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Description and gradient analysis of the coastal band vegetation in the Groen River mouth area (Namaqualand strandveld)

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Abstract:

Strandveld vegetation around the Groen river mouth was sampled using complementary ordination and classification techniques (DCA and TWINSPAN). Four communities can be recognised, although samples are primarily divided into inland and coastal plots. Two inland communities are: *Stoebaria utilis-Salvia lanceolata* community, characterised by tall vegetation (>1m), on deep, loose soils; *Hermannia spp- Lesertia diffusa* community of short (<0.6m) vegetation on shallow soils with a hardpan dorbank layer. Two coastal Strandveld communities are: *Vanzylia amulata-Limonium peregrinum* community which has short vegetation (<0.5m) on characteristic shallow soils with a calcrete layer at 50 cm deep; *Ruschia hutchensonia-Sasola nolothensis* community characterised by deep alkaline soils. Of the environmental variables sampled, soil resistance and the presence of calcium carbonate in the soil best explain the distribution of plots and species in ordination space. Communities classified in this study differ subtly from the Tall, Medium and Short Strandveld communities and Strand communities proposed by le Roux and Boucher, 1989 and 1993.

Introduction:

This thesis describes a survey of the vegetation present around the mouth of the Groen river, an area which forms part of the Namaqualand Strandveld District of the Succulent Karoo (Jürgens, 1991). The Succulent Karoo is a semi-arid region which receives winter rainfall (Milton et al. 1997). It stretches from 34° latitude in the South to the Skeleton Coast in northern Namibia (Jürgens, 1991). The Southern part of the Succulent Karoo region forms part of the Greater Cape Flora. The vegetation element defining this phytochorion is the large number of leaf succulent taxa (Jürgens, 1991). For a semi-arid area the Succulent Karoo is very species rich, with over 5000 plant taxa occurring here (Milton et al. 1997). This region has the world's largest succulent flora (Cowling et al. 1998a), and together with the rest of the Cape Flora has the largest diversity of geophytes (Esler et al. 1998).

Despite the uniqueness of the vegetation, very few studies have been carried out in the Succulent Karoo as a whole, and in the Strandveld in particular. le Roux and Boucher (1993) divide the Namaqualand Strandveld communities into northern and southern variants on either side of the Spoeg river. No floristic basis for this distinction is given. A study by Desmet (1996), on the vegetation between Port Nolloth and Alexander Bay, is the most rigorous work done on Namaqualand Strandveld to date. Unfortunately this study was performed in northern Namaqualand Strandveld. As yet no in-depth studies have been carried out on the southern Namaqualand Strandveld area. The only work that has been done on this area is descriptive and based on personal observations rather than rigorous objective sampling (le Roux and Boucher, 1989, 1993).

The Strandveld vegetation of the Succulent Karoo is described in Milton et al. (1997) as follows: "Dense to open shrub land of medium height with sclerophylls, evergreen and deciduous shrubs. The vegetation is on average taller than other vegetation types of the Succulent Karoo. Grasses and restios are present. Dominant succulent genera are: *Aloe, Euphorbia, Ruschia, Tetragonia,* and *Tylecodon.* Dominant non-succulent genera are: *Chrysanthemoides, Ehrharta, Euclea, Galenia, Grielim, Lebekia, Lycium, Limonium, Pelargonium, Pteronia, Nylandia, Rhus, Salvia, Wiborgia, Wildlenowia,*and *Zygophyllum.*"

Boucher and le Roux (1989) provide a brief description of the Strandveld vegetation between the Olifants and Spoeg river, an area which includes the vegetation surveyed in this study. They defined the following Strandveld communities:

i) Short Strandveld: occurs on shallow calcareous soils with little water storage potential. The vegetation varies from 10 cm to 30 cm in height. Plant cover is usually less than 50%. Characteristic species are *Cephalophyllum spongiosum, Galenia fruticosa, Mesembryanthemum barklyii, Othonna longifolia* and *Zygophyllum cordifolium.*

ii) Medium Strandveld: consists of vegetation taller than 50 cm. Dominant species include: *Arctotis merxmuelleri, Drosanthemum sp., Manoclamys albicans, Ruschia caroli, Ruschia robusta, Tetragonia fruticosa, Vanzylia sp.* and *Zygophyllum morgsana.* Medium Strandveld has a plant cover 50-60% and also occurs on calcareous soils.

iii) Tall Strandveld: is found on deep calcareous soils. Vegetation is tall, between 1m and 2m, and is fairly dense having a plant cover of 60-75%. Shrubs dominate with the species *Eriocephalus racemosus, Salvia aurea,* and *Zygophyllum morgsana.*

iv) White dune Strandveld: occurs on white dune fields which originate from river mouths.
Plants associated with this community are *Cladoraphis cyperoides, Arctotheca populifolia, Carpobrotus edulis, Hebenstretia cordata, Lebekia cinerea* and *Sporobolus virginicus.*

le Roux and Boucher (1993) also recognise a 200m wide littoral band of vegetation as a separate community, known as the Strand community zone. Namaqualand strand communities are characterised by the species: *Galenia fruticosa, Hypertelis salsoloides, Lycium ferocissimum, Psilocaulon dinterii* and *Sasola nollothensis.* This community is dominated by dwarf shrubs , less than 50 cm tall and grasses of up to 75 cm may also be present.

In this study only Strandveld vegetation present on Calcareous soils are surveyed. The objective of this study is to determine:

i)What vegetation communities occur in the Groen river area?

ii)Do published descriptions of the Strandveld plant communities adequately describe the vegetation present in the Groen River area?

iii)What environmental gradients affect species distribution?

iv)What patterns exist in the distribution of different functional growth forms in the study area?

Given that the Strandveld vegetation, like most of the Succulent Karoo, is very understudied, a research project of a descriptive nature was deemed appropriate. An understanding of the vegetation communities and the underlying gradients will greatly ease further ecological research in the Strandveld.

Methods:

Study site

The study area is situated near the mouth of the Groen river, on the Cape West coast of South Africa (30°51′S 17°34′E). The area receives predominantly winter rainfall, with an average annual rainfall of 140 mm. Fog and dew are regular occurrences and may contribute significantly to the total precipitation of the area. The frequency of fog is around 75 days per annum (Desmet and Cowling, 1998). As most plants adapted to arid conditions have well developed surface roots capable of absorbing small amounts of moisture from fog and dew, these two forms of precipitation should not be ignored (Desmet and Cowling, 1998). The temperature of the area is moderate with Summer maximum temperatures of 20°C and minimum Winter temperatures are around 9°C. Frost does not occur. Being a flat coastal plane, this area is subjected to wind for much of the year. Dry off-shore berg winds are common and play an important role in shaping the vegetation (Desmet, 1996.)

Sampled plots were located in Strandveld vegetation, which occurs on feldspathic sands of terrestrial origin These sands can be placed in two broad categories. The first is terrestrial sands that have been deposited in a Marine environment as a river load, and subsequently reworked and deposited on the sea-shore. The second is sands which have been deposited as river load but have never entered the marine environment (Desmet, 1996). As the study site is situated on the coast and on the banks of a river, both categories of sand substrate occur at the study site.

Vegetation sampling

Vegetation was sampled along three parallel transects perpendicular to the coast (Figure 1). Each transect was located within 5 km of the previous transect. Areas of homogenous vegetation were chosen along each transect and sampled. Rocky outcrops and white dune formations were specifically avoided and only vegetation on sands of marine origin were sampled. Sampling was conducted as follows: Sample "plots" along the main transect were composed of two or three smaller line transects

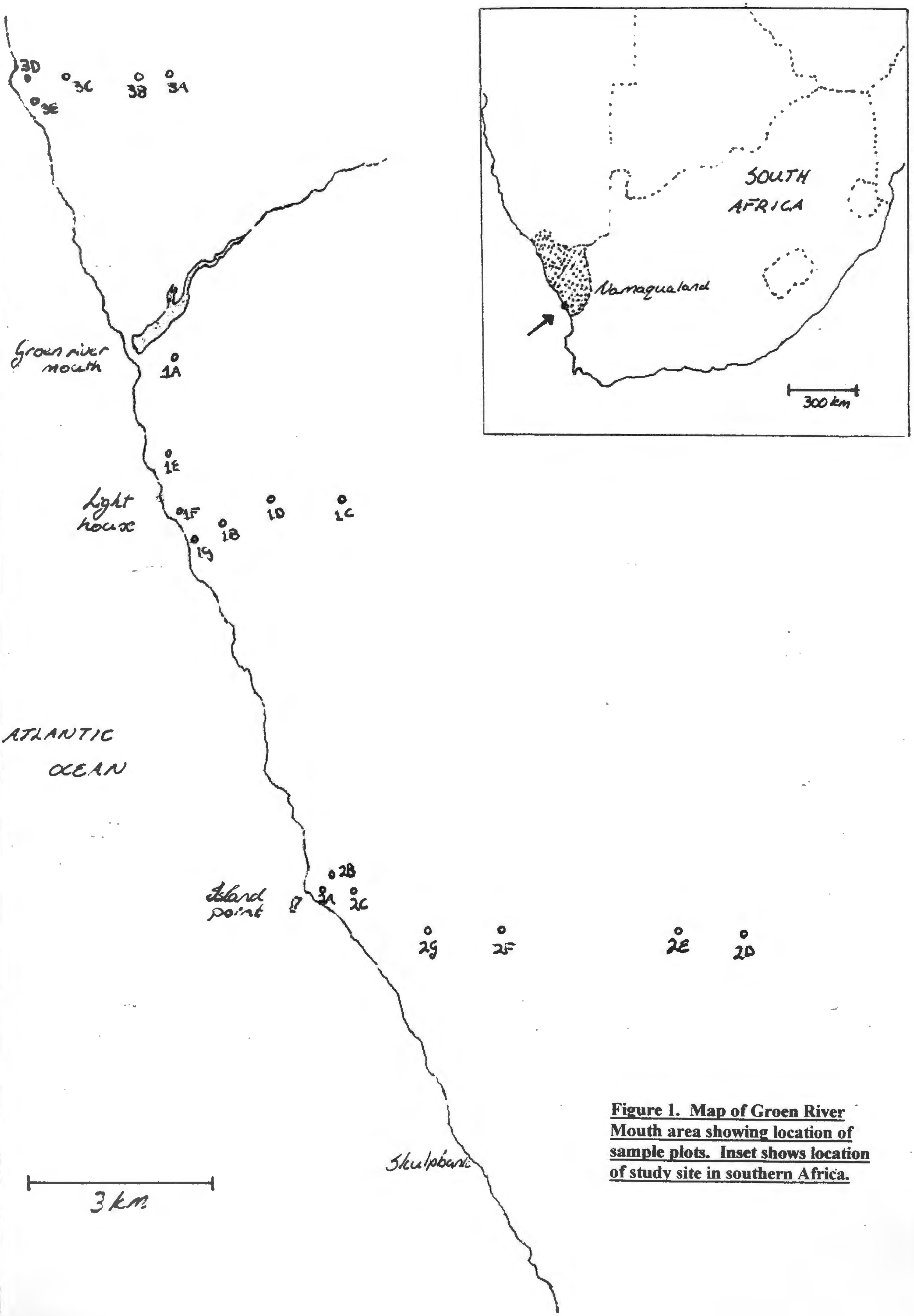

Figure 1. Map of Groen River Mouth area showing location of sample plots. Inset shows location of study site in southern Africa.

laid out at right angles to the main transect running inland. The length and number of these smaller transects in a sample plot was scaled to vegetation height, so that approximately the same number of individual plants occurred in each sample plot. For short vegetation (<1m), three 25 m transects were sampled. For vegetation ranging between 1m and 1.5m, three 50m transects were sample. Two 100m transects were sampled for vegetation reaching 2m. Sample plots composed of line transects were used so plant cover could be calculated rather than estimated. In arid environments where vegetation is patchy, this method of determining plant cover is more reliable.

Line transects within each plot were sampled in the following way. A tape measure was laid out over the vegetation, and the beginning and end point of each plant was recorded. Plant clumping is typical of this vegetation type, thus where more than one individual occupied a particular length of the transect, the distance of the line taken up by each species was recorded. Annuals and geophytes were not included in the sampling because of the ephemeral nature of these plants. 19 plots in total were sampled, 7 along each of transect 1 and transect 2, and 5 along transect 3 (Figure 1).

Environmental sampling

The following environmental features were recorded at each site: Soil depth , for which a soil pit was dug. The pit was dug until either a dorbank layer, or calcrete layer was reached. For very deep soils , the pit was only dug to 1.5 meters. If present, the depth of the dorbank, or calcrete layer was recorded. Two soil samples were collected at each plot; one from the bottom of the soil pit, the second from 5 cm below the surface. This second soil sample was collected from three randomly chosen areas. Soil samples collected from the bottom of the soil pit were tested for the presence of Calcium Carbonate ($CaCO_3$). Presence of $CaCO_3$ was tested by immersing soils in Hydrochloric acid (HCl). Depending on the amount of $CaCO_3$ present different amounts of effervescence was observed. The degree of effervescence was allocated state 0 to 4, with state values being indicative of more effervescence and hence more $CaCO_3$. Surface soil samples were analysed for the following measures. Soil texture; pH; Resistance; concentration of macro elements (Sodium (Na); Calcium (Ca); Magnesium (Mg); Phosphorus (P); and Nitrogen (N)); and trace elements (Boron (B), Copper (Cu), Manganese (Mn) and Zinc (Zn)). An average root depth measurement, (depth to which the majority of the roots extended) and maximum depth for the roots, (roots which extended the deepest into the soil) were measured from the soil pit. Other environmental variables collected included distance from the sea, slope, aspect, and average and emerging height of the sampled vegetation.

Analyses

For each sample plot, subsampled line transects were combined and treated as one long transect during the analysis.

Multivariate analysis

For each species in every plot, an importance value was calculated with two components, relative density and relative dominance. An importance value was used, so that both the size and density of individuals in an area could be taken into account. A density value for each species in a plot was calculated as the number of individuals on a transect multiplied by a scaling factor. The scaling factor allowed for comparison between plots with different length transects. The factor was the length of the transect being sampled divided the longest transect. For the importance value the relative density component was calculated as follows:

$$\text{Relative density} = \frac{\text{Density value for a species}}{\sum \text{Density value for all species}} \times 100$$

The dominance value for each species in a plot was calculated as the total distance of the line transect taken up by any one species divided, by the length of the transect. Hence a dominance per meter value was used and thus no scaling needed . The relative dominance component was calculated as:

$$\text{Relative Dominance} = \frac{\text{Dominance of a species}}{\sum \text{Dominance for all species}} \times 100$$

The importance value for each species in a plot was then calculated as the sum of the Relative density and Relative dominance values.

Phytosociological analysis

Two-way Indicator Species Analysis (TWINSPAN Hill, 1979), a polythetic divisive classification program and Detrended Correspondence Analysis (DCA) an indirect gradient analysis ordination technique in the package CANOCO (Ter Braak, 1987) were used to summarise the variation in the data set. These two complementary techniques for vegetation description and analysis are considered robust and reliable (Kent and Coker, 1992).

TWINSPAN (Hill, 1979) was used to classify the data. In order to test the robustness of vegetation communities described, this program was also run using species density, and species dominance values.

Detrended Correspondence Analysis (DCA, Ter Braak 1987) was used to determine the computational gradients in the data set, thereby enabling the assessment of relationships among communities identified in TWINSPAN. Sampled environmental variables were related to the DCA ordination in order to gain an understanding of which environmental variables were playing a role in community distribution. Indirect gradient analysis was used rather than direct gradient analysis where axes are constrained by sampled environmental variables. Strandveld vegetation is very understudied and driving environmental variables are not known. It was thus considered appropriate to use a technique which ordinates plots using only floristic data.

Correlation analysis

Plant cover and maximum clump size were calculated using the original data collected in the field. These measurements and average vegetation height were correlated with soil depth to infer whether soil depth is important in determinig vegetation structure.

Analysis of growth form distribution

To determine the distribution of certain plant growth forms in the study area, plant species were categorised into the following functional growth forms: Dwarf leaf succulents (< 0.4 m); non-dwarf leaf succulents (> 0.4m); stem succulents; non-succulent shrub; graminoids, forbs. The species co-ordinates for the DCA were replaced by the above functional group number and a biplot of functional group and sample plot was graphed.

Results:

Floristic classification

The results of the TWINSPAN are summarised in Figure 2 (the TWINSPAN output table is presented in Appendix 2) . TWINSPAN as a method is objective in its approach, but the manner of interpreting the output of this method is subjective (Kent and Coker, 1992). The communities shown in Figure 2. were chosen on the basis that each community shared a group of definitive species not present in the other communities (see Appendix 2).

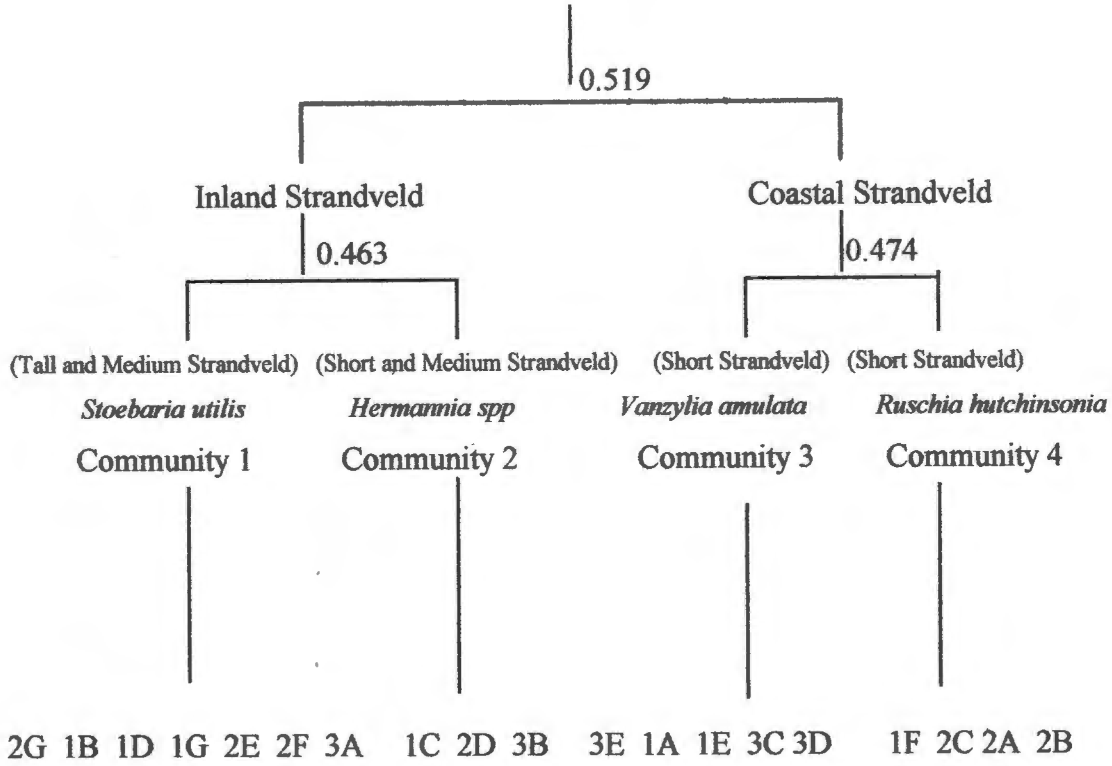

Figure 2: TWINSPAN divisions of the vegetation sampled around Groen river. The eigenvalue for each division is the number above each branch. Definitive species for each community are below the community group The type of vegetation according to le Roux and Boucher (1989) is included brackets.

All the communities delimited by TWINSPAN intergrade as they have the following species in common: *Zygophyllum morgsana*, *Tetragonia fruticosa*, *Othonna cylindrica*, *Helicrysum tricostatum* and *Cepahalophyllum spongiosum* (Appendix 2). The distribution of sample plots shown in the DCA ordination (Figure 3) further supports the lack of completely distinct communities in the study area. A change in one unit along a DCA ordination axis is approximately equal to a 50 % turnover in species composition (Gauch , 1982) and a difference of 4 ordination units therefore represents a complete species turn over. The largest difference between any two sample plots was just over one unit. The largest gap between any of the TWINSPAN Communities is about 0.75 of a unit. Even when a DCA ordination was run without an outlier plot (plot 3D), no better distinction between plot assemblages was obtained. There are however recognisable plant communities (Figure 2, Figure 3) in the

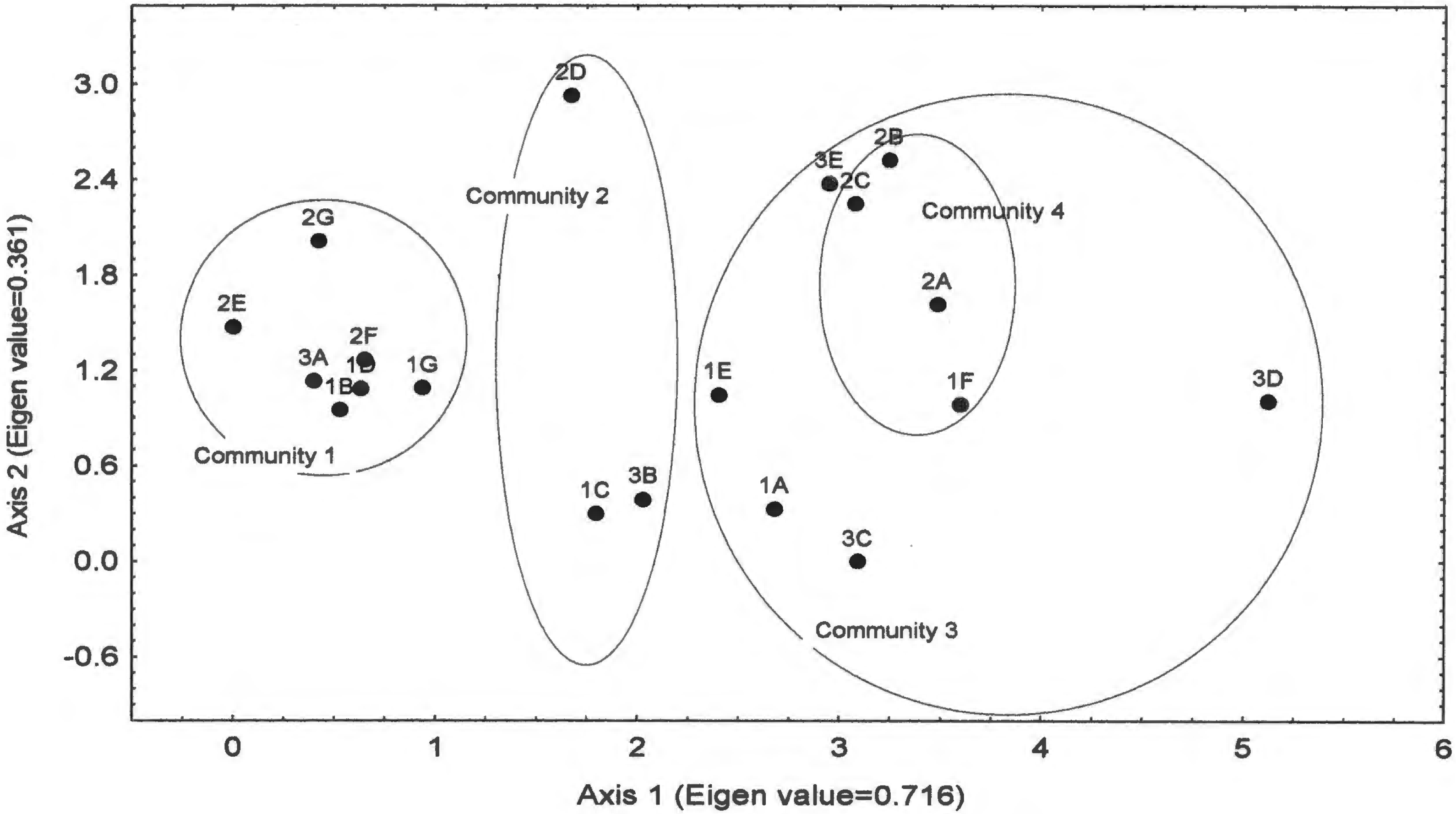

Figure 3: DCA ordination of sample plots showing the first two axes. TWINSPAN Communities are superimposed on the plot ordination.

sampled area. The plots in each community share a set of characteristic species (Appendix 2), and environmental conditions.

Strandveld communities in the Groen River area

Strandveld vegetation of the Groen River area can be divided into two groups (TWINSPAN division 1, Figure 2), on the basis of the distance of vegetation from the coast (Figure 1 and Figure 4d) . Distance from the coast affects the amount of ions found in the soil and hence soil conductivity (DCA axis 1 Figure 5). Differences in the amount of Calcium Carbonate found in these two groups (Figure 4 c) also supports distance from the coast as being an important factor. Typically soils close to the coast have high levels of Calcium Carbonate. Coastal plots (Community 3 and Community 4, Figure 2) are characterised by the presence of the species *Didelta carnosa*. Characteristic species for inland plots are *Conicosia sp.* and *Eriocephalus africana* .

Inland Strandveld can be further divided into two groups: Community 1: *Stoebaria utilis-Salvia lanceolata* and Community 2: *Hermannia spp- Lesertia diffusa* (TWINSPAN eigenvalue: 0.463). Coastal Strandveld can be divided into two Communities, Community 3: *Vanzylia amulata-Limonium peregrinum* and Community 4: *Ruschia hutchensonia-Sasola nolothensis* (TWINSPAN eigen value: 0.474).

Community 1: *Stoebaria utilis-Salvia lanceolata*

Community 1 is characterised by tall vegetation of, on average, greater 1 m (Figure 4 e). Soils are deep and loose with a depth greater than 1m. The soils of this community are neutral with an average pH of 7 (Figure 4 e and b). Plant vegetation cover is on average between 40 and 60%. Indicator species of this community are: *Stoebaria utilis, Salvia lanceolata, Maytenus heterophylla, Melianthus pectinatus, and Pteronia divericata* (Appendix 2). Species which occur here preferentially are *Pharnaceum lanatum, Zygophyllum morgsana* and *Manochlamys albicans.*

Community 2: *Hermannia spp- Lesertia diffusa.*

Community 2 is characterised by short vegetation of below 60 cm (Figure 4e). All sample plots of this Community are far from the coast (Figure 4 d) and occur on shallow soils of less than 60 cm deep (Figure 4 f). Soils are shallow because of the presence of a hardpan dorbank layer produced due by leached silica which forms a cemented layer in lower soil horizons. The dorbank layer causes soils to be slightly acidic (pH between 5.7 and 6.2). Plant canopy cover for Community 2 ranges from 50-60 % cover. Indicator species are: *Hermannia sp2; Ficinia nigrescens;* and *Lesertia diffusa.* Species which occur here preferentially are, *Limeum africanum,* and *Lebeckia sericea.*

Community 3: *Vanzylia amulata-Limonium peregrinum*

Community 3 is a coastal community characterised by soils with low resistance. The soils are shallow and overlay a hard calcrete layer. The vegetation is short (less than 40 cm) and plant canopy ranges between 40 and 65 % cover. Characteristic species are *Vanzjilia amulata, Limonium peregrinum,* and *Thesium sp2.* Preferential species are *Lampranthus hoerleinianus, Cephalophyllum spongiosum, Helicrysum tricostatum.*(Appendix 2, Figure 4).

Community 4: *Ruschia hutchensonia-Sasola nolothensis*

Community 4 is coastal with of short vegetation (<0.5cm). Unlike Community 3, the mean soil depth for this group is 2m (Figure 4f). pH of the soils of this community are high in comparison to the other three Communities. The soils are very alkaline, (mean pH = 8.2), all three other groups have neutral to slightly acidic soils with mean pH values of 6.5. The vegetation of this community is characterised by low species numbers and plant cover is between 4 and 60 %(Figure 4g). Characteristic species for this community are *Ruschia hutchensonia,* and *Sasola nolothensis* (Appendix 2, Figure 4). Preferential species are *Hypertelis salsoloides,* and *Odyssea paucinervis.*

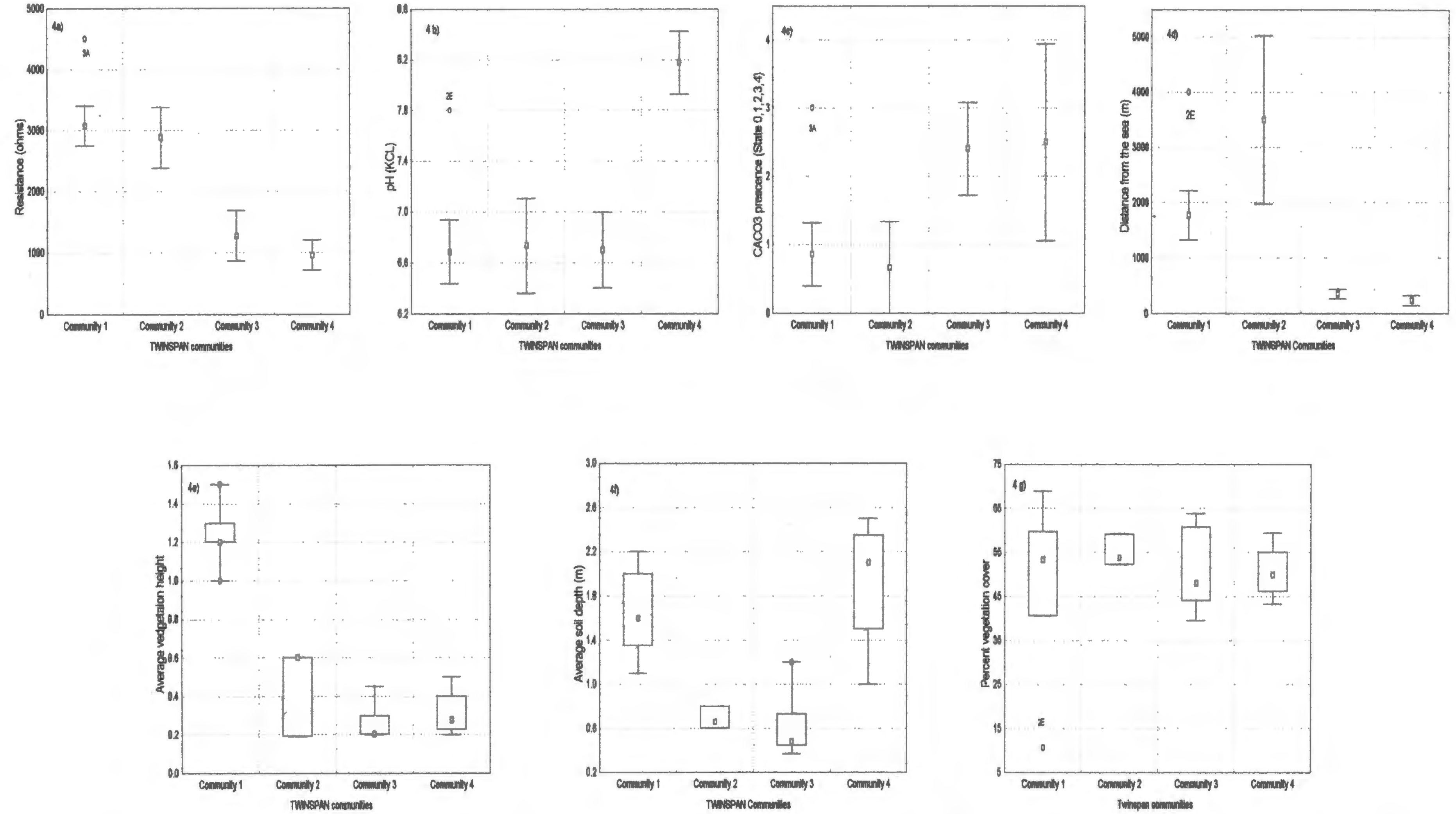

Figure 4: Summary environmental and biological variables for the four TWINSPAN Communities using mean and standard error bars. Where nominal data was used box and whisker plots are graphed. a) Soil Resistance (ohms), b) Soil pH (KCL), c) CaCO3 soil presence, d) Distance from the coast, e)Average vegetation height, f) Average soil depth g)Percentage vegetation cover.

Environmental gradient analysis:

Biplots of sample plots and environmental variables are presented in Figures 6. Soil resistance and the presence of Calcium Carbonate are the two important environmental variables most strongly correlated with axis 1: r = -0.7955 for resistance and r =0 .6338 for $CaCO_3$. Soil pH is the environmental variable most strongly correlated to the second DCA axis: r = 0.519. pH and resistance are both related to the amount of nutrient elements present in the soil. pH is strongly affected by Calcium (r = 0.667), Magnesium (r = .6103) and Boron (r = 0.6103). While resistance is affected by the amount of Sodium present in the soil (r = -0.618).

Soil depth relationships

There is no significant correlation between soil depth and vegetation height for all the plots in the study area (Figure 6). The vegetation height of inland communities does however appear to be related to soil depth. There is a highly significant correlation (r = 0.77 and p= 0.0096, Figure 7) between vegetation height and soil depth. Hence vegetation type and structure appears to be a function of soil depth for this group of samples. There is no apparent correlation between soil depth and vegetation height for the coastal plots. The vegetation structure of these plots is therefore dictated by some other factors. Given the coastal influence, wind and associated saline spray is a likely candidate for primary driving variables (Desmet, 1996). Vegetation clump size, r = 0.036 (p = 0.884), and plant cover, r = 0.3341 (p = 0.162), are also not correlated with soil depth.

Distribution of growth and functional life forms

Figure 8 shows the distribution of growth forms in the study area. If the two main TWINSPAN groups of Inland and Coastal Strandveld are compared the following trends in growth form distribution become apparent: Non-succulent shrubs such all the large species in the Asteraceae (*Eriocephalus africana, Chrysanthemoides monilifera, Chrysanthemoides incana,* and most of the *Pteronia* species), the large evergreen shrubs : *Maytenus heterophylla* and *Salvia lanceolata* occur mainly on inland Strandveld plots (Figure 8). Non-dwarf leaf succulents for example *Stoebaria* *utilis* and the members of the *Zygophyllaceae* occur more often on inland plots. Graminoids, Stem succulents and Forbs occur in equal abundance both at the coast and inland. While dwarf-succulents are typically found on coastal plots. The dwarf-leaf succulents (1) are most common in plots with soils of shallow depth: 1A (0.44 m), 3D (0.37 m) , and 3C (0.48 m).

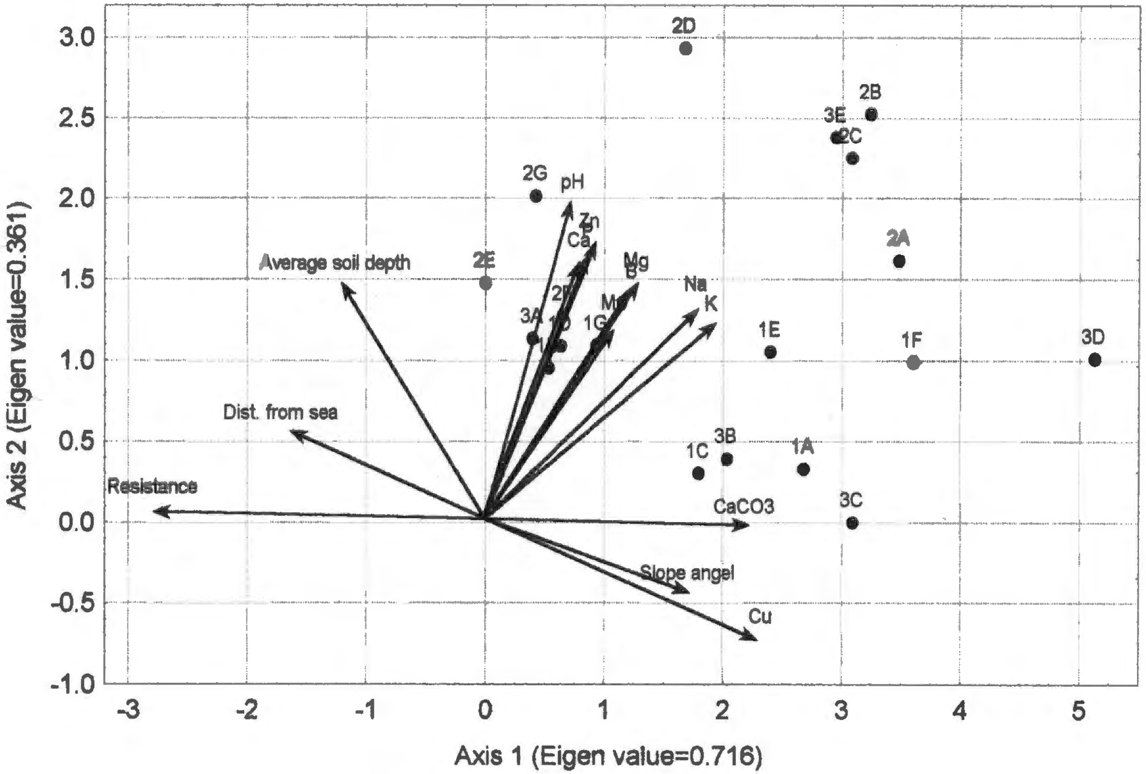

Figure 5: A biplot of environmental variables and sample plots with DCA axis 1 and 2.

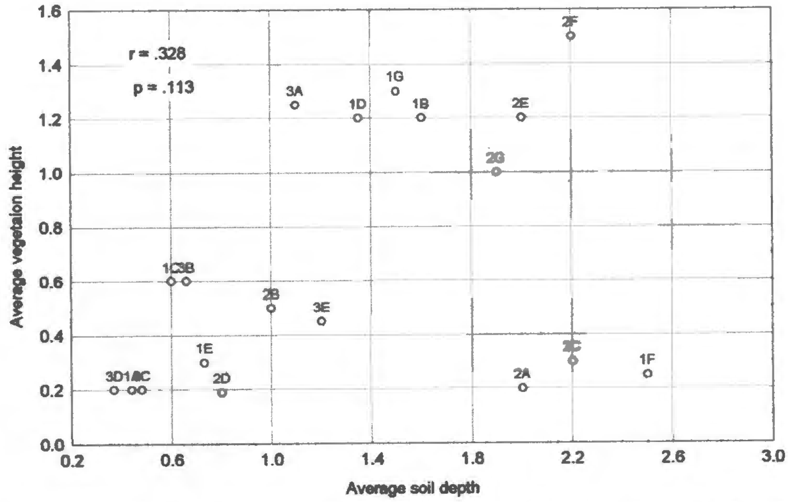

Figure 6: A correlation analysis of soil depth and vegetation height for the 19 sample plots. r = 0.328, p=0.113.

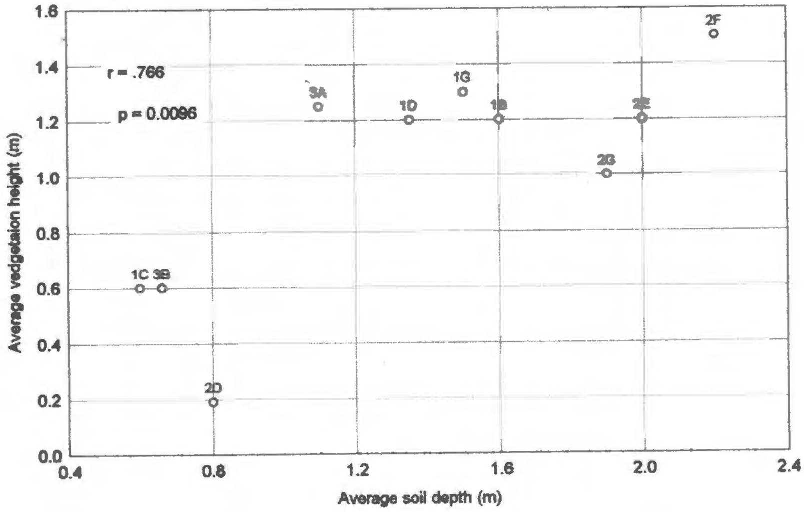

Figure 7: The correlation analysis of vegetation height and average soil depth, for the sample plots in Community 1 and Community 2. r = 0.766 and p = 0.0096.

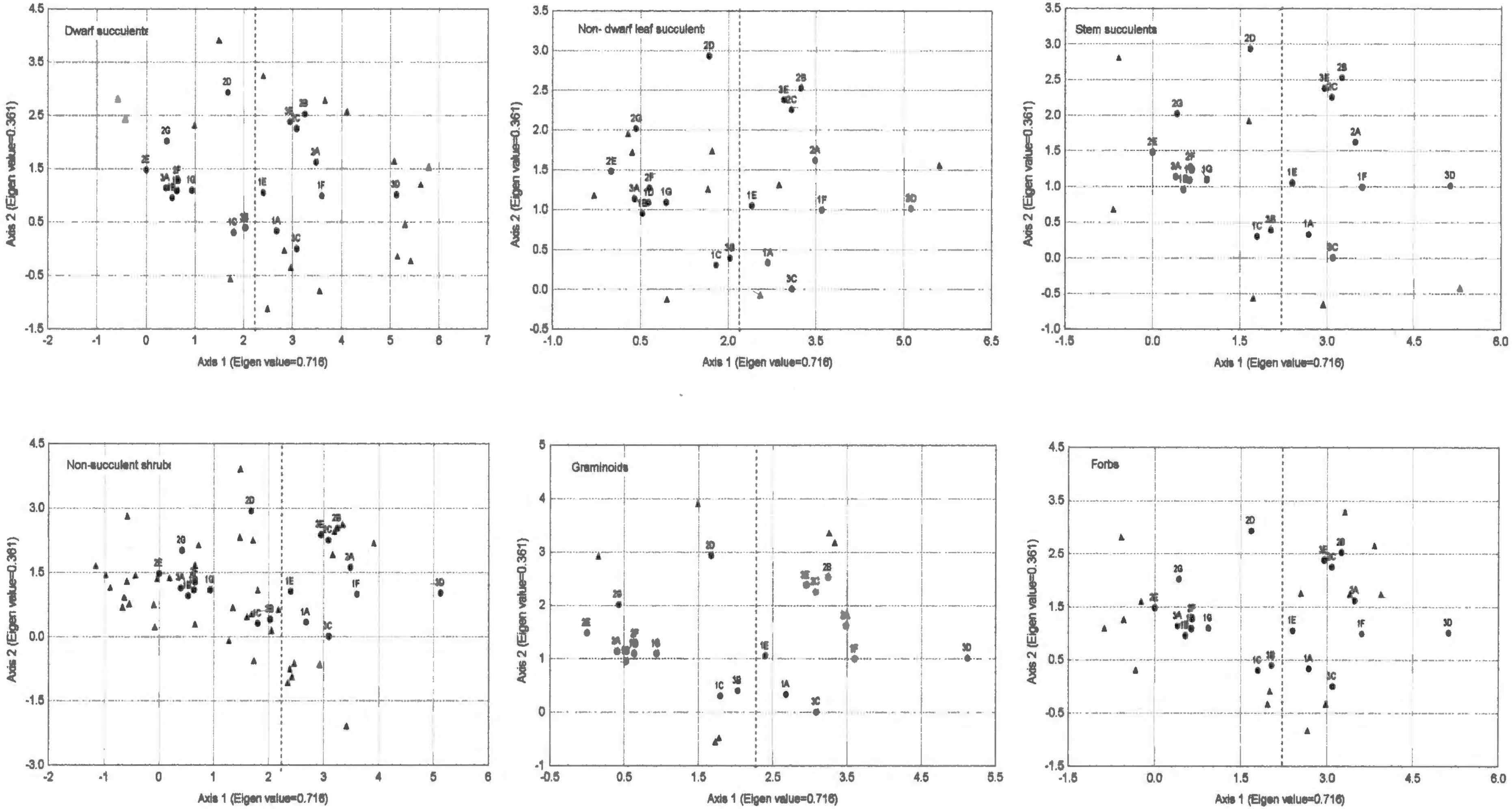

Figure 8: Biplots of functional groups (▲) with sample plots (●). The dashed line represents the first axis division of the TWINSPAN analysis and seperates inland plots from coastal plots.

Discussion:

There have been a number of criticisms of TWINSPAN and DCA as techniques for use in vegetation classification (van Groenewoud, 1992). Both techniques are however widely used for vegetation description and are generally considered to be reliable (Kent and Coker 1992, Gauch, 1982). Even a recent critique of both methods by van Groenewoud (1992) states that where the majority of the variability in vegetation data is explained by the first DCA axis, this axis adequately recovers the latent structure in the data. As the first axis of the DCA in this study has a high eigenvalue of 0.716, this floristic classification is considered reliable.

The four communities described in this study do not agree completely with those described by le Roux and Boucher (1989). Community 1: (*Stoebaria utilis-Salvia lanceolata*) according to this study, includes both the Tall and Medium Strandveld communities describe by le Roux and Boucher (1989). This is only the case if le Roux and Boucher's indicator species are used as community determinants. Indicator species of le Roux and Boucher's Medium Strandveld, are: *Arctotis merxmuelleri, Manoclamys albicans, Tetragonia fruticosa,* and *Zygophyllum morgsana*. All four species are present in Community 1 of this study and in most Strandveld plots sampled except those in Community 2. If vegetation height is used as a determinate, then Community 2 in this study corresponds to the Medium Strandveld described by le Roux and Boucher. Community 1 forms the most obvious group in the ordination space of the DCA.. Species presence rather than vegetation size should be used for community criteria, therefore we propose that the communities Medium and Tall Strandveld described by le Roux and Boucher are not true communities. We have also shown that the vegetation height of the plots present in Community 1 and Community 2 correlate with soil depth. This further shows that Medium Strandveld is not a community based on species composition but rather a subset of Tall Strandveld that varies in structure dependant on soil depth. These results indicate that using vegetation height for naming Strandveld communities is not an appropriate method. Another problem with le Roux and Boucher's (1989) description of Tall and Medium Strandveld is the amount of vegetation cover they described. Community 1 in this study had only 40-60 % plant cover as opposed to the 60-75% cover described by le

Roux and Boucher for Tall Strandveld. Such a difference calls into question the reliability of estimating plant cover rather than actually measuring it.

Community 3 (*Vanzylia amulata*) of this study corresponds to le Roux and Boucher's Short Strandveld community. Like le Roux and Boucher's community the soils of Community 3 are shallow. Both communities share similar indicator species.
The DCA ordination shows that Community 4 is a subset community which is nested within Community 3. This community is however does differ from Community 3 in having deep alkaline soils, on which only a few species can survive. Coastline proximity of plots in Community 4 and the presence of indicator species *Sasola nolothensis* and *Hypertelis salsoloides,* show that this community corresponds to le Roux and Boucher's Strand community.

Proximity to the coast is a major factor that separates vegetation communities in the Strandveld. The various plots that were classified as communities formed groups not on the basis of latitudinal proximity to one another but rather on their distribution in relation to the coast line. In the indirect gradient analysis, soil resistance and presence of calcium carbonate were the two most important environmental variables correlated with species turnover between communities in the Groen river area. Both of these are dependent on proximity to the coast. Resistance increases on a gradient inland from the coast (Appendix 4). This is due to the leaching of ions out of soils.

Community 4 is separated from the rest of Community 3 because of the high pH of the soils, a result of large amounts of calcium carbonate being present in the soil. The abundant calcium carbonate is evidence that these soils are of recent marine origin (Desmet, 1996). The more recent calcareous sands have high calcareous content because of finely divided shell fragments. Calcium carbonate buffers soil pH in the range of 7 and 8.5 (Marschner, 1988). High calcium carbonate levels induces deficiencies in the nine elements: aluminium, zinc, copper, iron, manganese, cobalt, boron, phosphorus and potassium by either making them insoluble or inhibiting their availability (Desmet, 1996) This may explain why plots in community 4 have only a few species.

Calcareous sands that are of older marine origin and that have been colonised by perennial growth are subject to the leaching of both carbonates and silicates. These soils typically have lower alkalinity (Desmet, 1996). The very slight acid nature of the inland communities (Community 1: average pH of 6.8 and Community 2: average pH of 6 are the result of leaching of both carbonates and silicates. Leaching may results in the formation of a hardpan layer as in community 2 and 3. Where this occurs species composition as well as structure may be effected, as the hardpan layer inhibits root penetration and thus limits available space for absorption of water and nutrients (Desmet, 1996).

Other environmental factors which were not measured in this study but which probably play a large role in the community structure found here are; wind and the deposition of salt from aerosols carried by onshore winds. These two factors may especially explain the patterns present in coastal Strandveld communities.

The functional plant growth forms are distributed unevenly along a gradient away from the sea. Dwarf succulents typically occur on shallow soils, and on soils which are close to the coast. The most common family of plants in the dwarf succulent functional group are the Mesembryanthemaceae. This family along with other leaf succulents in the families Crassulaceae, Euphorbiaceae, Asteraceae and Asclepiadaceae form the most important component of the Succulent Karoo vegetation (Cowling et al. 1998). The Mesembryanthemaceae are particularly speciose on shallow soils as they are shallow rooted and compete very efficiently for soil moisture (Cowling et al. 1998, Milton et al. 1997). Many members of the Mesembryanthemaceae are able to survive in soils with high concentrations of salts (Milton et al. 1997), this may also explain why dwarf succulents occur on coastal Strandveld plots in this study.

Non-succulent shrubs, do occur in the rest of the succulent Karoo. However shrubs of average height 1 and 2 meters typical of Tall Strandveld are unusual (Cowling et al.

1998). The tall vegetation of the Strandveld is due to the deep soils which have been stabilised by vegetation and had calcium and other ions leached out of them.

Conclusion:

The area around the Groen river has four recognisable plant communities, with two inland and two coastal communities. Inland vegetation size and species composition appears to be dependent on soil depth, with a hardpan dorbank layer playing an important role. The inland Strandveld communities of Tall and Medium Strandveld described by le Roux and Boucher (1989) are not reliable. We suggest new names for inland Strandveld. Community 1 of this study should be called Tall Strandveld and Community 2 should be called Short Strandveld. The medium Strandveld described by le Roux and Boucher should be included within Tall Strandveld.

The coastal plots from this study form communities that agree with those described by le Roux and Boucher (1993 and 1989). However the fact that one community is nested within the other in this study suggests that these communities are very closely associated. We suggest referring to them broadly as strand communities. This name is appropriate as both communities 3 and 4 are very affected by marine influences. We also suggest that further sampling of Strand communities takes place. This study showed that soil depth does not effect coastal plant communities, thus environmental variables related to the coastal position of these communities such as wind, aerosol spray should be measured.

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References:

Boucher, C and le Roux, A. (1989). Heavy mineral sand mining project assessment vegetation report. Anglo American Corporation West Coast Heavy Minerals Sands Project Supplementary Report. EEU Report No. 4/90/49.

Boucher, C and le Roux, A. (1993) Dry coastal ecosystems of the South African coast. In: van der Maarel, E. (ed.) Dry Coastal Ecosystems. Africa, America, Asia and Oceania. Ecosystems of the Worlds 2B. Elsevier, Amsterdam.

Cowling, R.M., Rundel, P.W., Desmet, P.G., and Esler, K.J. (in press a). Extraordinarily high regional-scale diversity in southern African arid lands: subcontinental and global comparisons. *Plant Ecology.*

Cowling, R.M., Esler, K.J. and Rundel, P.W. (in press b), Namaqualand, South Africa- an overview of a unique winter rainfall desert ecosystem. *Plant Ecology.*

Desmet, P.G. (1996) Vegetation and restoration potential of the arid coastal belt between Port Nolloth and Alexander Bay, Namaqualand, South Africa. MSc Thesis, University of Cape Town.

Desmet, P.G. and Cowling, R.M. (1998). The Climate of the Karoo- A functional approach. In: Dean, W.R.J. and Milton, S.J. (eds), The Karoo: ecological patterns and processes. Cambridge University press, Cambridge.

Esler, K.J., Rundel, P.W. and Voster, P. (1998). Biogeography of prostrate leafed geophytes in semi-arid South Africa: hypotheses on functionality. *Plant Ecology* in press.

Hill, M.O. (1979). TWINSPAN. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

Jürgens, N. (1991). A new approach to the Namib Region . I: Phytogeographic subdivision. *Vegetatio* 97: 21-38.

Kent, M. and Coker, P. (1992). Vegetation description and Analysis. A Practical Approach. CRC Press, Boca Raton.

Marschner, H. (1995). Mineral Nutrition of Higher plants. Academic press. London.

Milton, S.J; Yeaton, R.I; Dean, W.R.J. and Vlok, J.H.J. (1997). Succulent Karoo. In: Cowling, R.M., Richardson, D.M. and Pierce, S.M. (eds.) The vegetation of Southern Africa. Cambridge University Press, Cambridge.

Ter Braak, C.J.F. (1987) CANOCO- a FORTRAN program for canonical community ordination by correspondence analysis, principle component analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Statistics Department Wageningen, The Netherlands.

van Groenewoud, H. (1992). The robustness of Correspondence, Detrended Correspondence, and TWINSPAN Analysis. *Journal of Vegetation Science* **3**: 239-246.

Appendix 1: Species codes used in the TWINSPAN and DCA analyses.

Species code	Species	Family	Functional group
ALOARE	*Aloe arenicola*	Asphodelaceae	non-dwarf leaf succulent
AMETEN	*Amellus tenuifolius*	Asteraceae	forb
ANTsp1	*Antimima sp*	Mesembryanthemaceae	dwarf leaf succulent
APIsp1	*Dasispermum suffruticosum*	Apiaceae	forb
ARCMER	*Arctotis merxmuelleri*	Asteraceae	forb
ASPAET	*Asparagus aetheopicus*	Asparagaceae	non-succulent shrub
ASPCAP	*Asparagus capensis*	Asparagaceae	non-succulent shrub
ASPFAS	*Asparagus fasicularis*	Asparagaceae	non-succulent shrub
ASPJUN	*Asparagus juniperoides*	Asparagaceae	non-succulent shrub
ASTsp1	Asteraceae sp	Asteraceae	non-succulent shrub
ATRsp1	*Atriplex sp*	Chenopodiaceae	forb
BALAFR	*Ballota africana*	Lamiaceae	forb
CEPSPO	*Cephalophyllum spongiosum*	Mesembryanthemaceae	dwarf leaf succulent
CHAINV	*Chaetobromus inv*	Poaceae	graminoid
CISCAP	*Cissampelos capensis*	Menispermaceae	forb
CLACYP	*Cladoraphis cyperoides*	Poaceae	graminoid
CONsp1	*Conicosia sp*	Mesembryanthemaceae	dwarf leaf succulent
CRAMUS	*Crassula muscosa*	Crassulaceae	dwarf leaf succulent
CRATOM	*Crassula tomementosa*	Crassulaceae	dwarf leaf succulent
CRYINC	*Chrysanthemoides incanum*	Asteraceae	non-succulent shrub
CRYMON	*Chrysanthemoides monilifera*	Asteraceae	non-succulent shrub
CRYsp1	*Chrysocoma sp*	Asteraceae	non-succulent shrub
CRYsp3	*Chrysocoma sp*	Asteraceae	non-succulent shrub
DIDCAR	*Didelta carnosa*	Asteraceae	forb
DROINT	*Drosanthemum intermedium*	Mesembryanthemaceae	dwarf leaf succulent
EHRCAL	*Ehrharta calycina*	Poaceae	graminoid
ERIAFR	*Eriocephalus africanus*	Asteraceae	non-succulent shrub
EUCRAC	*Euclea racemosa*	Ebenaceae	non-succulent shrub
EUPBUR	*Euphorbia burmannii*	Euphorbiaceae	stem succulent
EUPMAU	*Euphorbia mauritanica*	Euphorbiaceae	stem succulent
EUPTUB	*Euphorbia tuberculata*	Euphorbiaceae	stem succulent
FICNIG	*Ficinia nigrescens*	Cyperaceae	graminoid
GALFRU	*Galenia fruticosa*	Aizoaceae	forb
HEBCOR	*Hebenstretia cordifolia*	Selaginaceae	forb
HELspnon-dwa	*Helichrysum sp*	Asteraceae	non-succulent shrub
HELTRI	*Helichrysum tricostatum*	Asteraceae	non-succulent shrub
HERsp1	*Hermannia sp*	Sterculiaceae	non-succulent shrub
HERspnon-dwa	*Hermannia sp*	Sterculiaceae	non-succulent shrub
HERsp3	*Hermannia sp*	Sterculiaceae	non-succulent shrub
HERsp4	*Hermannia sp*	Sterculiaceae	non-succulent shrub
HERsp5	*Hermannia sp*	Sterculiaceae	non-succulent shrub
HYPSAL	*Hypertelis salsoloides*	Aizoaceae	dwarf leaf succulent
LAMHOE	*Lampranthus hoerliana*	Mesembryanthemaceae	dwarf leaf succulent
LEBSER	*Lebeckia sericea*	Fabaceae	non-succulent shrub
LESDIF	*Lessertia diffusa*	Fabaceae	non-succulent shrub
LIMAFR	*Limeum africanum*	Aizoaceae	forb
LIMEQU	*Limonium equisetinum*	Plumbaginaceae	forb
LIMPER	*Limonium perigrinum*	Plumbaginaceae	forb
LYCDEC	*Lycium decumbens*	Solanaceae	non-succulent shrub
LYCFER	*Lycium ferocissimum*	Solanaceae	non-succulent shrub
MANALB	*Manochlamys albicans*	Chenopodiaceae	forb
MAYHET	*Maytenus heterophylla*	Celastraceae	non-succulent shrub
MELEXU	*Melolobium exudans*	Fabaceae	non-succulent shrub

Appendix 1: Species codes used in the TWINSPAN and DCA analyses.

MELPEC	*Melianthus pectinatus*	Melianthaceae	non-succulent shrub
MESspx	*Mesembryanthemaceae sp*	Mesembryanthemaceae	dwarf leaf succulent
MICSAG	*Microloma sagittatum*	Asclepiadaceae	non-succulent shrub
MURsp1	*Muraltia sp*	Polygalaceae	non-succulent shrub
ODYPAN	*Odysea paniculata*	Poaceae	graminoid
OSTOPP	*Osteospermum oppositifolium*	Asteraceae	non-succulent shrub
OSTspnon-dwa	*Osteospermum sp*	Asteraceae	non-succulent shrub
OTHARB	*Othonna arborescens*	Asteraceae	stem succulent
OTHCYL	*Othonna cylindrica*	Asteraceae	non-dwarf leaf succulent
OTHRET	*Othonna retrofractum*	Asteraceae	non-dwarf leaf succulent
OTHsp4	*Othonna sp*	Asteraceae	non-dwarf leaf succulent
PELFUL	*Pelarganium fulgidum*	Geraniaceae	stem succulent
PELGIB	*Pelargonium gibbosum*	Geraniaceae	stem succulent
PELPUL	*Pelargonium pulchellum*	Geraniaceae	stem succulent
PHABRA	*Pharnaceum brachy?*	Aizoaceae	forb
PHALAN	*Pharnaceum lanatum*	Aizoaceae	forb
PHYsp1	*Phyllobolus sp*	Mesembryanthemaceae	dwarf leaf succulent
PSIDIN	*Psilocaulon dinterii*	Mesembryanthemaceae	dwarf leaf succulent
PTEDIV	*Pteronia divaricata*	Asteraceae	non-succulent shrub
PTEGLA	*Pteronia glabrata*	Asteraceae	non-succulent shrub
PTEONO	*Pteronia onobromoides*	Asteraceae	non-succulent shrub
PTEOVA	*Pteronia ovalifolia*	Asteraceae	non-succulent shrub
PTEPAN	*Pteronia paniculata*	Asteraceae	non-succulent shrub
PTEsp7	*Pteronia sp*	Asteraceae	non-succulent shrub
RHULON	*Rhus longispina*	Anacardiaceae	non-succulent shrub
RUSFUG	*Ruschia fugitans*	Mesembryanthemaceae	dwarf leaf succulent
RUSHUT	*Ruschia hutchensonia*	Mesembryanthemaceae	dwarf leaf succulent
RUSPER	*Ruschia perforata*	Mesembryanthemaceae	dwarf leaf succulent
RUSsp4	*Ruschia sp*	Mesembryanthemaceae	dwarf leaf succulent
RUSsp5	*Ruschia sp*	Mesembryanthemaceae	dwarf leaf succulent
RUSSUB	*Ruschia subpaniculata*	Mesembryanthemaceae	dwarf leaf succulent
SALLAN	*Salvia lanceolata*	Lamiaceae	non-succulent shrub
SALNOL	*Salsola nolothensis*	Chenopodiaceae	non-succulent shrub
SCRsp1	*Scrophulariaceae sp*	Scrophulariaceae	forb
SENCOR	*Senecio corymbiferus*	Asteraceae	non-dwarf leaf succulent
SENsp1	*Senecio sp*	Asteraceae	non-dwarf leaf succulent
SOLsp1	*Solanaceae (subterranean sp)*	Solanaceae	non-succulent shrub
SPEMED	*Spegularia media*	Caryophyllaceae	dwarf leaf succulent
SPHsp1	*Sphalmanthus sp*	Mesembryanthemaceae	dwarf leaf succulent
STIZEY	*Stipogrostis zeyerii*	Poaceae	graminoid
STOUTI	*Stoeberia utilis*	Mesembryanthemaceae	non-dwarf leaf succulent
TETFRU	*Tetragonia fruticosa*	Aizoaceae	non-dwarf leaf succulent
THEALI	*Thesium aliatus*	Santalaceae	non-succulent shrub
THEspnon-dwa	*Thesium sp*	Santalaceae	non-succulent shrub
THESPI	*Thesium spinosum*	Santalaceae	non-succulent shrub
TYLFRA	*Tylecodon fragilis*	Crassulaceae	stem succulent
TYLWAL	*Tylecodon wallichii*	Crassulaceae	stem succulent
VANAMU	*Vanzijlia amulata*	Mesembryanthemaceae	dwarf leaf succulent
VISCAP	*Viscum capense*	Viscaceae	non-succulent shrub
WAHASP	*Wahlenbergia asparagoides*	Campanulaceae	forb
WILINC	*Willdenowia incurrata*	Restionaceae	forb
ZYGMOR	*Zygophyllum morgsana*	Zygophyllaceae	non-dwarf leaf succulent
ZYGspnon-dwa	*Zygophyllum sp*	Zygophyllaceae	non-dwarf leaf succulent
ZYGsp3	*Zygophyllum sp*	Zygophyllaceae	non-dwarf leaf succulent

Appendix 2: Twinspan output, pseudospecies 1,2, 3, and 4 represent increasing importance values for ag specie.1=imp. valuebetween 0 and 0.1, 2 between 0.1-0.5, 3 between 0.5 and 1 and 4 an imp. value greater than 1.

SPECIES	2G	1B	1D	2E	3A	1G	2F	1C	2D	3B	3E	1A	1E	1C	3D	2C	1F	2B	2A
ASTspX	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
CONsp1	2	-	-	1	-	1	1	3	2	-	-	-	-	-	-	-	-	-	-
CRYsp3	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
EHARTA	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
EUPTUB	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-
FICNIG	-	-	-	-	-	-	-	4	-	2	-	-	-	-	-	-	-	-	-
HERsp2	-	-	-	-	-	-	-	3	2	2	-	-	-	-	-	-	-	-	-
HERsp4	-	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	-	-	-
LESDIF	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
LYMAFR	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
MURsp1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
PELKAR	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
PHYLAB	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
PHYsp1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
PTEGLA	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
STIZEY	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
THEALI	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CRYMON	2	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-
LEBSER	-	-	-	-	-	4	2	3	2	4	-	-	2	-	-	-	-	-	-
LIMAFR	-	-	-	-	-	-	1	2	-	1	-	1	-	-	-	-	-	-	-
AMETEN	-	-	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-
APIsp1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ASPAET	2	2	3	1	3	-	2	-	-	1	-	-	-	-	-	-	-	-	-
ASPJUN	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
BALAFR	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CHAINV	-	-	-	2	-	-	2	-	3	-	-	-	-	-	-	-	-	-	-
CRYsp1	-	-	1	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
ERIAFR	-	4	2	3	4	-	3	2	-	-	-	-	-	-	-	-	-	-	-
HERsp5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MANALB	2	2	1	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-
MAYHET	-	-	2	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
MELsp1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OSTsp2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OTHARB	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PELGIB	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PHALAN	-	2	2	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-
PTEDIV	-	2	2	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
RHULON	-	-	-	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
RUSsp4	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
RUSsp5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SALLAN	-	2	3	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
STOUTI	2	3	3	1	2	3	3	-	-	-	-	-	-	-	-	-	-	-	-
VISCAP	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRYINC	-	-	-	2	2	2	2	1	-	3	2	2	-	-	-	-	-	-	-
GRIGRA	4	-	-	1	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-
KEDSAM	-	2	1	2	-	-	1	-	2	-	-	2	-	-	-	-	-	-	-
LYCFER	2	1	2	1	3	2	2	1	-	-	-	-	-	-	-	-	-	-	2
SENsp1	-	2	1	-	1	-	1	1	-	-	-	1	-	-	-	-	-	-	-
TETFRU	4	3	4	3	4	4	3	2	1	2	1	2	3	-	1	2	-	2	-
ZYGMOR	4	3	4	4	3	4	3	2	-	2	2	1	2	-	-	1	-	2	2
HERsp1	-	-	-	1	1	-	2	1	2	1	-	2	-	1	-	1	-	-	-
HERsp3	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-
MELEXU	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-
OSTOPP	2	4	4	1	4	4	2	4	-	4	2	2	3	4	-	-	-	-	-
THESPI	-	-	-	-	-	-	-	3	-	3	-	-	-	3	-	-	-	-	-
EUPBUR	-	1	1	-	2	-	-	-	1	-	-	1	-	-	1	-	-	-	-
MICSAG	-	2	2	2	2	1	-	1	-	-	2	-	2	-	-	-	-	-	-
PTEONO	1	4	4	-	-	2	2	3	-	1	2	3	2	-	-	-	-	-	-
RUSSUB	2	-	2	2	2	-	2	-	3	-	3	-	2	-	-	4	-	-	-
OTHCYL	3	3	4	2	2	3	3	2	-	3	2	2	3	1	-	1	2	3	2
ARCMER	1	-	-	1	-	2	3	3	-	-	2	3	2	2	-	-	-	-	-
OTHRET	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
ANTsp1	-	-	-	-	-	-	-	2	-	1	-	-	-	2	-	-	-	-	-
CRATOM	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	-	-
LESsp1	-	-	-	-	-	-	-	2	-	-	-	2	-	1	-	-	-	-	-
HELTRI	-	2	2	3	2	3	-	-	-	1	2	4	3	-	-	1	3	-	-
CEPSPO	1	-	1	-	-	2	-	2	-	4	1	4	4	4	2	3	1	-	-
LAMHOE	-	-	-	-	-	-	-	2	-	1	2	1	-	3	-	1	2	-	-
OTHsp3	-	-	-	-	-	-	-	-	-	2	-	2	2	-	-	-	-	-	-
PTEsp3	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
RUSFUG	-	-	-	-	-	-	-	3	-	3	-	4	3	4	3	1	-	-	-
GRIHUM	-	-	-	-	-	-	1	-	-	-	-	1	2	-	-	-	-	-	-
HELsp2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
LIMPER	-	-	-	-	-	-	-	-	-	-	2	3	2	2	-	-	-	-	-
MESspx	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
PELFUL	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-
PHABRA	-	-	1	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-
PTEOVA	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
PTEPAN	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-
SCRsp1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
SPHsp1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	-
THEsp2	-	-	-	-	-	-	-	-	-	-	3	1	-	2	-	-	-	-	-
TYLFRA	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
VANAMU	-	-	-	-	-	-	-	-	-	-	-	3	2	2	4	-	-	-	-
ATRsp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
CLACYP	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	3
DIDCAR	-	-	-	-	-	-	-	-	-	-	4	3	4	4	2	2	4	4	4
DROINT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	2	-	-
GALFRU	-	2	-	-	-	-	-	-	2	-	2	3	-	3	2	3	4	-	4
HEBCOR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
HYPSAL	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	1	2	2
LIMEQU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
LYCDEC	2	-	-	-	-	-	-	-	-	-	1	1	2	-	-	-	-	3	3
ODYPAN	-	-	-	-	-	-	-	-	3	-	4	-	-	-	-	4	-	4	-
PSIDIN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2
RUSHUT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	3	4	4
SASNOL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
ZYGsp2	-	-	2	-	-	-	-	1	-	2	2	2	2	2	-	3	2	2	-
ZYGsp3	-	-	-	1	-	-	-	1	-	-	-	2	-	-	4	-	2	2	-
ASPCAP	-	2	2	-	-	-	-	2	2	3	2	-	1	-	2	2	3	2	-
TWINSPAN	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Grouping	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1
Code	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	1	1
		0	0	0	0	1	1	0	1		0	1	1	1		0	1	0	1

Appendix 3: Soil variables for the 19 sample plots and the four TWINSPAN Associations.

Plot	twinspan group	Soil texture	pH (KCL)	Resistance (ohms)	Sodium (mg/kg)	Phosphorus (mg/kg)	Potassium (mg/kg)	Calsium (mg/kg)	Magnesium (mg/kg)	Copper (mg/kg)	Zinc (mg/kg)	Manganese (mg/kg)	Boron (mg/kg)	Soil colour	CaCO3 present
1B	1	SAND	6.9	3600	27	18	29	1.25	0.43	0.19	0.96	45.26	0.29	Orange/Grey	0
1D	1	SAND	7	3100	39	17	42	1.92	0.62	0.23	1.05	66.47	0.42	Light orange	0
1G	1	SAND	7	2300	65	24	40	2.54	1.09	0.26	1.06	41.33	0.76	Orange grey	1
2E	1	SAND	6.7	3200	24	15	37	0.97	0.3	0.12	0.62	22.38	0.25	Dark red	0
2F	1	SAND	7.2	3600	31	27	39	1.75	0.49	0.15	0.76	43.38	0.33	Dark orange	0
2G	1	SAND	7.8	3150	43	38	46	6.41	1.59	0.23	1.35	107.4	1.41	Orange/Grey	0
3A	1	SAND	6.5	2430	36	20	48	3.81	1.05	0.19	1.11	71.5	0.91	Dark red	0
1C	2	SAND	6.2	2120	51	15	80	1.06	0.54	0.23	0.57	12.03	0.46	Dark red	2
2D	2	SAND	5.7	4500	31	7	51	0.59	0.36	0.19	0.5	8.15	0.25	Dark red	3
3B	2	SAND	6	1930	59	15	54	1.28	0.63	0.26	0.44	6.99	0.35	Dark orange/grey	2
1A	3	SAND	5.8	2840	44	13	36	0.64	0.45	0.24	0.81	24.03	0.24	Brown red	3
1E	3	SAND	7.5	880	96	17	56	0.85	0.89	0.23	1.03	62.6	0.64	Light orange grey	3
3C	3	SAND	6.3	800	82	20	59	1.89	1.46	0.36	1.11	84.44	0.99	Dark red/grey	2
3D	3	SAND	6.9	560	142	16	134	1.57	1.83	0.54	0.96	91.8	0.84	Dark orange	4
3E	3	SAND	7	1300	66	21	53	1.27	0.7	0.32	3.41	195.8	0.68	Dark grey	0
1F	4	SAND	7.8	750	104	25	44	1.17	1.05	0.3	2.24	161.9	0.84	Dark brown	0
2A	4	SAND	8.7	1310	148	153	80	23	2.56	0.1	0.44	1.95	0.89	Grey	5
2B	4	SAND	8.5	370	430	363	245	39.3	7.95	0.16	1.23	20.48	1.78	Grey	5
2C	4	SAND	7.7	1410	75	42	66	2.19	1.27	0.3	1.98	148.9	0.91	Dark red	0

Appendix 4: Biotic variables collected ateach sample plot.

Plot	twinspan group	Percent total vedgetaion cover	Average clump size	Maximum clump size	Ave. Soil depth (m)	Ave. root depth (cm)	Deepest root depth (cm)	Distance from sea (m)	Lichens absent=0 present=1 abundant =2	Slope angle (degrees)	Vedge height average (m)	Vedge Height emerging (m)	Emerging species
1B	1	59.7	1.148	5.05	1.2	60	120	1500	0	0	1.2	2	LYCFER
1D	1	59.2	1.557	7.3	1.35	50	100	2500	0	0	1.2	2	SALLAN,LYCFER,MYTHET
1G	1	68.95	1.8635	9	1.22	60	100	60	2	20	1.3	1.8	ZYGMOR,LYCFER,STOUTI
2E	1	10.62	1.14	3	2	50	80	2500	0	0	1.2	2.85	RHULON,SALLAN
2F	1	40.56	0.659	3.8	2.3	70	110	1500	0	0	1.5	2	STOUTI,LYCFER,SALLAN
2G	1	43.01	0.81	6.5	1.9	40	100	800	1	5	1	1.5	ZYGMOR
3A	1	53.35	1.35	4.1	1.1	40	80	1500	0	0	1.25	2	RHULON,LYCFER,ERIAFR,STOUTI
1C	2	52.22	0.42	2.25	0.62	30	40	2500	0	10	0.6	1	ZYGMOR,ERIAFR
2D	2	59.2	1.56	7.3	0.8	20	40	3000	0	0	0.19	0.5	LEBSER,RUSSUB
3B	2	53.83	0.727	4	0.66	20	40	1000	1	0	0.6	0.8	OTHCYL,HERsp1,ZYGMOR
1A	3	47.94	0.399	2.25	0.44	20	40	200	0	10	0.2	0.5	ASPCAP, RUSFUG,LIMPER
1E	3	44.03	0.718	3	0.73	25	40	200	1	15	0.3	0.75	ZYGMOR
3C	3	60.73	0.52	9.2	0.48	20	40	600	1	0	0.2	0.4	DIDCAR,OSTOPP,LAMHOE
3D	3	63.8	0.48	1.9	0.37	30	35	300	1	25	0.2	0.35	ZYGsp3,ASPCAP
3E	3	39.6	0.33	2	1.2	35	70	150	2	10	0.45	0.8	ZYGMOR
1F	4	43.24	0.4769	2.2	2.2	20	100	150	2	10	0.25	0.5	LAMHOE
2A	4	59.44	0.874	5.8	2	20	40	100	2	10	0.2	0.5	ZYGMOR
2B	4	49.04	0.34	4.9	1	35	95	200	2	0	0.5	1.5	LYCFER
2C	4	50.68	0.51	3.52	2	40	120	500	1	0	0.3	1	ZYGMOR,OTHCYL