5	7
Savanna	14	14
Central Arid Region	21	26
Generalist	34	25
Succulent Karoo	6	7
Total	100	100

Centre of Endemism and the Kalahari-Highveld Transition Zone, as well as the Tongaland-Pondoland Regional Mosaic of White (1983) and the Natal, Eastern Karoo and Cape phytochoria of Linder et al. (2005). Cluster B mainly represents the Zambezi Regional Centre of Endemism of White (1983) and the Zambezi Central, Natal and Kalahari phytochoria of Linder et al. (2005). Lastly, Cluster C is mainly represented by the Karoo-Namib Regional Centre of Endemism and the Kalahari-Highveld Transition Zone of White (1983) and the Namib-Karoo and Eastern Karoo phytochoria of Linder et al. (2005).

Notwithstanding the removal of QDGCs containing one species, a Generalist group formed. This is a non-specific group, i.e. represented in all biomes and bioregions (Table 2) with 53% of assigned QDGCs containing less than five grass species and 81% with less than 10 species (data not presented). Because it was ecologically uninformative, this group will henceforth be excluded from discussions as a grasschorion, although it has been included in a table (see Table 7), because it contributes towards the dataset on grass species richness. The six remaining grasschoria are mapped (Figure 2) and broadly described in Table 2, delineated by the key biomes



**Figure 1:** Dendrogram of southern African (South Africa, Lesotho and Eswatini) grasschoria delimited by Multivariate Agglomerative Hierarchical Clustering. A1: Grassland; A2: Indian Ocean Coastal Belt; A3: Fynbos; B: Savanna; C1: Central Arid Region; C2: Generalist; C3: Succulent Karoo



**Table 2:** Summary of classification of grasschoria (A–C) of southern Africa (South Africa, Lesotho and Eswatini). Key biomes and bioregions from Rutherford et al. (2006) with additional descriptions accessed from published literature. Only key bioregions with representation values higher than 10% within a grasschorion are shown

Cluster	Grasschorion	Key biomes <sup>1</sup> and bioregions <sup>2</sup>	Additional description <sup>3</sup>
A1	Grassland	<sup>1</sup> AT, GL, SAV <sup>2</sup> DG, DHG, MHG, SEG	Bankenveld, N-E Sandy Highveld, <i>Themeda-Festuca</i> Alpine Veld (Ac); Alpine, Moist subtropical (Kr); Forest Biome; Rocky Highveld Grassland (Lo); Drakensberg Alpine Centre (Va)
A2	Indian Ocean Coastal Belt	<sup>1</sup> IOCB <sup>2</sup> IOCB, SES	Moist and humid subtropical (Kr); Coastal Bushveld-Grassland (Lo); Maputaland-Pondoland Region (Va)
A3	Fynbos	<sup>1</sup> F, FB <sup>2</sup> EFR, NWF, SWF, WFR	Coastal Fynbos, Coastal Renosterveld, False Sclerophyllous Bush types (Ac); Karoo Mountain-, Langebaan-, Agulhas Plain-, Southeastern-, Southwestern- and Northwestern Centre (Go); Maritime, Mediterranean (Kr)
B	Savanna	<sup>1</sup> SAV <sup>2</sup> CBV, M, LV	Springbok Flats Turf Thornveld, Sour Bushveld (Ac); Dry and moist tropical, Moist subtropical (Kr); Mopane Bushveld, Mixed Lowveld Bushveld, Mixed Bushveld (Lo)
C1	Central Arid Region	<sup>1</sup> D, GL, NK, SAV <sup>2</sup> BML, DHG, EKB, UK	Kalahari Thornveld (Ac); Cold and warm desert, Dry subtropical (Kr); Kimberley Thorn Bushveld, Kalahari Plateau Bushveld (Lo); Nama-Karoo and Western Savanna biomes (Ru); Griqualand West Centre (Va)
C2	Generalist	All bioregions and biomes; minimally in: <sup>1</sup> FB, IOCB, SK <sup>2</sup> NWF, SWF and NHV	Non-specific
C3	Succulent Karoo	<sup>1</sup> D, FB, SK <sup>2</sup> NHV, NSV, RVK, T- ESK	Namaqualand Broken Veld, Succulent Karoo, Strandveld (Ac); Warm desert (Kr); Gariep Centre (Va)

<sup>1</sup>AT: Albany Thicket; D: Desert; F: Forest; FB: Fynbos; GL: Grassland; IOCB: Indian Ocean Coastal Belt; NK: Nama-Karoo; SAV: Savanna; SK: Succulent Karoo

<sup>2</sup>BML: Bushmanland; CBV: Central Bushveld; DG: Drakensberg Grassland; DHG: Dry Highveld Grassland; EFR: Eastern Fynbos-Renosterveld; EKB: Eastern Kalahari Bushveld; IOCB: Indian Ocean Coastal Belt; LV: Lowveld; M: Mopane; MHG: Mesic Highveld Grassland; NHV: Namaqualand Hardeveld; NSV: Namaqualand Sandveld; NWF: Northwest Fynbos; RVK: Rainshadow Valley Karoo; SEG: Sub-Escarpment Grassland; SES: Sub-Escarpment Savanna; SWF: Southwest Fynbos; T-ESK: Trans-Escarpment Succulent Karoo; UK: Upper Karoo; WFR: West Coast Renosterveld

<sup>3</sup>Ac: Acocks (1988); Lo: Low and Rebelo (1996); Kr: Kruger (1999); Va: Van Wyk and Smith (2001); Go: Goldblatt and Manning (2002); Ru: Rutherford et al. (2006)

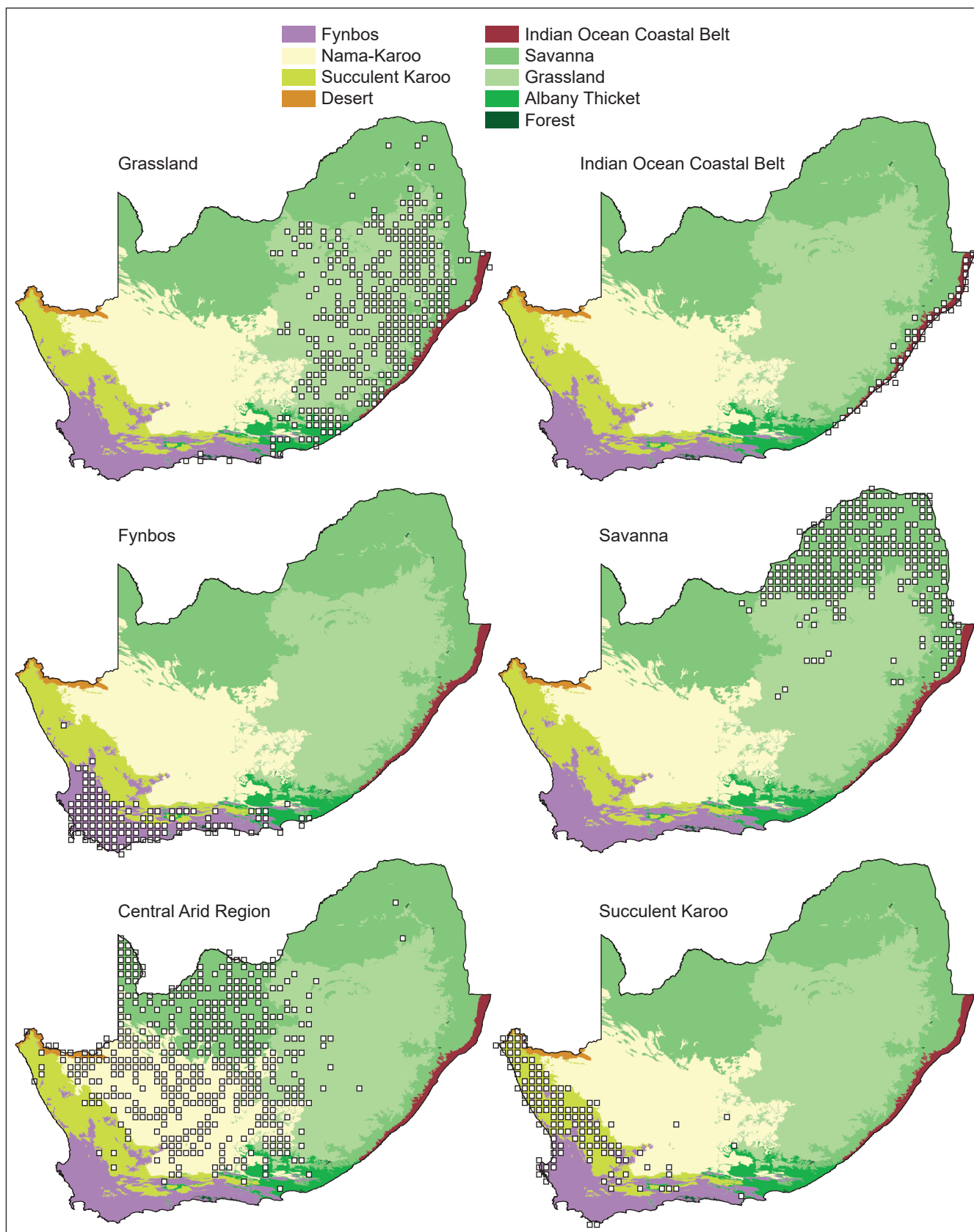
and bioregions defined by Rutherford et al. (2006) with additional vegetational descriptions from Acocks (1988), Low and Rebelo (1996), Kruger (1999), Van Wyk and Smith (2001) and Goldblatt and Manning (2002).

### Grassland (A1)

The Grassland Grasschorion includes grass species mainly found in the Grassland Biome (82%) and more specifically the Mesic Highveld Grassland Bioregion (34%) (see definition in 'Material and methods'), evident from Figure 2 and Table 3. Rutherford et al. (2006) describes this biome with a summer rainfall, cooler elevated interior, and with several plant species to be found only in this region.

The western border of the Grassland Grasschorion does not fully match that of the Grassland Biome (Figure 2). In order to determine the overlap of the Savanna and Central Arid Region grasschoria into the western region of the Grassland Grasschorion, the percentage overlay in designated DS is presented in Table 4. The Central Arid Region Grasschorion represents 81% and the Savanna 8% of the DS bordering the Grassland Biome. The eastward dwarf shrubland expansion concept of the Karoo into grasslands is an accepted theory as a result of either overgrazing or inappropriate land management (Acocks 1953; Meadows 2003) or, perhaps more controversially, hotter, drier conditions with higher incidences in fire and

CO<sub>2</sub> concentrations (Midgley et al. 2008; Masubelele et al. 2014, 2015; Du Toit et al. 2015). Hoffman and Cowling (1990) and Du Toit and O'Conner (2014) claim the reverse, namely that the Nama-Karoo has become grassier with a westward movement of grassland boundaries, because of an apparent increase in rainfall and a shift in seasonality of rainfall, namely from late to early season. Masubelele et al. (2014) also concluded that grass and not dwarf shrub cover increased over a 50-year period in the ecotone between the Grassland and Nama-Karoo biomes. They suggest that an increase in early summer rainfall in the Nama-Karoo Biome and a reduction in stocking rates are factors that could influence this trend. Our study shows that grass species adapted to arid conditions shifted their range into the grassland regions. Indigenous grass species adapted to arid and semi-arid conditions, such as *Aristida congesta*, *Eragrostis lehmanniana*, *Enneapogon scoparius* and *Tragus koelerioides* (Supplementary material 2) were recorded to a large extent in the DS referred to in Table 4. The eastern boundary of this grasschorion follows the Grassland Biome boundary closely, but overlap with the Savanna Biome (south-easterly) and in terms of bioregions more specifically with the Sub-Escarpment Savanna Bioregion. The southern boundary of the Grassland Grasschorion overlaps with the Albany Thicket Biome and will be discussed separately.



**Figure 2:** The grasschoria of southern Africa (South Africa, Lesotho and Eswatini) superimposed on the biomes of South Africa defined by Rutherford et al. (2006)

**Table 3:** Representation percentages of key biomes and bioregions (Rutherford et al. 2006) within grasschoria of southern Africa (South Africa, Lesotho and Eswatini)

Biome	GL	IOCB	Fynbos	SAV	CAR	SK
Albany Thicket	2	4	5		1	
Desert					2	7
Fynbos	2		<b>94</b>			17
Grassland	<b>82</b>	4		7	13	
Indian Ocean Coastal Belt	1	<b>82</b>				
Nama-Karoo					<b>42</b>	7
Savanna	13	10		<b>93</b>	40	
Succulent Karoo			1		2	<b>69</b>
<b>Bioregion</b>						
Albany Thicket	2	3	7		1	
Bushmanland					21	3
Central Bushveld	2			<b>60</b>		
Drakensberg Grassland	12					
Dry Highveld Grassland	13			4	11	
Eastern Fynbos-Renosterveld	2		<b>24</b>			
Eastern Kalahari Bushveld				1	<b>32</b>	
Gariep Desert					2	4
Indian Ocean Coastal Belt	2	<b>85</b>				
Kalahari Duneveld					9	
Knervlakte						5
Lower Karoo					4	3
Lowveld	6			20		
Mesic Highveld Grassland	<b>34</b>			3	1	
Mopane				11		
Namaqualand Sandveld						3
Namaqualand Cape Shrubland			2			
Namaqualand Hardeveld						<b>23</b>
Namaqualand Sandveld						14
North West Fynbos						1
Northwest Fynbos			16			3
Rainshadow Valley Karoo			4		1	10
Richtersveld						6
South Coast Fynbos			5			
South Strandveld			2			
Southern Namib Desert						4
Southwest Fynbos			<b>24</b>			3
Sub-Escarpment Grassland	21					
Sub-Escarpment Savanna	6	12		1		
Trans-Escarpment Succulent Karoo						10
Upper Karoo					18	3
West Coast Renosterveld			12			
West Strandveld			2			5
Western Fynbos-Renosterveld			2			

Note: Bold-formatted values indicate the biome and bioregion with the highest percentage representation in a particular grasschorion. GL: Grassland; IOCB: Indian Ocean Coastal Belt; SAV: Savanna; CAR: Central Arid Region; SK: Succulent Karoo

A summary of the predominant climate and soil characteristics for this grasschorion is given in Table 5. The mean annual rainfall is mainly >800 mm, but also covers regions with <400 mm. Moderate mean annual minimum (<8 °C) and mean annual maximum (25–29 °C) temperatures further denote this grasschorion as an agriculturally highly productive region. The extreme maximum summer temperatures of 36–42 °C recorded in low-lying, westerly parts are further noted for this grasschorion (Supplementary material 3). Species are adapted to soil with low pH (<6.4), low phosphorus content (<10 mg kg<sup>-1</sup>) and to non-sodic soils. This grasschorion represents the USDA PHZs 8 and 9, the hardiness

zones with the lowest mean annual extreme minimum winter temperatures in the study area, namely –12 to –1 °C. Additional information regarding climatology and agrohydrology (Schulze 2007) for all the grasschoria described is shown in Supplementary material 3.

The Grassland Grasschorion has key species in common with all grasschoria, except for the Succulent Karoo, for example, *Eragrostis curvula* and *Themeda triandra* (Table 6). Two species, namely *Aristida junciformis* and *E. capensis*, are key species in the Grassland and Indian Ocean Coastal Belt grasschoria only, whereas *Koeleria capensis* is a key species in the Grassland and Fynbos grasschoria only. High occurrences of different species

**Table 4:** The percentage grasschoria of southern Africa (South Africa, Lesotho and Eswatini) assigned to biomes in designated degree squares (DS)

Biome borders (designated DS)	Grasschorion	Percentage of DS
Grassland/Savanna>Nama-Karoo <sup>1</sup> (2525, 2625, 2725, 2726, 2825, 2925, 3025, 3026)	Grassland	11
	Savanna	8
	Central Arid Region	81
Fynbos/Succulent Karoo <sup>2</sup> (3218)	Fynbos	42
	Succulent Karoo	58
Albany Thicket <sup>1</sup> (3224, 3225, 3226, 3227, 3324, 3325, 3326, 3327)	Grassland	46
	Indian Ocean Coastal Belt	14
	Fynbos	24
	Central Arid Region	16

<sup>1</sup>±86 400 km<sup>2</sup>; <sup>2</sup>±10 800 km<sup>2</sup>

of *Eragrostis* are also noted, with *E. racemosa* and *E. plana* not present as key species in other grasschoria. The distribution patterns of key species *Eragrostis plana*, *Harpochloa falx* and *Tristachya leucothrix* are also known to be predominantly found in the Grassland Biome (Fish et al. 2015). There are 123 grass species recorded in this grasschorion that are endemic/near endemic to southern Africa (Fish et al. 2015) (Supplementary material 4) with *Pentameris basutorum*, *P. exserta*, *P. galpinii* and *P. oreodoxa* strictly confined to the Drakensberg region.

This grasschorion covers the Core Afromontane and Drakensberg Alpine phytochoria of Steenkamp et al. (2005) and the Natal phytochorion of Linder et al. (2005). In a study describing the Leguminosae of southern Africa (Trytsman et al. 2016), the Sourveld (for definition see Trollope et al. 1990) and Mixed Veld Group (that include leguminochoria Southern Afromontane, Albany Centre, Northern Highveld Region, Drakensberg and Alpine Centre) enclosed a similar region to this grasschorion.

### Indian Ocean Coastal Belt (A2)

The Indian Ocean Coastal Belt Biome and Bioregion are almost completely congruent with this grasschorion (82 and 85%, respectively) (Figure 2 and Table 3). The relatively recently distinguished Indian Ocean Coastal Belt Biome (based mainly on floristic and climatic rather than conventional vegetation criteria) is, according to Rutherford et al. (2006), distinct, because it is the 'southernmost extent of the wet, tropical and subtropical seaboard of East Africa'. The Savanna Biome and especially the Sub-Escarpment Savanna Bioregion, minimally overlaps with this grasschorion (10–12%).

High mean annual rainfall (mainly regions with 600–1 000 mm), high mean annual minimum temperatures (>6 °C) and moderate to high mean annual maximum temperatures (25–35 °C) represent the climatic conditions of this grasschorion. The soils are predominantly acidic (pH<6.4) with low P content and non-sodic. This grasschorion represents USDA PHZs 11 and 12, the zones with the highest mean annual extreme minimum winter temperatures in the study area, namely 4–16 °C. Information from Schulze (2007) indicates that this is mainly a sourveld and frost-free region, enclosing tropical areas (Supplementary material 3). The fact that this grasschorion lies in a frost-free area with extreme maximum temperatures of >40 °C could be

important when selecting grass species for further agronomic evaluation.

Key species present in the Indian Ocean Coastal Belt and other grasschoria (not mentioned under Grassland), is *Ehrharta erecta* (Fynbos) and *Panicum maximum* (Savanna), with both *Melinis repens* and *Setaria sphacelata* having a high occurrence in the Indian Ocean Coastal Belt and Savanna grasschoria (Table 6). *Dactyloctenium australe*, *Stenotaphrum secundatum* and *Sporobolus virginicus*, are species noted for their presence in exclusively coastal areas, the former two species mainly in the eastern coastal regions and the latter along most of southern Africa's coastlines (Fish et al. 2015). Only 35 grass species in this grasschorion were recorded as being endemic/near-endemic to southern Africa (Fish et al. 2015) (Supplementary material 4) with *Panicum sancta-luciense* exclusively found in the Maputaland Centre (Trytsman et al. 2020). Hoveka et al. (2020) noted the Maputaland-Pondoland-Albany Hotspot, defined by Steenkamp et al. (2004), to have a high projected endemic richness and a call is made to correct previously biased sampling in order to capture South Africa's extraordinary diversity.

The Indian Ocean Coastal Belt Grasschorion forms part of the Tongaland-Pondoland Region of Goldblatt (1978), the Maputaland-Pondoland Region of Van Wyk and Smith (2001), the Natal phytochorion of Linder et al. (2005) and the Core Afromontane and Greater Maputaland of Steenkamp et al. (2005). This grasschorion is almost congruent with the Coastal Region Leguminochoria described by Trytsman et al. (2016).

### Fynbos (A3)

The Fynbos Grasschorion is largely congruent with the Fynbos Biome, especially the Eastern Fynbos–Renosterveld and Southwest Fynbos bioregions (Figure 2 and Table 3).

The mean annual rainfall for the Fynbos Grasschorion lies predominantly between 200 and 600 mm (Table 5). A minimum mean annual temperature of 2–8 °C and maximum of 25–29 °C could be expected in this region with USDA PHZs 10 and 11 (mean annual extreme minimum winter temperature –1 to 10 °C). A wide range of soil pH is noted within this grasschorion, varying from the range <6.4 to 6.5–8.4. The soil P status is mainly grouped in the <10 range, but 29% lies in the 5–20 range. A relatively high percentage of soils are medium sodic, indicating poor



**Table 5:** The predominant climate and soil conditions associated with grasschoria of southern Africa (South Africa, Lesotho and Eswatini) shown as a percentage and USDA Plant Hardiness Zones (PHZs) (Daly et al. 2012; Glen and Van Wyk 2016). Climatic conditions include mean annual rainfall (MAR), mean minimum and maximum temperatures (Temp Min and Temp Max). The soil properties shown are pH level, phosphorus content and sodicity

MAR (mm)	<400	200–600	600–1 000	>800	
Grassland	25	23	13	39	
Indian Ocean Coastal Belt	3	32	51	14	
Fynbos	24	50	21	5	
Savanna	2	24	51	23	
Central Arid Region	58	36	4	2	
Succulent Karoo	42	26	15	17	
Temp Max (°C)	<27	25–29	27–35	>33	
Grassland	23	54	23	0	
Indian Ocean Coastal Belt	0	59	41	0	
Fynbos	9	68	23	0	
Savanna	2	32	65	2	
Central Arid Region	1	9	64	26	
Succulent Karoo	1	36	61	2	
Temp Min (°C)	<2	0–4	2–8	>6	PHZs
Grassland	31	26	29	14	8, 9
Indian Ocean Coastal Belt	0	0	10	90	11, 12
Fynbos	0	14	63	23	10, 11
Savanna	7	9	56	28	10, 11
Central Arid Region	49	27	20	3	8, 9
Succulent Karoo	8	11	40	40	10, 11
Soil pH (H <sub>2</sub> O)	<6.4	5.5–7.4	6.5–8.4	>7.5	
Grassland	51	32	16	1	
Indian Ocean Coastal Belt	62	34	3	0	
Fynbos	31	31	30	7	
Savanna	38	30	29	3	
Central Arid Region	2	6	41	50	
Succulent Karoo	1	9	45	45	
Soil P (mg kg <sup>-1</sup> )	<10	5–20	10–35	20–35	>35
Grassland	86	8	6	0	0
Indian Ocean Coastal Belt	93	3	3	0	0
Fynbos	44	29	16	8	2
Savanna	87	5	8	0	0
Central Arid Region	39	7	18	29	7
Succulent Karoo	6	9	26	38	21
Sodicity (percentage exchangeable sodium)	Non-sodic (1–6)	Medium (6–15)	Highly (>15)		
Grassland	96	4	0		
Indian Ocean Coastal Belt	100	0	0		
Fynbos	62	34	3		
Savanna	100	0	0		
Central Arid Region	85	12	2		
Succulent Karoo	12	51	37		

infiltration and drainage, with resultant loss of soil (Qadir and Oster 2004). This grasschorion lies in an all year to winter rainfall area, mostly frost-free (Supplementary material 3).

The Fynbos Grasschorion has many key species in common with the Succulent Karoo, namely *Bromus pectinatus*, *Ehrharta calycina*, *Pentameris airoides*, *Stipagrostis zeyheri* and *Tribolium hispidum* (Table 6). Two genera, namely *Ehrharta* and *Pentameris*, are well presented as key species. Key species unique to the Fynbos Grasschorion are *Cymbopogon marginatus*, *Ehrharta capensis*, *Ehrharta ramosa*, *Ehrharta villosa*, *Pentameris curvifolia* and *Pentameris eriostoma* (Fish et al. 2015). Similarly, as had been the case with the leguminochoria described by Trytsman et al. (2016), many Fynbos key

species are not associated with any other grasschoria and hence reflects its unique floristic composition. This grasschorion contains the most grass species endemic/near endemic to southern Africa (164 species) (Fish et al. 2015) with 30 species of *Pentameris* exclusively recorded in the Fynbos (Supplementary material 4).

This grasschorion forms part of the Cape Region phytogeographical region (Goldblatt 1978), the Worcester-Robertson Karoo and Hantam-Roggeveld Centres (Van Wyk and Smith 2001), the Cape phytocorion (Linder et al. 2005) and the North-western and South-eastern Fynbos (Steenkamp et al. 2005). This grasschorion is almost congruent to the Lower and Higher-Rainfall Cape Floristic Region leguminochoria described in Trytsman et al. (2016).

**Table 6:** List of key species recorded in grasschoria of southern Africa (South Africa, Lesotho and Eswatini) with the total number of occurrences (# Occ) of the individual species within each grasschorion. Key species followed by a bullet (•) are present as key species in the designated grasschorion only

Grassland	# Occ	Fynbos	# Occ	Central Arid Region	# Occ
<i>Alloteropsis semialata</i> •	122	<i>Bromus pectinatus</i>	53	<i>Aristida adscensionis</i>	147
<i>Andropogon appendiculatus</i> •	136	<i>Cymbopogon marginatus</i> •	57	<i>Aristida congesta</i>	229
<i>Aristida congesta</i>	123	<i>Ehrharta calycina</i>	92	<i>Chloris virgata</i>	114
<i>Aristida junciformis</i>	146	<i>Ehrharta capensis</i> •	49	<i>Digitaria eriantha</i>	165
<i>Brachiaria serrata</i> •	116	<i>Ehrharta erecta</i>	50	<i>Enneapogon desvauxii</i> •	157
<i>Elionurus muticus</i> •	149	<i>Ehrharta ramosa</i> •	57	<i>Enneapogon scaber</i>	116
<i>Eragrostis capensis</i>	190	<i>Ehrharta villosa</i> •	48	<i>Eragrostis curvula</i>	176
<i>Eragrostis curvula</i>	256	<i>Eragrostis curvula</i>	84	<i>Eragrostis lehmanniana</i> •	215
<i>Eragrostis plana</i> •	136	<i>Festuca scabra</i> •	68	<i>Eragrostis obtusa</i> •	126
<i>Eragrostis racemosa</i> •	150	<i>Koeleria capensis</i>	55	<i>Fingerhuthia africana</i>	142
<i>Harpochloa falx</i> •	121	<i>Pentameris airoides</i>	61	<i>Heteropogon contortus</i>	137
<i>Heteropogon contortus</i>	142	<i>Pentameris curvifolia</i> •	64	<i>Melinis repens</i>	104
<i>Hyparrhenia hirta</i> •	147	<i>Pentameris eriostoma</i> •	74	<i>Sporobolus fimbriatus</i> •	141
<i>Koeleria capensis</i>	114	<i>Pentameris pallida</i> •	150	<i>Stipagrostis ciliata</i>	138
<i>Melinis nervigumis</i> •	134	<i>Stipagrostis zeyheri</i>	59	<i>Stipagrostis obtusa</i>	158
<i>Microchloa caffra</i> •	118	<i>Tenaxia stricta</i> •	84	<i>Stipagrostis uniplumis</i> •	153
<i>Setaria incrassata</i>	118	<i>Themeda triandra</i>	57	<i>Themeda triandra</i>	116
<i>Setaria sphacelata</i>	158	<i>Tribolium echinatum</i> •	47	<i>Tragus berteronianus</i>	119
<i>Themeda triandra</i>	194	<i>Tribolium hispidum</i>	79	<i>Tragus koelerioides</i> •	109
<i>Tristachya leucothrix</i> •	134	<i>Tribolium uniola</i> •	77	<i>Tragus racemosus</i> •	121
Percentage of total number of records	27		31		36
Indian Ocean Coastal Belt		Savanna		Succulent Karoo	
<i>Aristida junciformis</i>	26	<i>Aristida adscensionis</i>	124	<i>Bromus pectinatus</i>	64
<i>Cymbopogon nardus</i> •	31	<i>Aristida congesta</i>	210	<i>Chaetobromus involucreatus</i> •	60
<i>Dactyloctenium australe</i> •	27	<i>Brachiaria nigropedata</i> •	124	<i>Cladoraphis cyperoides</i> •	28
<i>Digitaria natalensis</i> •	31	<i>Chloris virgata</i>	132	<i>Cladoraphis spinosa</i> •	34
<i>Diheteropogon amplexens</i> •	25	<i>Cynodon dactylon</i> •	131	<i>Ehrharta brevifolia</i> •	31
<i>Ehrharta erecta</i>	25	<i>Digitaria eriantha</i>	209	<i>Ehrharta calycina</i>	90
<i>Eleusine coracana</i> •	28	<i>Eragrostis curvula</i>	158	<i>Ehrharta delicatula</i> •	49
<i>Eragrostis capensis</i>	33	<i>Eragrostis superba</i> •	162	<i>Ehrharta longiflora</i> •	28
<i>Eragrostis curvula</i>	31	<i>Eustachys paspaloides</i> •	124	<i>Ehrharta triandra</i> •	33
<i>Hyparrhenia filipendula</i> •	27	<i>Heteropogon contortus</i>	196	<i>Enneapogon scaber</i>	33
<i>Ischaemum fasciculatum</i> •	27	<i>Melinis repens</i>	185	<i>Fingerhuthia africana</i>	39
<i>Leersia hexandra</i> •	26	<i>Panicum maximum</i>	195	<i>Pentameris airoides</i>	44
<i>Melinis repens</i>	26	<i>Perotis patens</i> •	125	<i>Pentameris patula</i> •	27
<i>Panicum deustum</i> •	31	<i>Pogonarthria squarrosa</i> •	161	<i>Schismus barbatus</i> •	80
<i>Panicum maximum</i>	32	<i>Schmidtia pappophoroides</i> •	127	<i>Schismus schismoides</i> •	37
<i>Setaria sphacelata</i>	35	<i>Setaria incrassata</i>	143	<i>Stipagrostis ciliata</i>	39
<i>Sporobolus africanus</i> •	34	<i>Setaria sphacelata</i>	136	<i>Stipagrostis obtusa</i>	31
<i>Sporobolus virginicus</i> •	26	<i>Themeda triandra</i>	151	<i>Stipagrostis zeyheri</i>	30
<i>Stenotaphrum secundatum</i> •	28	<i>Tragus berteronianus</i>	124	<i>Tribolium hispidum</i>	29
<i>Themeda triandra</i>	26	<i>Urochloa mosambicensis</i> •	131	<i>Tribolium tenellum</i> •	28
Percentage of total number of records	24		22		52

### Savanna (B)

The Savanna Grasschorion lies largely in the Savanna Biome, especially in the Central Bushveld Bioregion with the Lowveld Bioregion listed as a minor component (Figure 2 and Table 3). The Savanna Biome is the summer rainfall part of the largest African biome, as described by Rutherford et al. (2006).

The mean annual rainfall in this grasschorion is mainly within the 600–1 000 mm range and the mean annual minimum and maximum temperatures are 2–8 °C and 27–35 °C, respectively, with USDA PHZs 10 and 11 (mean annual extreme minimum winter temperature –1 to 10 °C) (Table 5). Soils are generally acidic, low in phosphorus and non-sodic. This grasschorion has had 16 occurrences of heat waves of >30 °C on three or more consecutive days per year in some areas (Supplementary 3).

The Savanna has several key species in common with the Central Arid Region Grasschorion namely *Aristida adscensionis*, *Chloris virgata*, *Digitaria eriantha* and *Tragus berteronianus* (Table 6). The only key species with a distribution range almost exclusively in the Savanna is *Urochloa mosambicensis* (Fish et al. 2015), whereas many key species are present in both the Savanna and Central Arid Region grasschoria. At least 82 grass species in the Savanna Grasschorion are endemic/near-endemic to southern Africa (Fish et al. 2015) (Supplementary material 4), with *Enneapogon spathaceus*, *Melinis drakensbergensis* and *Sorghastrum nudipes* exclusively recorded here.

This grasschorion is included in the Zambezi and the Tongaland-Pondoland Regions (Goldblatt 1978), the Zambezi-central (Linder et al. 2005). The Greater

Maputaland phytoschorion of Steenkamp et al. (2005) covers the eastern part of this grasschorion. The Northern and North-eastern Savanna Region Leguminoschorion described by Trytsman et al. (2016) is almost congruent to this grasschorion.

### Central Arid Region (C1)

This grasschorion forms in the Nama-Karoo Biome, as well as the eastern part of the Savanna Biome (Figure 2 and Table 3). It is, however, also clear from this table that the more arid bioregions defined by Rutherford et al. (2006), namely the Eastern Kalahari Bushveld, Bushmanland and Kalahari Duneveld together with the Upper and Lower Karoo connects this grasschorion. The Nama-Karoo Biome is described as mainly a summer rainfall region with a low species richness (Rutherford et al. 2006), although in our view species richness and endemism is quite high for this biome. The low occurrence of  $C_3$  grass species in the western compared with the eastern parts of the Savanna Biome (Trytsman et al. 2020) could contribute to the inclusion of this western region in the Central Arid Region Grasschorion rather than with the Savanna Biome.

The low mean annual rainfall of <400 mm recorded in this grasschorion (Table 5) is reflected in the climatology description as a semi-arid to arid region, with USDA PHZs 8 and 9 (mean annual extreme minimum winter temperature  $-1$  to  $-12$  °C). A low mean annual minimum ( $<2$  °C) and relatively high mean annual maximum temperature (27–35 °C) is also noted in Table 5. The largely high soil pH ( $>7.5$ ), low soil phosphorus ( $<10$  mg  $kg^{-1}$ ) and non-sodic soil described here are expected, considering the low mean annual rainfall.

The Central Arid Region has four key species in common with the Succulent Karoo, namely *Enneapogon scaber*, *Fingerhuthia africana*, *Stipagrostis ciliata* and *Stipagrostis obtusa*. *Enneapogon desvauxii* and *Tragus koelerioides* are key species mainly found in the Central Arid Region Grasschorion (Table 6). A total of 107 grass species in the Central Arid Region Grasschorion are endemic/near endemic to southern Africa (Fish et al. 2015) (Supplementary material 4), with four *Eragrostis* spp. exclusively documented here, namely *Eragrostis brizantha*, *E. macrochlamys*, *E. pilgeriana* and *E. truncata* (Fish et al. 2015).

The Central Karoo phytoschorion of Steenkamp et al. (2005) covers this grasschorion well, with the eastern border, similar to the current study, also extending into the Grassland Biome. Only seed plant genera, endemic to the southern African region, were included in this study and Poaceae was represented by 60 species. According to Gibbs Russell (1987) the Nama-Karoo Biome has stronger floristic links with the Savanna and Desert biomes at species, genus and family level than with the Succulent Karoo (species, family level) and fynbos (genus level). The Karoo-Namib Region and the Kalahari-Highveld Transition Zone phytogeographical regions of Goldblatt (1978), Griqualand West Centre (Van Wyk and Smith 2001), the Namib-Karoo and Eastern Karoo phytoschoria (Linder et al. 2005) and the Central Arid Region Leguminoschorion of Trytsman et al. (2016) are represented in this grasschorion.

### Succulent Karoo (C3)

The Succulent Karoo Biome is well represented within this grasschorion; whereas the Fynbos Biome is also represented to a lesser extent (Figure 2 and Table 3). Rutherford et al. (2006) describes this biome as the most species rich semi-desert and with the highest diversity of succulents in the world. The Namaqualand Hardeveld and Namaqualand Sandveld bioregions are the two main bioregions represented in this grasschorion.

A low mean annual rainfall (<400 mm) with relatively high mean annual minimum (2–8 °C to  $>6$  °C) and maximum (27–35 °C) temperatures denotes the Succulent Karoo Grasschorion (Table 5). This grasschorion includes USDA PHZs 10 and 11 (mean annual extreme minimum winter temperature of  $-1$  °C to 10 °C), similar to the Fynbos and Savanna grasschoria. Schulze (2007) described this region as mainly a winter rainfall area with extremely high maximum temperatures, exceeding 44 °C (Supplementary material 3). The high soil pH ( $>6.5$ ) and phosphorus content (mainly 20–35 mg  $kg^{-1}$ ) is to be expected in the light of the region's low mean rainfall (Smet and Ward 2006). This grasschorion is also noteworthy for its medium to highly sodic soils.

The Succulent Karoo Grasschorion has key species in common with the bordering Fynbos and Central Arid Region grasschoria, as listed earlier (Table 6). Most of the key species in this grasschorion have distribution patterns exclusively in the Succulent Karoo, for example, species of *Cladoraphis* and *Ehrharta* (Fish et al. 2015). At least 104 grass species in this grasschorion are endemic/near endemic to southern Africa (Fish et al. 2015) (Supplementary material 4), with *Stipagrostis dregeana*, *S. lutescens* and *S. schaeferi* exclusively found in the coastal border with Namibia.

The Northern and Southern Succulent phytoschoria of Steenkamp et al. (2005) are more or less congruent with this grasschorion. The northern border of the Fynbos Biome included in this grasschorion, instead of the Fynbos Grasschorion, are similarly defined by Steenkamp et al. (2005) as part of the Southern Succulent Karoo phytoschorion. Table 4 indicates that 58% of the 3218 DS that fall mainly within the Fynbos biome, linked with the Succulent Karoo Grasschorion. The Karoo-Namib phytogeographical region (Goldblatt 1978), the Namaqualand-Namib Domain (Cowling et al. 1998), the Gariep, Kamiesberg and Knersvlakte Centres (Van Wyk and Smith 2001), the Namib-Karoo phytoschorion (Linder et al. 2005) and the Arid Western Region (Trytsman et al. 2016) largely represent this grasschorion.

### Desert, Forest, Nama-Karoo and Albany biomes

The minor Desert and Forest biomes were not resolved as grasschoria. The scale of the current study (1 648 QDGCs included), compared with the low number of QDGCs enclosed by the Desert (represented by  $<1.1\%$  QDGCs) and Forest (represented by  $<0.2\%$  QDGCs) biomes most likely resulted in their exclusion in a study based on a single plant family, as in the case of the current one. The Desert Biome, which contains at least 62 grass species with numerous species of *Ehrharta*, *Eragrostis* and *Stipagrostis* present (Fish et al. 2015), were included

in the Succulent Karoo Grasschorion. The Forest Biome are represented in the Grassland, Indian Ocean Coastal Belt, Savanna and Fynbos grasschoria and accordingly depends on the location of the relict forest patches and the matrix vegetation (e.g. fynbos or grassland) of the particular QDGC in which it is located. Typical grass species found in the Forest Biome are *Stipa dregeana*, *Oplismenus hirtellus*, *Brachypodium flexum* and *Setaria megaphylla* (Fish et al. 2015), with the former the widest and the latter the narrowest distribution pattern of those mentioned. The highest collection intensities of forest species, as shown in Figure 3, are recorded along the coastal areas (Indian Ocean Coastal Grasschorion), along the transitional zone between the Grassland and Savanna grasschoria and the in Northern Mistbelt Forest (Mucina and Geldenhuys 2006). Some of these forest grasses are occasionally found in other biomes but then microclimatic pockets, reminiscent of a forest habitat, often exist and therefore the possibility that such outlier distributions may include distinct ecotypes is most likely. The Nama-Karoo Biome forms part of the Central Arid Region, as is also the case with the leguminoschoria (Trytsman et al. 2016), with species, for example, *Sporobolus nebulosus* and *Stipagrostis fastigiata* found in the Nama-Karoo Biome (Fish et al. 2015).

The Albany Thicket Biome, also not resolved as a distinct grasschorion, is part of a region described as a complex transition zone with major vegetation formations (Lubke et al. 1986) where floristic elements of many other regions converge (Van Wyk and Smith 2001). According to Rutherford et al. (2006), the Albany Thicket Biome has an unusual floristic and evolutionary ancient nature in the southern region. As indicated in Table 4, four grasschoria converge in this biome, largely the Grassland Grasschorion (46%), followed by the Fynbos Grasschorion (24%). At least 239 grass species were recorded in the Albany Thicket Biome with *Diheteropogon filifolius*, *Eragrostis obtusa*, *Leptochloa eleusine*, *Panicum deustum*, *Sporobolus nitens*, *Stipa dregeana* var. *dregeana* and *Tribolium curvum* more or less confined to this region (Fish et al. 2015). According to Potts et al. (2015), the Albany Subtropical Thicket–Nama-Karoo boundary is one of the least researched boundaries in South Africa. The earlier indigenous legume study, in contrast to this study, distinguished an Albany Centre Leguminoschorion with a high legume species richness (Trytsman et al. 2016).

#### **Species richness, species range, growth form and species association**

Table 7 presents relevant information on grass species richness and the highest number of grasses collected in the QDGCs within each grasschorion. Even though the Generalist cluster (C2 in Figure 1) is affirmed a residual group, it does largely contribute to the dataset presented in Table 7. The smallest grasschorion, namely the Indian Ocean Coastal Belt (2.4% of QDGCs) has the highest grass species richness (56.2), followed by the Savanna Grasschorion (52.7), whereas the Central Arid Region and the Succulent Karoo grasschoria have the lowest, 17.4 and 12.4, respectively. The Indian Ocean Coastal Belt and Savanna grasschoria were recorded as having predominantly medium to high mean annual rainfall

(Table 5) and the Central Arid Region and Succulent Karoo grasschoria both a low rainfall range. Species richness has been positively correlated with water availability (Pausas and Austin 2001; Whittaker et al. 2007; Li et al. 2013) and Visser et al. (2012) confirmed that apart from precipitation, temperature, fire frequency and grazing pressure, it strongly influence the species richness of some C<sub>4</sub> grass lineages.

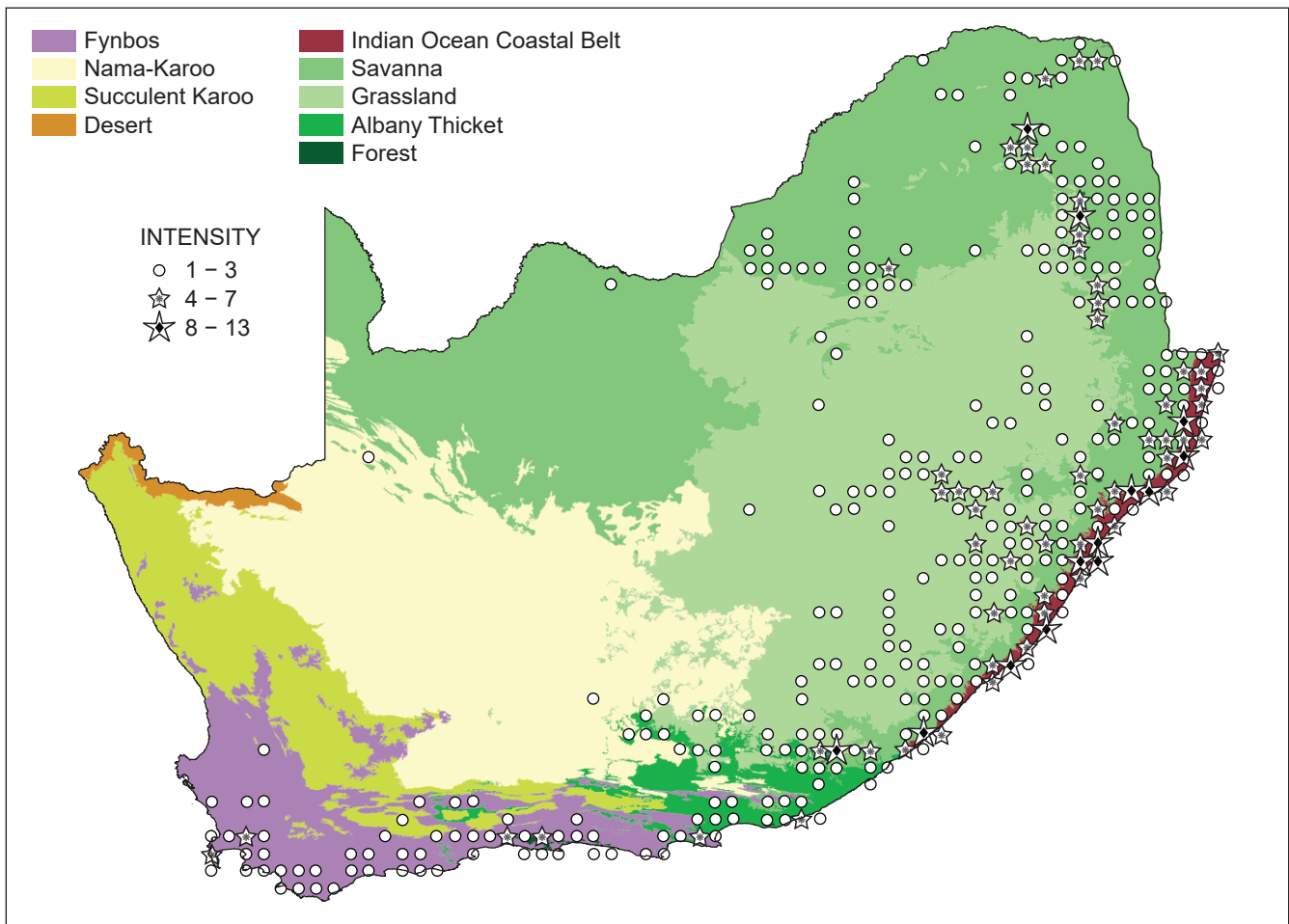
The highest number of grass species per QDGC is recorded in the Savanna Grasschorion (Table 7) followed by the Indian Ocean Coastal Belt, Grassland and Fynbos grasschoria with relatively similar figures. These grasschoria encloses major cities, namely Mbombela and Pretoria (Savanna), Durban (Indian Ocean Coastal Belt), Bloemfontein (Grassland) and Cape Town (Fynbos). Grasses in QDGCs near these urban areas were usually well represented as herbarium specimens. Such excessive sampling owing to geographical bias limits the use of herbarium collection data, as was also highlighted by Fish and Steyn (2002), Robertson and Barker (2006) and De la Estrella et al. (2012). Considering the richness of the southern African flora and the fact that many QDGCs are not optimally sampled, geographical bias in collecting not only leads to an increase in the number of specimens per species, but also an increase in the number of species. The Succulent Karoo Grasschorion does not enclose any densely populated urban areas.

Most of the growth forms (as described by Gibbs Russell et al. 1990) listed in Table 8 is represented in all the grasschoria, with tufted, rhizomatous/tufted and rhizomatous the most commonly found forms. Genera mostly represented by these growth forms are *Eragrostis*, *Hyparrhenia* and *Sporobolus*, respectively. The more unusual grass growth forms, for example, tufted/trailing, rhizomatous/woody, cushion/tufted, geophyte growth form is present in especially the Fynbos Grasschorion. Genera with members representing these growth forms are *Ehrharta*, (rhizomatous/woody), *Pentameris* (all mentioned forms) and *Tribolium* (tufted/trailing). The tufted growth form was shown to be an attribute of the majority of grass pasture species (Trytsman et al. 2020) and therefore, together with rhizomatous grasses, an important consideration in prioritising future collection and conservation efforts.

The percentage annuals found in the more mesic grasschoria (e.g. Grassland and Indian Ocean Coastal Belt) are lower than in the more arid grasschoria (e.g. Central Arid Region and Succulent Karoo) (Table 8). Gibbs Russell et al. (1990) stated that not only are perennial grasses more abundant in mesic regions and annuals in the dry western region, but that some species behave as perennials in more mesic regions and as annuals in arid regions, giving the example of *Fingerhuthia africana* (perennial/occasional annual) and *Centropodia glauca* (annual/weak perennial).

The environmental variables significantly discriminate between grasschoria (pseudo- $F = 3\ 627$ ,  $p = 0.001$ ) with the first four axes individually accounting for 59.9%, 19.5%, 15.3%, and 5.1%, respectively, and cumulatively, 99.8% of the total variability (Table 9). The predictors, mean annual rainfall and soil pH, followed by mean annual minimum and maximum temperature, then soil P, had the strongest





**Figure 3:** The collection intensity of grass forest species, indigenous to southern Africa (South Africa, Lesotho and Eswatini), superimposed on the biomes of South Africa as defined by Rutherford et al. (2006)

**Table 7:** Quarter degree grid cell (QDGC) ratios, species richness and the highest number of species recorded in a QDGC of grassschoria of southern Africa (South Africa, Lesotho and Eswatini). Species richness = #Species/#QDGC within a grassschorion

Grassschorion	% QDGC	Species richness	Highest #spp. in given QDGC
Grassland	18.4	32.8 ± 23.9	131 (2929BB)
Indian Ocean Coastal Belt	2.4	56.2 ± 26.9	139 (2930DD)
Fynbos	6.6	36.2 ± 21.9	127 (3318CD)
Savanna	14.4	52.7 ± 34.7	234 (2528CA)
Central Arid Region	25.6	17.4 ± 15.5	85 (2926AA)
Generalist	25.4	6.4 ± 4.2	26 (2929AA)
Succulent Karoo	7.2	12.4 ± 7.8	42 (3119AC)
Total/Mean	100.0	34.6	126

correlations ( $p = 0.001$ ) with the first canonical variate axis in the discriminant analysis whereas mean annual minimum temperature was the most influential variable on the second axis (Table 9). The main gradient distinguishing grassschoria was a rainfall-temperature gradient, with the Grassland and Indian Ocean Coastal Belt grassschoria occurring at the wettest, cool end of the gradient, Succulent Karoo and Central Arid Region in the driest, hottest regions, and

Fynbos and Savanna grassschoria at intermediate rainfall and temperatures (Figure 4). The latter two grassschoria were further distinguished by occurring in areas with higher than mean annual minimum temperatures. Soils tended to be basic, with higher P content towards the dry, hot end of the environmental gradients.

The Indian Ocean Coastal Belt Grassschorion contain species adapted to high mean annual rainfall and low

**Table 8:** The different growth forms present in the grasschoria of southern Africa (South Africa, Lesotho and Eswatini) as described by Gibbs Russell et al. (1990) with the number of annual and perennial grass species recorded in each grasschorion

Growth form	GL	IOCB	FB	SAV	CAR	SK
Tufted	244	141	183	261	191	121
Rhizomatous/tufted	86	50	42	76	48	23
Rhizomatous	38	23	22	39	31	17
Trailing	10	10	8	11	4	2
Rhizomatous/stoloniferous	10	6	6	13	6	5
Stoloniferous	10	8	6	8	8	3
Stoloniferous/tufted	9	4	6	9	7	3
Hydrophyte/rhizomatous/stoloniferous	8	4	4	6	3	3
Hydrophyte/rhizomatous/stoloniferous/tufted	3	3	3	3	2	2
Hydrophyte/stoloniferous/tufted	4	3	3	5	1	
Hydrophyte/tufted	4	1	4	2	4	1
Rhizomatous/stoloniferous/tufted	2	3	1	5	4	1
Hydrophyte/rhizomatous/tufted	2	3	1	3	3	1
Cushion	2		6	1	1	1
Hydrophyte/trailing	3	3		3		
Hydrophyte/rhizomatous	2	1	1	3	1	
Tufted/trailing			4			2
Hydrophyte	2			2		
Rhizomatous/woody	1		1			1
Cushion/tufted			2			
Geophyte			1		1	
Life cycle						
Annuals	55	41	44	80	63	39
Perennials	349	201	238	335	228	130
% Annuals	14	17	16	19	22	23

GL: Grassland; IOCB: Indian Ocean Coastal Belt; FB: Fynbos; SAV: Savanna; CAR: Central Arid Region; SK: Succulent Karoo

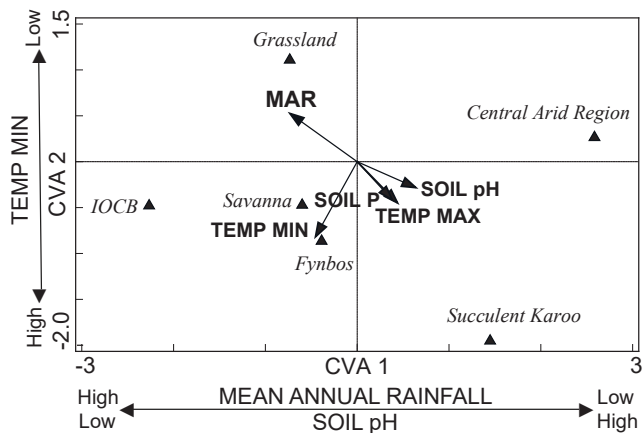
**Table 9:** Correlations between predictor environmental variables and canonical variate axes in a discriminant analysis of southern African (South Africa, Lesotho and Eswatini) grasschoria

Variable	Canonical variate axis			
	1	2	3	4
Mean annual rainfall (mm)	-0.684	0.280	-0.083	0.100
Mean annual maximum temperature (°C)	0.464	-0.271	-0.393	0.029
Mean annual minimum temperature (°C)	-0.470	-0.484	-0.030	0.085
Soil phosphorus (mg kg <sup>-1</sup> )	0.427	-0.265	0.298	0.174
Soil pH (H <sub>2</sub> O)	0.655	-0.165	0.009	0.130

soil pH, the Central Arid Region Grasschorion species to low mean annual rainfall and high soil pH and the other grasschoria species with an intermediate adaptation (Figure 4). The Grassland and the Succulent Karoo grasschoria contains grass species adapted to extremes in terms of mean annual minimum temperatures, the former to low and the latter to high mean annual minimum temperatures, and the other grasschoria with intermediate adaptations. The importance of moisture and temperature as abiotic factors influencing the distribution of African vegetation were reported by Skarpe (1986), Ruiz-Vega (1994), Bond et al. (2003), Greve (2011) and Bocksberger et al. (2016). The growth responses of grasses to climate, soil and management factors to improve their adaptive traits through selection have also been a major target for pasture researchers worldwide (Chapman et al. 2011; Truter et al. 2015).

## Conclusion

The boundaries of grasschoria in southern Africa distinguished by agglomerative hierarchical clustering are mainly congruent with existing biome vegetation units, with the exception of the Albany Thicket, Desert and Forest biomes that were not resolved. This lack of resolution is, at least to some extent, ascribed to the scale of the relatively large Operational Taxonomic Units (in this case QDGC) used in the current study. The Grassland, Indian Ocean Coastal Belt and Fynbos grasschoria formed a main cluster, found in relatively high rainfall regions. The Savanna Grasschorion formed as a separate main cluster in the eastern part of the Savanna Biome and the third main cluster, namely the Central Arid Region and Succulent Karoo grasschoria in the arid to semi-arid regions of southern Africa. The high number of grass species in



**Figure 4:** The position of six southern African (South Africa, Lesotho and Eswatini) grassschoria along the first two canonical variate axes in a discriminant analysis. Arrows indicate the direction of influence of the environmental variables: MAR: mean annual rainfall; Temp Max: mean annual maximum temperature; Temp Min: mean annual minimum temperature; soil pH and soil phosphorus (P). IOCB: Indian Ocean Coastal Belt

the Savanna Grassschorion, i.e. within the QDGC 2528CA, is proposed as a starting point for collecting seed of grass species identified as important pasture crops by the SA-NFG. In the light of anticipated environmental change, an effort to collect and evaluate the 107 endemic/near endemic species to southern Africa associated with the Central Arid Region is proposed.

The western boundary of the Grassland Grassschorion does not follow that of the Grassland Biome and the probability of arid-adapted grass species, being in the process of shifting their range eastwards into the grassland regions is inferred. Analysing herbarium specimens and rangeland monitoring data of indigenous grass species recorded in southern African over time might corroborate the eastward shift of arid grass species.

The recording of infraspecific taxa in ecological vegetation datasets, such as PHYTOBAS, could assist in phenotypic groupings of grasses into smaller ecogeographical regions. Despite the biased collection of the BODATSA database, data presented here confirm that resulting geographical ranges can successfully be interpreted ecologically. Williams and Crouch (2017) supported the inclusion of herbaria data, captured by private institutions, with those of the National Herbarium (included in BODATSA) and will accordingly be an important service in terms of monitoring biodiversity at a finer scale, especially if all collections are digitised.

The advantage of identifying and formally labelling infraspecific genetic variants (both physiological and morphological) within especially species of potential economic significance, such as *Eragrostis curvula* and *Digitaria eriantha*, is evident. In this regard, the distribution patterns of grass species in relation to the grassschoria recognised for southern Africa in the current study may be used as a reflection of potential genetically based variation in environmental tolerance, accordingly assisting in identifying ecotypes of grasses for specific applications.

Despite the in-depth research in southern Africa to identify suitable ecotypes for soil reclamation and restoration during the latter part of the last century (e.g. Dawson 1987), unfortunately none of the genetic material thus assembled has survived and consequently no progress has been made to use it to the advantage of systematics or breeding grasses for agricultural purposes. Results from this study should enable the SA-NFG to develop a strategy for the acquisition, conservation and evaluation of valuable grass genetic resources and therefore assist in directing future pasture research in South Africa.

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