FERTILE ISLAND EFFECTS IN A SUCCULENT DESERT ECOSYSTEM IN NORTHERN NAMAQUALAND

T.S. Dlamini

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Supervisors: Prof. R.M. Cowling

and A/Prof. W.D. Stock

University of Cape Town

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ABSTRACT

Soil nutrients of three desert shrubs ranging from relatively short-lived to medium-lived and long lived were measured under the canopies and compared to open spaces in a succulent plant community in northern Namaqualand. The hypothesis that the development of islands of fertility islands is less likely to be strongly effected on relatively short-lived desert plants which are characteristic of the biome was tested using these comparisons. Soil nutrients were higher in soils under the canopies of *Stoeberia utilis* and *Ruschia* sp. nov. (relatively long and medium-lived to each other respectively) compared to the outside. Under the relatively short-lived *Ruschia cyathiformis* soil nutrients did not differ from soil outside the canopy. In surface (0-10 cm) soil nutrients were the same as in deeper soils (20-30 cm) for all variables measured. Comparisons to other arid ecosystems where plants are long-lived and strongly associated with fertile islands were made and conclusions about fertile island effects on the three shrubs were drawn.

INTRODUCTION

Desert ecosystems are usually characterised by a diversity of plant growth forms (Polis, 1991) which are able to survive in extreme environmental conditions including, temperature extremes, low and unpredictable rainfall, low humidity and sometimes high rates of evaporation (Garcia-Moya and Mckell, 1970). Faced with such a hostile environment most desert ecosystems are characterised by two(suites of plant species in terms of lifestyles) plant guilds; those that are long-lived and endure drought and short-lived (mainly annual) species that avoid drought (Noy-Meir, 1985; Inouye, 1991, Rundel and Gibson, 1996).

The succulent karoo of Namaqualand is, however, an unusual desert since it includes many relatively short-lived (3-50 years) and succulent shrubs (mainly Mesembryanthemaceae) as well as longer lived species. Long-lived species such as trees are rare and confined to water courses or dry river beds. The short-lived lifestyle is a consequence of predictable rainfall and fog ameliorated summers (Cowling *et al.*, 1994, Cowling and Hilton-Taylor, 1997, Esler *et al.*, 1997). Regular, albeit low winter rainfall has selected for species that emphasise reproduction and regeneration rather than persistence. Relatively mild winters result in winter growth; plants have shallow roots and consequently are vulnerable to mortality in response to occasional severe droughts (Esler *et al.* 1997, Cowling and Hilton-Taylor, 1997). Population turnover among this shrub guild is high - dead individuals and seedlings are a common feature for most communities.

Most desert soils are relatively infertile (Charley and West, 1975; Rundel and Gibson, 1996; Schlesinger, 1996), an observation which raises numerous questions about life survival strategies employed by plants growing there. One answer could be that longevity and the ability of shrubs to create fertile islands beneath canopies plays an important role in determining patterns of survival under these conditions.

Long-lived plants accumulate nutrients, especially organic matter, and cause significant modification of soil chemistry beneath their canopies. This is an autogenic process that may promote the persistence of shrubs in arid and semi-arid communities for many years (Belsky, 1989; Tiedemann and Klemmedson, 1977; Schlesinger, 1996). While it has been acknowledged that trees and shrubs affect the nutrient status of an ecosystem in several ways (Zak and Freckman, 1991), the formation of islands of fertility is associated with long-lived species (Crawford and Gosz, 1982, Noir-Mey, 1985). Though it is difficult to age plants, the fertility island- effect is expected to be more pronounced under longer than shorter lived species.

Fertile islands are primarily due to localisation of litter fall by plants (Strojan, 1979). The ability of shrubs and trees to reduce soil erosion (Belsky, 1989) also contributes to the process and is of particular importance in desert ecosystems where regularly high velocity winds are a common phenomenon (Garcia-Moya and McKell, 1970). In addition, litter is accumulated from annual grasses and forbs growing under the protection of shrubs which further add to the pool of soil nitrogen and carbon under the their canopy when they die. Plants also improve soil fertility when they eventually die (Tiedemann and Klemmedson, 1977, Barnes and Archer, 1996). In the past many publications have attempted to quantify and describe in detail the structure of such shrub-induced chemical alterations (Garcia-Moya and McKell, 1970; Charley and West, 1975, Belsky, 1989, Belsky *et al.* 1992). For example, Belsky *et al.* (1992) has shown that these differences lead to higher nutrient concentrations in understorey plants compared to plants growing in the open in the East African savanna. Similar patterns have been reported for northern American deserts (Charley and West, 1975).

To date no work on nutrient patterns has been undertaken in the arid succulent shrub-dominated regions of southern Africa.

However, given the apparent high rate of turnover of plant species (Cowling and Hilton-Taylor, 1997) it is predicted that nutrient patterns would differ from the above mentioned studies for two reasons. Though north American deserts resemble the succulent karoo of Namaqualand in climatic regimes in a number of ways, for example, the Mojave desert in southern California is also a winter rainfall area (Rundel and Gibson, 1996), growth from domninance differs. The succulent karoo of Namaqualand is arguably the richest arid region in the world for plant species diversity (Cowling *et al.*, 1989, Cowling *et al*, 1997), however, growth form diversity is low as compared to the neighbouring Nama karoo biome and other desert ecosystems of the world (Cowling *et al.*, 1989, Cowling and Hilton-Taylor, 1997). Other deserts are usually characterised by high structural diversity for adaptation purposes (Rundel and Gibson, 1996).

The aims of the project were as follows: Firstly, to test the hypothesis that due to high rate of species turnover in the succulent karoo, fertile islands are not expected to exist under typical short-lived and medium-lived shrubs. In order to do this we, sampled soils beneath three shrubs belonging to the family Mesmembryanthemaceae which range from a short lived species (*Ruschia cyathiformis*) to medium lived species (*R.* sp. nov.) and to a relatively long-lived species (*Stoeberia utilis*). Secondly, the aim was to use these results to compare the results to soil fertility patterns reported in the north American deserts which experience similar climates but differ in vegetation by being dominated by long-lived shrubs.

MATERIALS AND METHODS

STUDY AREA

The study site is located at an altitude of about 80m about 50 km north of Port Nolloth (Fig. 1). The climatic variables and life form characterises of the area are typical of the arid fringe of the succulent karoo biome (Rutherfold and Westfall, 1986). Three weather stations in the vicinity of the study site provide climatic indicators which suggest a cool, dry desert climate. The data is based firstly on a weather station that was situated in Alexander Bay town (28°37'S 16°29'E, alt 12m) which operated between 1931 and 1950 then moved to Alexander Bay airport which was in operation from 1951 till 1984. The rest of the data is recorded in a station that is placed just north of Port Nolloth (29°14'S 16°52' E, alt 4m). The area receives an average rainfall between 63 mm at Port Nolloth, 41 mm at Alexander Bay town and 46 mm at Alexander Bay airport, respectively. The peak rainfall period is April to the end of August (Fig. 2a-e) hence the area is one of the Winter rainfall deserts of the world. Rainfall is low but highly predictable for its total amount (Figs. 2f) when compared to other winter rainfall areas (Esler *et al.*, 1997).

The study site is located within the fog zone of the arid west coast of southern Africa. Precipitation brought about by fog. Fog accounts for ca. 130 mm of rainfall per year which is more than seven times the amount of mean annual rain (Werger, 1978, Desmet, 1996). The occurrence of fog peaks in spring and autumn when wind velocities are low and flow of air is still and directed onshore and its occurrence is more predictable than rain thus it contributes significantly to the available amount of moisture (Werger, 1986, Desmet, 1996). Dew is common and it also contributes to the moisture pool of the area (Werger, 1978).

Soils are classified as calcareous sands (sand content 96-98%) and are basic (soil pH of ca. 8.0) (Desmet, 1996). They lie on an impermeable layer (less than 1m deep) called dorbank. The vegetation of the study site falls within the *Ruschia ruspis-arcuatae-R.* aff.*supaniculata* transitional veld of the succulent karoo (Desmet, 1996). The plant community is described as a tall deciduous to open shrubland called Vye sandveld or *Stoeberia utilis* sand veld. Vegetation cover is about 20% and dominant species include: *Tetragonia fruiticosa, Arctotis diffusa, Chaetobromus* involucratus, *Stoeberia utilis*, *R. cyathiformis*, *R.* sp. nov. and *Osteospermum oppositifolium.*

EXPERIMENTAL DESIGN

To investigate the occurrence of fertile islands in the study area (and in order to make a comparison of the fertility of soils at the different locations), soil samples were collected under and beyond the canopies of three shrub species. Sampling was carried out in a uniform area of ca. 1 ha. For this purpose three dominant species in the site were chosen, namely *Ruschia cyathiformis* a perennial dwarf shrub growing up to 30 cm high with succulent leaves and an erect to weakly decumbent growth habit, *Ruschia* sp. nov. an erect, spreading leaf succulent shrub up to 1 m high and *Stoeberia utilis* an erect leaf succulent shrub growing up to 1.5m.

All three species belong to the family Mesemembryamthemaceae and were chosen on the basis of their assumed longevity. *R. cyathiformis* had more dead plants than living ones in the community and was treated as a short-lived shrub whereas *S. utilis* had fewer dead plants and was treated as a long-lived plant, whilst *R.* sp. nov. appeared to be an intermediate between the two. In order to quantify these observations, the proportion of dead plants to living plants was estimated by counting a hundred plants of each species along a sampling transect. Dead plants included those which appeared to be at the final stage of senescence whereas seedlings and plants which appeared vigorous were scored as alive.

Shrubs contribute directly to the nutrient pool under their canopies due to litter fall, hence soil fertility under shrubs is expected to be a function of plant size (Barnes and Archer, 1996). We thus estimated volumes for each of the 100 plants counted in the line transect, by measuring the height and two diameters of the canopy. Volumes of shrubs were calculated as cylinders for *R. cyathiformis* and *S. utilis* and as a cone for *R.* sp. nov. because of the respective shapes of the shrubs.

Soil sampling procedures

A total of 15 plants, representing five replicates of each of the species, were sampled. Soil samples were taken from three locations: (i) under their canopy (canopy zone), (ii) at the edge of the canopy (one canopy distance), and (iii) in the open space surrounding the shrubs (two canopy distances). The average canopy distances of *S. utilis*, *Ruschia. sp. nov.* and *R. cyathiformis* plants were 82, 52 and 48 cm, respectively. In addition to the horizontal sampling, soils were also taken along a vertical gradient at two different depths i.e. at 0-15 cm and (ii) at 20-30 cm below the soil surface. This was carried out with the aim of testing if there is a significant increase of nutrients in deeper soils due to accumulation and leaching.

To obtain top layer samples, superficial organic matter (litter) was carefully removed and about 10 portions of soil were scooped out along the circumference of the sampling distance. These portions were then bulked to make a representative sample of about 1 kg of soil. Below surface samples were obtained in a similar way but in their case, holes (ca. 20-30 cm deep) were dug with a spade making them as wide as possible to avoid surface sand falling back into the hole. A total of 90 samples representing different species, locations and depths were collected. All soil samples were air dried and then stored at room temperature for six weeks before they were passed through a 2 mm sieve to remove gravel and litter in preparation for analysis.

LABORATORY ANALYSIS

In the laboratory each sample was analysed for several soil fertility indices including total N and P which are the most commonly limiting biological elements in desert ecosystems (Crawford and Gosz, 1982). Other soil variables analysed were organic matter, electrical conductivity and soil pH. Since the study focuses on shrub-induced soil heterogeneity, cations which are normally considered in evaluating the importance of physical processes in determining soil fertility (cation exchange capacity) (Schlesinger, 1996), were not included. Details of each analysis are discussed below:

Total N and P

Total nitrogen was analysed by digestion of 1g samples of soils using the Kjeldahl method followed by colorimetric determination in phenol. Total Phosphorus was determined colorimetrically by ammonium molybdate blue procedure using stannous chloride as a reductant (Murphy and Riley, 1962).

Organic matter

Soil organic matter (C) was determined by dry combustion of 10g samples in a muffle furnace at 450°C for 16 hours. Afterwards, samples were cooled down in a dessicator and weighed. The weight lost during the combustion process was then calculated and expressed as the percentage of organic matter in the samples.

pH

To measure pH, for each sample ca. 20g of soil was weighed into a small bottle and 50 ml of 0.01M $CaCl_2$ solution was added prior to shaking were placed in an automatic shaker for 30 minutes. A potable pH meter was calibrated with buffers for pH 7 and 10 before soil pH's were measured. The probe was washed in distilled water between readings in order to get accurate results.

Electrical conductivity

A 1:1 suspension was prepared by weighing 25g of soil into a bottle and adding 25 ml deionised water in order to compare the total amount of dissolved solids in solution by measuring electrical conductivity. Before readings were taken, the mixture was shaken vigorously for two minutes and the probe was rinsed in deionised water in between readings. These values were referenced to 0.01M NaCl solution.

STATISTICAL ANALYSIS

All data have been analysed by three-way analysis of variance for the purpose of exploring effects of species, location and depth. In the cases where there were significant species and location effects the results were further analysed by two way or one way analysis of variance where appropriate. An LSD (95%) multiple range test was used to show differences between means in all cases where there were significant differences. Different volumes of shrubs, which further leads to differences in canopy distances 1 and 2, were also taken into account as covariates.

RESULTS

Plant size mortality relations

Plant mortality results show that 70% of *R. cyathiformis* plants counted along the sampling transect were dead (Fig.3a). In this case, the size distribution structure of live plants is skewed to the left since more than 25% of individuals were still in the seedling stage (0-0.1m^3). Mature plants measured at least 0.3 m^3 and were poorly represented in the population. On the other hand a different ratio of dead to alive plants was observed in *R.* sp. nov. and *S. utilis* where only about 10 % of plants were dead (Fig 3b& c). Consequently, there is a similarity in distribution of plants into size classes between the three shrubs in that there is a high proportion of seedlings in each case.

Soil nutrient patterning

A three way analysis of variance showed that there were significant species and location effects between and within shrubs for N, SOM:N, pH and electrical conductivity but depth had no significant effect on nutrient patterns. (Fig. 4a, b, C, (Tables 1a-d). Three-way analysis of variance also showed that there are no species-location-depth interactions among the significantly different soil variables, except for soil pH (Tab. 1c). There were no significant differences in SOM and P concentrations. A comparison of soils found at different locations showed that there were higher concentrations of N on surface soils under the canopy of *S. utilis* and *R.* sp. nov.than soils outside the canopy whereas N concentration in soils under the canopy of *R. cyathiformis* did not differ significantly from soils outside the canopy (Fig 4). N concentration declined from 0.4 to 0.24 $mg.g^{-1}$ in *S. utilis* from the canopy to the open and from 0.4 to 0.2 $mg.g^{-1}$ in *R.* sp. nov.

When the SOM:N ratio was calculated by dividing the concentration of SOM by N (in % dry weight), *R. cyathiformis* had the highest value followed by *R.* sp. nov. and *S. utilis* had the lowest value. There were no significant differences between the soil salinity levels (as indicated by electrical conductivity measurements) found under the canopies of the three species, though differences with location were noted in each species (Tab. 1d). When pH results were analysed, there were significant interactions between species and locations (Tab. 1c). A two way analysis of the pH results showed that soils at two canopy distance are the same in all three species but soil under canopies and at the edge of the canopies differ significantly (Fig.4). Distribution of soil nutrients in spaces between shrubs in the community appears to be uniform as there were no significant differences in soils obtained outside the canopy of each shrub (Fig. 5). All results did not change when plant volumes were included as covariates in the data analysis.

DISCUSSION

Population dynamics

The high mortality rate observed in the population structure of *R. cyathiformis* in the studied community indicates that the shrub lives for shorter periods of time compared to the other two shrubs (Fig.3c). Contrary, to expectations held before the study was initiated, that the population structure of *R.* sp. nov. should follow a pattern that is somewhat intermediate between the two, its structure resembles the structure of *S. utilis* in a number of ways. This is illustrated by its equal number of dead plants (less than 10 % of counted individuals) (Fig.3a-b). Therefore, though it is difficult to age the plants, it can be seen from the results that *R. cyathiformis* is relatively short-lived compared to the other two shrubs since it has a more dynamic population structure.

The plant size distribution structures of the three species is uneven and clearly depicts a successful recruitment profile since all the size classes are fairly well represented and the seedling stage had the highest number of individuals per class (Figs.3a-c). All the study species had a unimodal population distribution structure that is skewed to the left because of high seedling representation which could indicate that recruitment is not delayed until late stages of growth (senescence). This community is highly dynamic and there is little competition between and among succulent shrubs which leads to assumptions that species are functionally equivalent and community membership is determined by a lottery process (Werger, 1986, Cowling and Hilton-Taylor, 1997). The patterns of high turnover suggested here are characteristic of plants adapted to the study area and are widely attributed to predictable winter rainfall and fog ameliorated summers (Esler *et al.*, 1997). Occasional droughts play a crucial role in shaping the population structure of the community because they cause mass death of species and re-arrange emerging competitive hierarchies (Von Willer *et al.*, 1992).

In other deserts of the world where vegetation is dominated by big, long-lived plants and turnover is low, population structures are usually uneven and skewed to the right and thus different from the situation in this study (Rundel and Gibson, 1996, Noy-Meir, 1985).

Soil nutrient patterning

The exact age when plants begin to create fertile islands is unknown but since N is a limiting nutrient of plants in arid areas, sharp concentration gradients in typical long-lived plants are expected to begin show as the plants approach maturity. This invokes the notion that *S. utilis* which is relatively longer lived should modify soil characteristics under its canopy more than relatively short-lived perennial plants of the succulent karoo. Therefore, since *R. cyathiformis* had the highest rate of turnover (Fig.3a), as it showed highest seedling recruitment and had more dead individuals, it is expected that fertile island effects should be minimal in *R. cyathiformis*, highest in *S. utilis* and intermediate between the two in *R.* sp. nov. Species in the studied community had significant effect on some soil nutrients (Table 2a-d). Significantly different soil variables under the shrubs were not the same for all three species (Fig. 4). Furthermore, soil fertility under the three different species did not decrease at the same rate from root to canopy crown. As expected there was no difference in N concentration in the three different locations in *R. cyathiformis*, a moderate gradient in *R.* sp. nov. and a relatively steeper gradient in *S. utilis*. Thus data from this study clarifies the hypothesis under test to a large extent because N accumulation is supposed to be induced by shrubs and the species under test are not expected to show an equal ability to carry out the process.

Apparently, all the species regardless of the expected extent of fertile island effects showed similar patterns of a reduction in salt contents with increasing distance from the canopy though there were slight differences in the gradients.

The similarity between the three species regardless of marked differences in N content means soil reaction under all the study shrubs and their surrounding follows a uniform pattern which is not necessarily determined by type of species. The best explanation for these trends could be that the desert shrubs invariably localise salts that are carried by sea winds by trapping them together with dust particles in the nutrient build up process discussed in the introduction. There is not enough evidence in this study to support the idea that accumulation of salts under shrubs may be primarily due to depletion of sources in its surroundings as suggested by Garcia-Moya and Mckell (1970). The soils in the area are generally alkaline as all soils samples examined in this study had pH in excess of 7.5 which does not deviate from our expectations because the soils are classified as calcareous sands. On the other hand the significant differences in soil pH between the species is surprising and these differences could indicate that soil reaction is characterised by species to some degree in the studied community.

Though direct comparison of soil nutrients with other studies may be of limited utility because of differences in soil types and differential enrichment as a function of species, worthwhile observations in relation to similar undertakings have been made. The low N values found in the study area are comparable to figures reported by Charley and West (1975) for three semi-desert sites in Utah (southern USA), as ranging between 0.03 and 0.24 % dry weight for surface soils. They however also found sizeable vertical gradients which is not the case in this study. Garcia-Moya and Mckell (1970) studied nutrient patterning of soils in the Gold Valley of Mojave desert and found a three-fold decline of soil N from surface soils to 45 cm depths under *Larrea divaricata*. They also reported significant reductions in soils under the canopies of *Acacia gregii* (0.05 to 0.02 %) and *Cassia armata* (0.03 to 0.013%). In a similar study carried out in six communities of the Mojave and Utah deserts, Charley and West (1975) noted moderate to steep concentration declines of SOM, N and SOM:N values beneath the canopies of four woody species from surface to subsoils which they largely attributed to lack of soil mixing.

If soil mixing is of special significance as implied in these studies, the sandy soil texture of our study site could partly account for these differences. In this study, a uniform distribution of nutrients, especially nitrogen, at different depths was found. These soil patterns especially N could indicate that there is no significant removal from surface soils by leaching. The maintenance of N under shrubs may be a consequence of shrub growth, litter fall and re-establishment (Rundel and Gibson, 1996). Therefore, one would expect the *R. cyathiformis* which according to our hypothesis is not associated with fertile islands to show less ability to retain N under its canopy compared to *S. utilis*, which is not the case however. The effect of desert shrubs in creating heterogeneous soil distribution by accumulation of nutrients under their canopies (as implied in the study) may promote the persistence of shrubs in the community and the desertification of grasslands that are invaded by shrubs (Schlesinger, 1996).

According to Garcia-Moya and Mckell (1970), the total nitrogen content of desert soils is in shallow surface layers where it remains tied to the organic matter of living plants. When organic matter is mineralised the nitrogen is released and leaches through sandy soil where it is later recovered by an extensive root system of shrubs. Data obtained in this study is not sufficient to validate or contradict these claims because sampling was limited to 30 cm below the surface. However, the fact that nutrient concentrations were similar at the surface and at depth treatments suggests that leaching does not occur. A detailed study of the rooting systems of the study species could help explain this trend since it is documented that differential root systems may influence the patterns of nutrient availability along the soil profile (Garcia-Moya and Mckell, 1970; Belsky, 1989, Belsky *et al.* 1992). A sharp decrease in soil N from surface to subsoils is expected for plants which have shallow roots and limited ability to recover nutrients along the soil profile whereas deep rooted plants provide relatively high soil N to greater depths. Apparently, plants in the study community effectively harvest water resources from shallow soil horizons.

Since rain falls in winter and no significant storage are accumulated to allow growth in the spring and summer months (Esler *et. al.*, 1997). The shallow rooting patterns in these desert shrubs are a sign that they are drought intolerant and accounts for the mass deaths during occasional droughts that play a role in shaping the highly dynamic population structure discussed above (Cowling and Hilton-Taylor, 1997).

There is a significant reduction of N from canopy to open spaces in *S. utilis* and *R.* sp. nov. while in *R. cyathiformis* a uniform distribution of N in soils under shrubs and the open was observed (Fig. 4). N concentration was reduced two-fold in *R.* sp. nov. while in *S. utilis* the reduction was more significant (Table 4). Although the exact source of the nutrient enrichment of the soils under the two shrubs was not investigated empirically, it is very likely that it is due to nutrient inputs by litter and other factors discussed such as the role of shrubs in reducing the effects of soil erosion. The soil nutrient gradients noted in *S. utilis* and *R.* sp. nov. confirm that shrubs affect redistribution of nutrients between their canopies and their surroundings to some extent as suggested by Charley and West (1975) and Belsky (1989). Unlike in south American deserts where good correlations between total C and N in soils under tree canopies have been noted (e.g. Charley and West (1975), the N results in this study are not consistently matched by SOM. When these variables were analysed separately, SOM concentrations did not decline significantly with increasing distance from the centre of the canopy in all the three species whereas SOM and SOM:N values did. This is surprising because in *S. utilis* one would have expected a declining SOM trend similar to the one observed in N concentrations because the two nutrients are the main components of organic matter which accumulates under shrubs when fertile islands are formed. A possible factor behind this is wind action which removes the lighter material of litter which may contain a high proportion of organic matter whereas SOM may remain in the soil when mineralisation is already initiated.

Therefore, decomposition of litter by soil micro-organisms beneath shrubs may partly account for the observed distribution of SOM and N.

CONCLUSION

The results of this study show that the fertile island effect is more intensely expressed in the longer-lived *S. utilis* as compared to the relatively short-lived *R. cyathiformis*. This is in support of the hypothesis that due to the high rate of turnover, plants of the succulent karoo of Namaqualand biome are not expected to form strong or clearly defined islands of fertility because they do not persist for periods long enough to enrich the soil properties under their canopies. Plants in this semi-desert type survive by means of producing seedlings in large quantities. Such a mode of recruitment differs from other deserts where recruitment is low and plants persist in the environment. Survival is by means of utilisation of limited resources by fewer long-lived plants with expensive adaptive means to survive drought and other desert hardships. The nutrient patterning data is in agreement with prior predictions and is complemented by the plant mortality results.

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Captions for figures

Figure 1: Location of study area and sampling site (Modified from Desmet, 1996).

Figure 2: Climatic diagrams developed from records of three weather stations near the study area (Modified from Desmet, 1996).

Figure 3: Population structure of the three study species showing proportions of dead plants to living ones and their distriibutions into different volume classes.

Legends: Alive dead

Volume (m^3) of shrubs in each class shown in Fig. 3.

Species	Shrub classes					
	1	2	3	4	5	6
S.utilis	0-1	1-2	2-3	3-4	4-5	>5
R. sp. nov.	0-.2	.2-.4.	4-.6	.6-.8	.8-1	1-1.2
R. cyathiformis	0-.1	.1-.2	.2-.3	.3-.4	.4-.5	.5-.6

Figure 4: Chemical characteristics of soils sampled from study area. The left bar represents surface soils (0-10 cm) and the right bar represents deeper soils (20-30 cm). Locations 1, 2 and 3 stand for under, at the edge and outside the canopy of each shrub, respectively.

Figure 5: A comparison of soils taken outside the canopies of *Sutilis, R.* sp. nov. and *R. cyathiformis*, represented as species 1,2 and 3 respectively

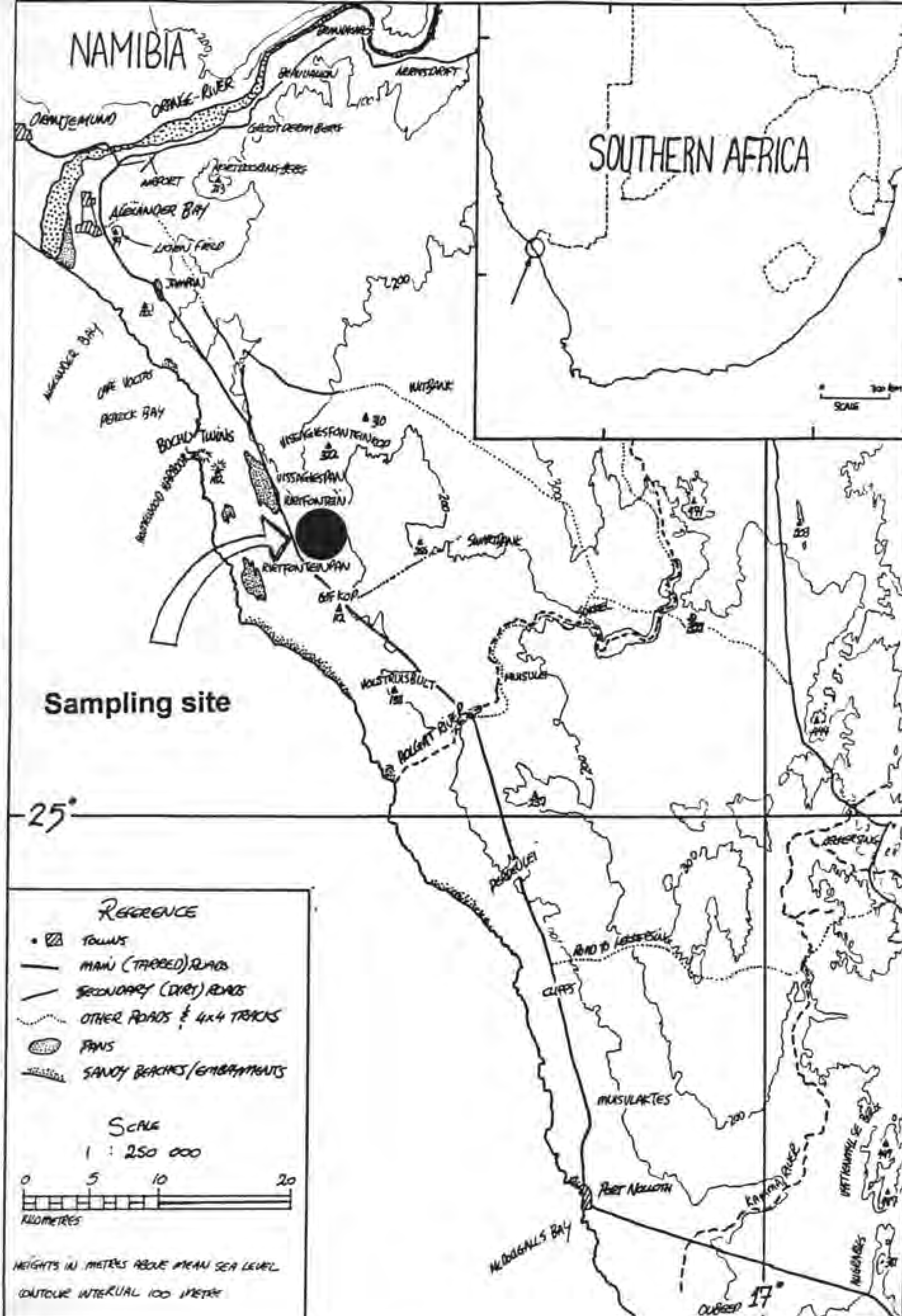

NAMIBIA
ORANGE RIVER
ORANJEMUND
ALEXANDER BAY
SOUTHERN AFRICA
Sampling site
25°
17°
PORT NOLLOTH
McDOUGALLS BAY
REFERENCE
TOWNS
MAIN (TARRED) ROADS
SECONDARY (DIRT) ROADS
OTHER ROADS & 4x4 TRACKS
PANS
SANDY BEACHES/EMBANKMENTS
SCALE
1 : 250 000
0 5 10 20
KILOMETRES
HEIGHTS IN METRES ABOVE MEAN SEA LEVEL
CONTOUR INTERVAL 100 METRE

Figure 1

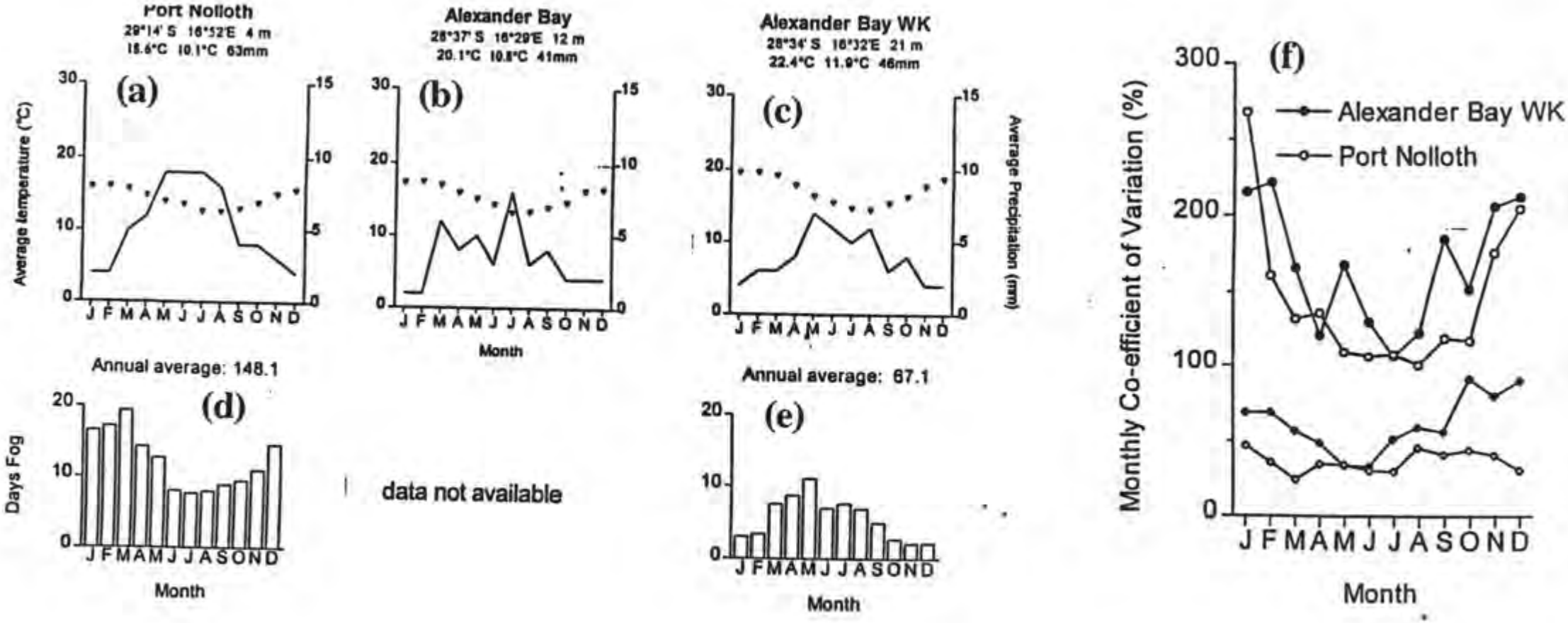

Port Nolloth
29°14' S 16°52'E 4 m
18.6°C 10.1°C 63mm
Alexander Bay
28°37' S 16°29'E 12 m
20.1°C 10.8°C 41mm
Alexander Bay WK
28°34' S 16°32'E 21 m
22.4°C 11.9°C 46mm
(a)
(b)
(c)
(d)
(e)
(f)
Average temperature (°C)
Average Precipitation (mm)
Days Fog
Monthly Co-efficient of Variation (%)
J F M A M J J A S O N D
Month
Annual average: 148.1
Annual average: 67.1
data not available
Alexander Bay WK
Port Nolloth

Figure 2

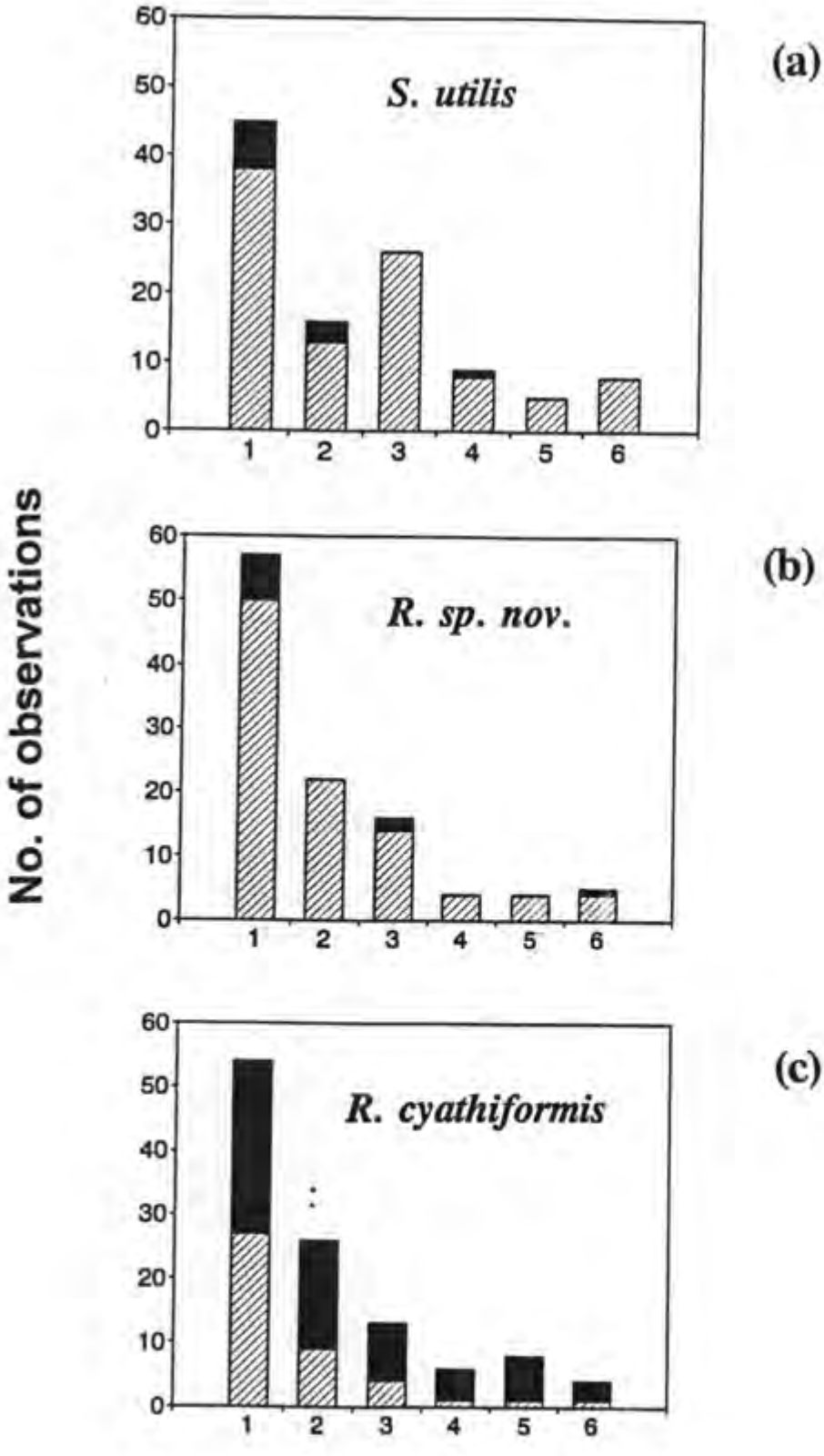

No. of observations
(a)
S. utilis
(b)
R. sp. nov.
(c)
R. cyathiformis
60
50
40
30
20
10
0
1
2
3
4
5
6
Shrub size classes

Figure 3

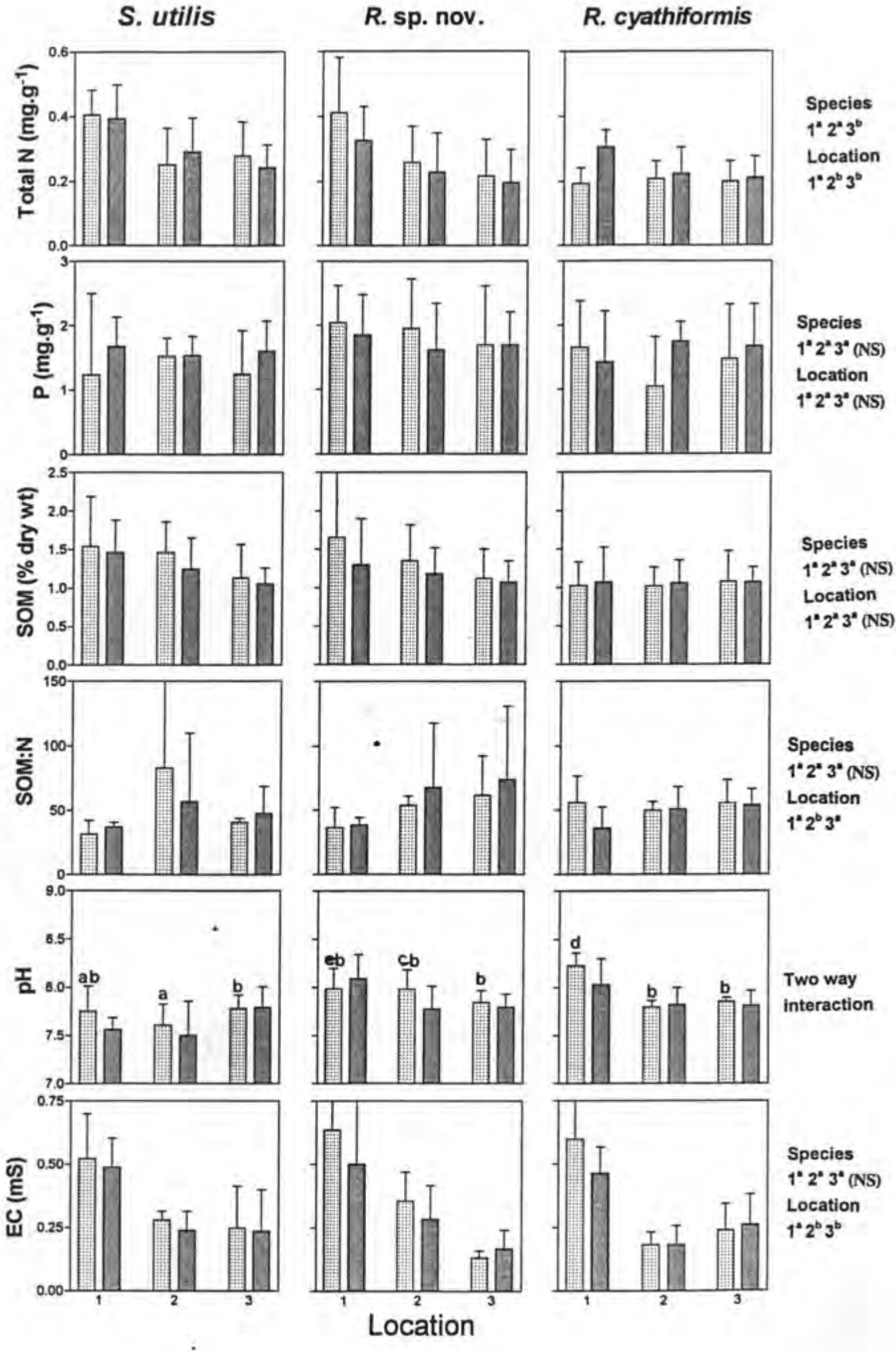

S. utilis
R. sp. nov.
R. cyathiformis
Total N (mg.g-1)
P (mg.g-1)
SOM (% dry wt)
SOM:N
pH
EC (mS)
Species
1a 2a 3b
Location
1a 2b 3b
Species
1a 2a 3a (NS)
Location
1a 2a 3a (NS)
Species
1a 2a 3a (NS)
Location
1a 2a 3a (NS)
Species
1a 2a 3a (NS)
Location
1a 2b 3a
Two way
interaction
Species
1a 2a 3a (NS)
Location
1a 2b 3b
ab
a
b
eb
cb
b
d
b
b
Location

Figure 4

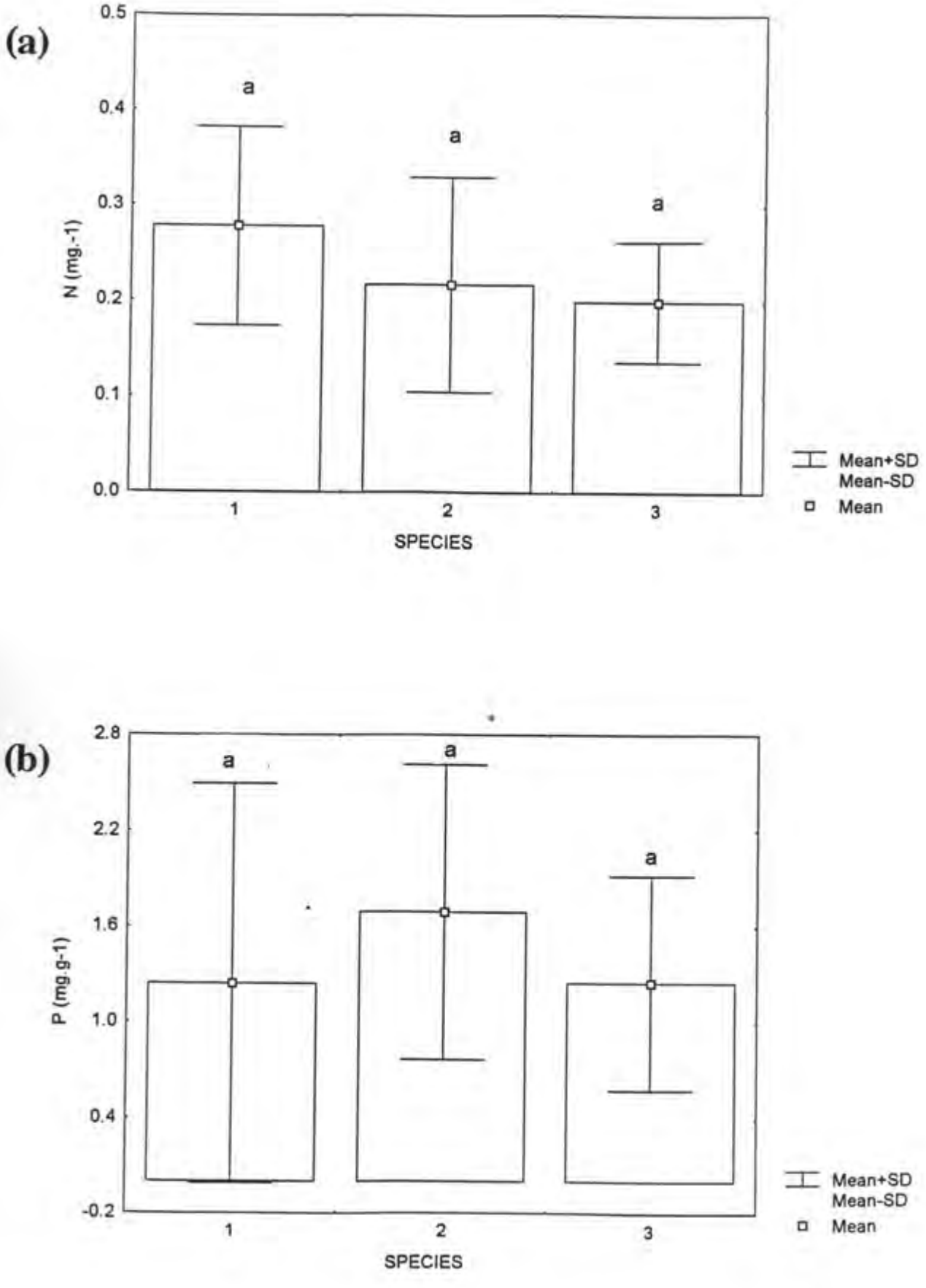
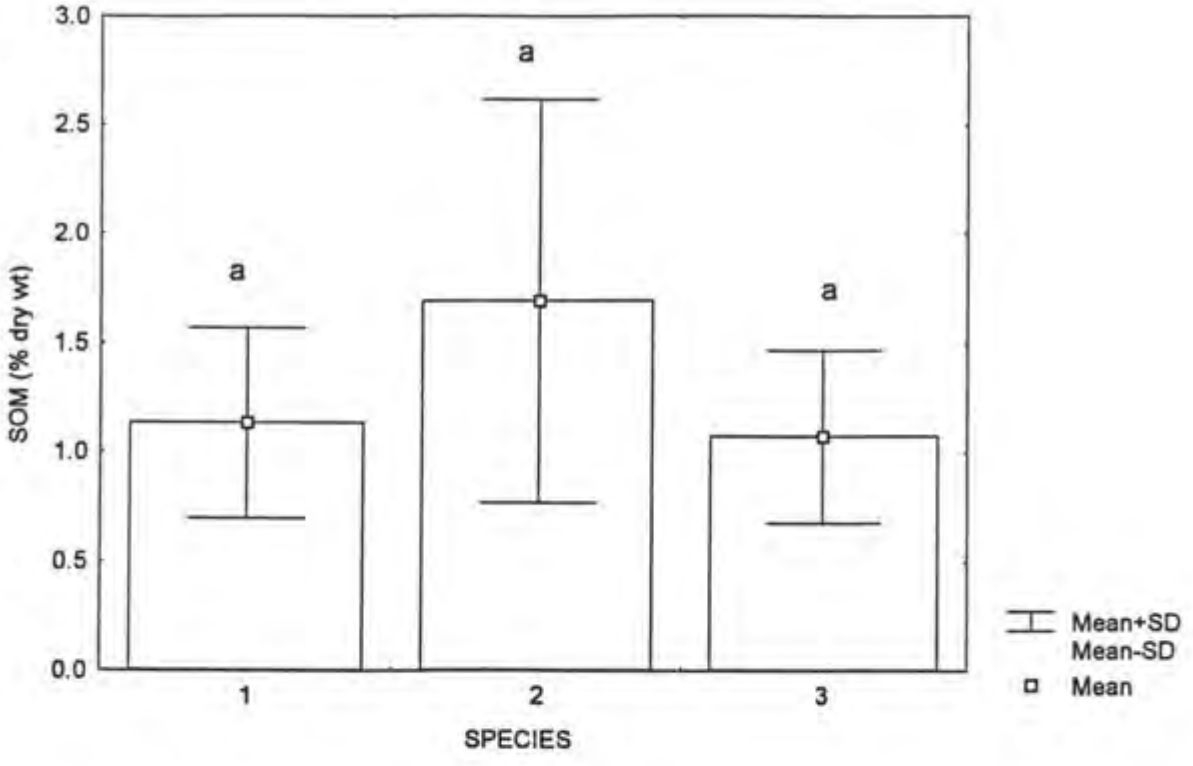
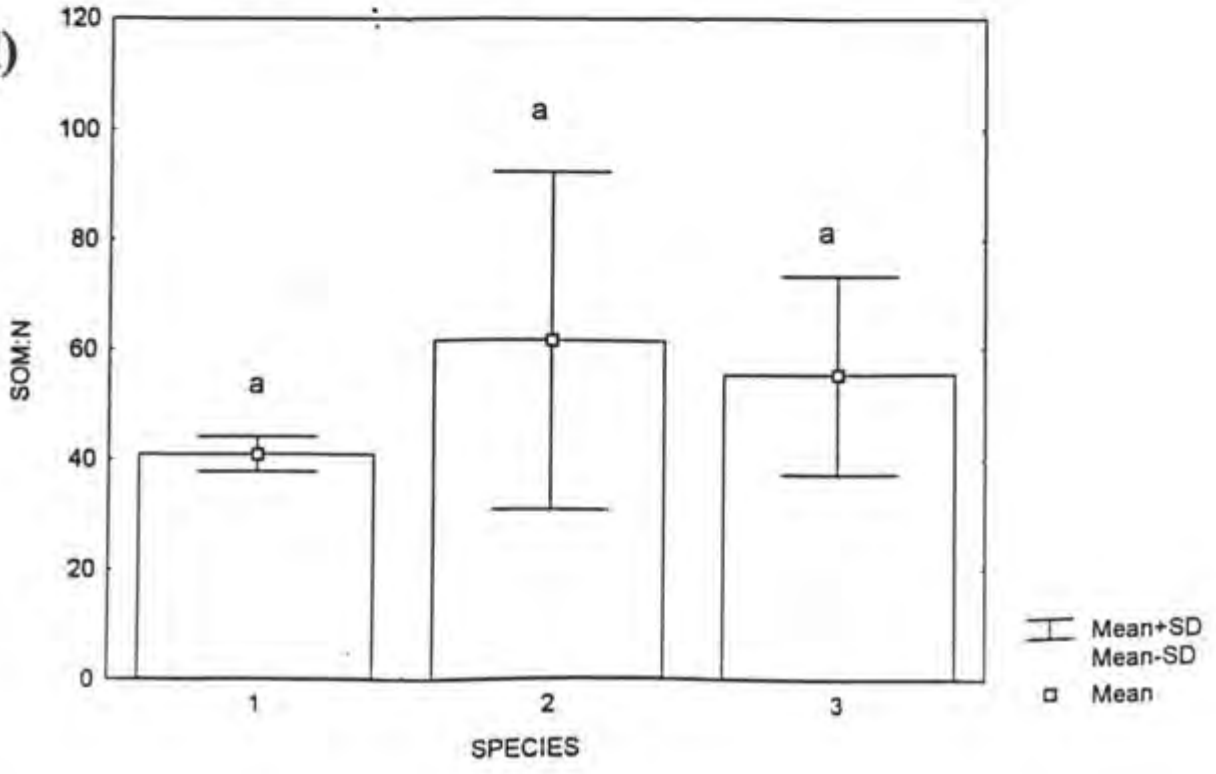

(a)
0.5
0.4
0.3
0.2
0.1
0.0
N (mg.-1)
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean
(b)
2.8
2.2
1.6
1.0
0.4
-0.2
P (mg.g-1)
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean

Figure 5

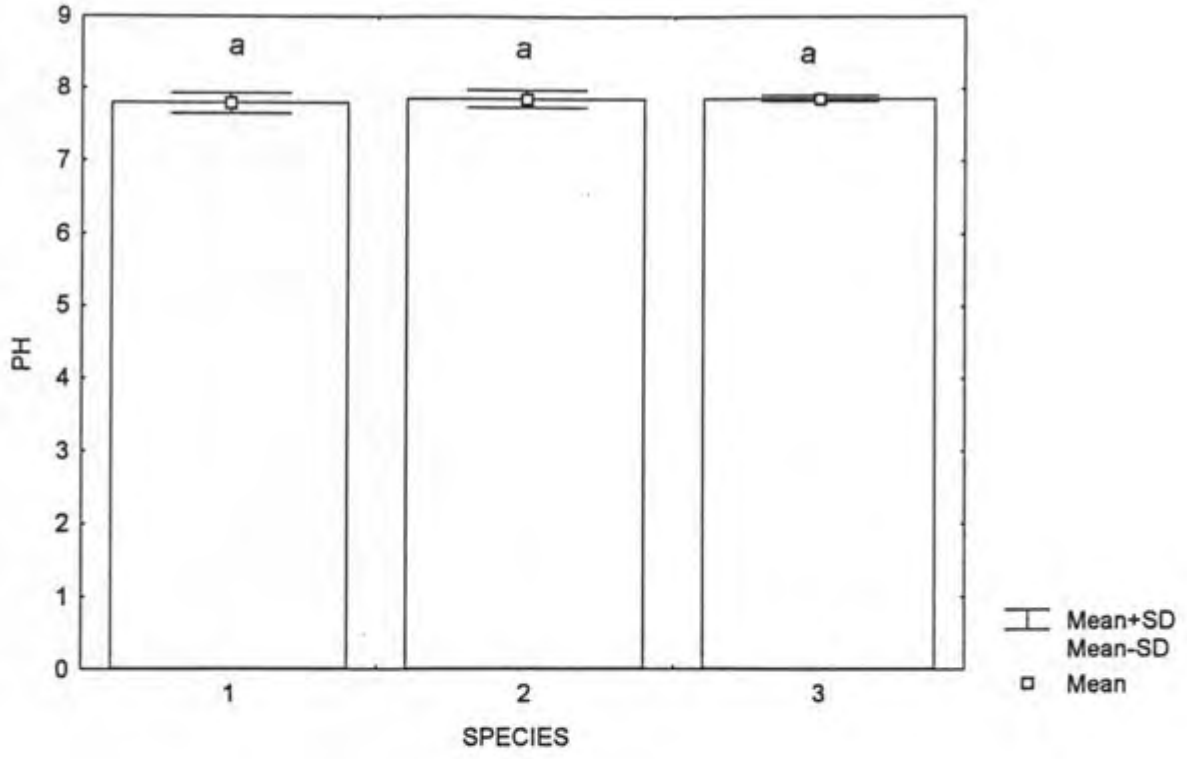
(c)


3.0
2.5
2.0
1.5
1.0
0.5
0.0
SOM (% dry wt)
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean

(d)


120
100
80
60
40
20
0
SOM:N
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean

(e)


9
8
7
6
5
4
3
2
1
0
PH
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean

(f)

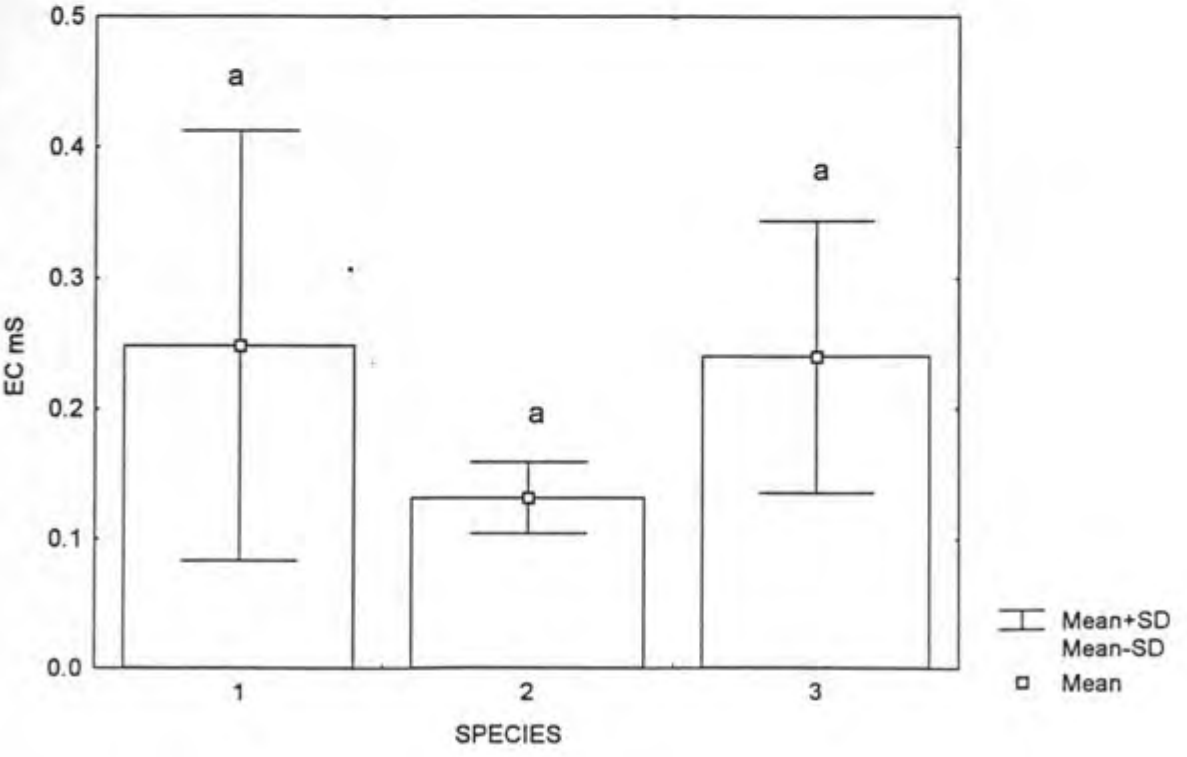

0.5
0.4
0.3
0.2
0.1
0.0
EC mS
a
a
a
1
2
3
SPECIES
Mean+SD
Mean-SD
Mean

Table 1.: Results of three-way analysis of variance for effect of species, location and depth for so variables in study area. *** $P<0.001$, **$P<0.01$, *$P<0.05$, NS = non significant.

(a) Total nitrogen

Main effects	df (effect)	df (error)	F-ratio	Significance
Species	2	72	6.640	**
Location	2	72	12.528	***
Depth	1	72	0.265	NS
Interactions			F-ratio	Significance
Species x location			1.574	NS
Species x depth			1.572	NS
Location x depth			0.221	NS
Species x location x depth			0.960	NS

(b) SOM:N ratio

Main effects	df (effect)	df (error)	F-ratio	Significance
Species	2	72	0.294	NS
Location	2	72	3.604	*
Depth	1	72	0.098	NS
Interactions			F-ratio	Significance
Species x location			1.181	NS
Species x depth			0.572	NS
Location x depth			0.239	NS
Species x location x depth			0.525	NS

(C) pH

Main effects	df (effect)	df (error)	F-ratio	Significance
Species	2	72	15.76	***
Location	2	72	7.342	**
Depth	1	72	0.098	NS
Interactions			F-ratio	Significance
Species x location			3.599	**
Species x depth			0.111	NS
Location x depth			0.282	NS
Species x location x depth			1.359	NS

(d) Electrical Conductivity

Main effects	df (effect)	df (error)	F-ratio	Significance
Species	2	72	1.580	NS
Location	2	72	3.589	*
Depth	1	72	0.900	NS
Interactions			F-ratio	Significance
Species x location			1.523	NS
Species x depth			0.394	NS
Location x depth			0.071	NS
Species x location x depth			0.135	NS

Table 2: Results of two way analysis of variance for effect of species and location for soil pH in t succulent karoo. *** $P<0.001$, ** $P<0.01$, * $P<0.05$, NS = non significant.

Main effects	df (effect)	df (error)	F-ratio	Significance
Species	2	81	15.723	***
Location	2	81	7.322	***
Interactions			F-ratio	Significance
Species x location			3.589	***