Rockiness and Response to Rest:

How do semi-arid perennial species respond over the short-term to rest from grazing, along a gradient of rockiness?

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Abstract

This study explored the short-term dynamics of four Succulent Karoo growth forms in response to rest from grazing pressure along a gradient of rockiness in Paulshoek, Namaqualand, South Africa. The area was fenced off in November 2005, and measurements of height and breadth for individual plants within 16 paired plots were taken annually between January and March from 2006-2011. Ordination was used to see the effect of rockiness in multivariate space, and percentage mortality, recruitment and population change were analysed for the seven dominant species. There was no significant difference between protected and grazed plots, though palatable species had noticeably higher volumes in the protected plots. In general there was little response to rainfall in terms of number of individuals and plant volume over the 6 year period. However, increase in percent rockiness correlated with an increase in number of individuals and volume of all species in general and for most of the seven dominant species. This supports the theory that rocky uplands (i.e. more micro-sites) are important in accelerating vegetation recovery from grazing and in maintaining the high compositional variability found in the Succulent Karoo. Overall, the non-significance of most of the results indicates that 6 years is not long enough to see considerable responses in Succulent Karoo vegetation. This implies that decadal times-scales are the shortest period to consider in conservation and range management as this will be when climatic/episodic events may prompt responses in vegetation.

Introduction

The effects of livestock grazing on plant communities has been widely researched, with some authors showing positive results such as an increase in plant diversity, but many stressing the negative outcomes (Anderson & Hoffman, 2007). The negative outcomes are reflected in rangelands in the Succulent Karoo with an overall decrease in plant cover and compositional shifts (Anderson & Hoffman, 2007), decrease in above-ground biomass (Anderson, Hoffman, & O'Farrell, 2010) and change in the plant growth forms from perennial to annual (Todd & Hoffman, 2009). Responses of recruitment and changes in biomass vary in relation to altitude, rainfall, gradient and habitat type (Anderson, Hoffman & O'Farrell, 2010) but over long periods of time, certain differences have been noted between lightly and heavily grazed areas (Todd & Hoffman, 2009). Systems have changed to dominance by less palatable species (Anderson & Hoffman,

2007), especially dramatic increases in unpalatable *Galenia africana* in heavily grazed areas of the Succulent Karoo (Todd & Hoffman, 2009).

Namaqualand has been grazed by livestock for thousands of years but the intensities have greatly increased in the last 200 years, as nomadic pastoralism has been replaced by more sedentary grazing, creating noticeable fence-lines between areas of different grazing intensities (Allsopp et al., 2007). Namaqualand is unusual in South Africa because of its distinctive cultural, social and environmental conditions (wide inter-annual variability in rainfall and frequent droughts) (Rohde & Hoffman, 2008). In Paulshoek, the past history of land use and land tenure has resulted in areas experiencing heavy grazing (from sheep and goats) in the communal areas while across the fence are the relatively less impacted commercial areas (Todd & Hoffman, 2009). Thus the high species richness and endemism of the Succulent Karoo is considered threatened by livestock grazing (Hendricks et al., 2005).

It is a widely held belief in range management discipline that in arid and semi-arid areas, changes in shrub populations occur mostly during wet episodes rather than just over the long term (Westoby, Walker, & Noy-Meir, 1989; Watson, Westoby, & Holm, 1997; Anderson & Hoffman, 2007). Ecological processes in arid and semi-arid shrublands (in Australia and America) are thought to be more reliant on 'event-driven' change (episodic, infrequent and/or sporadic) compared to gradual change (Watson, Westoby & Holm, 1997). But in the Succulent Karoo, change can be both slow and incremental, and unpredictably short and rapid (Watson, Westoby & Holm, 1997). Often recruitment and establishment rates are used to establish these processes, rather than mortality as it is more time consuming to measure (Watson, Westoby, & Holm, 1997).

Environmental variability across the Kamiesberg (the escarpment in the Succulent Karoo biome where the study site, Paulshoek, is located) results in highly heterogeneous biomass at a broad scale in response to variable rainfall (Fig.1) and more locally in response to habitat variability (Anderson, Hoffman & O'Farrell, 2010). Namaqualand comprises about a quarter of the Succulent Karoo with ~3500 species in 135 families and 724 genera (Desmet, 2007) and is unusual amongst the world's deserts in that the vegetation is dominated by relatively short-lived leaf succulent shrubs (mainly Aizoaceae and Crassulaceae) (Jürgens et al., 2011). While there may be an increase in annual biomass in communal areas, it is short-lived and does not compensate for loss of persistent perennial species. Studies have reported a shift from perennial plants to annual plants, mainly reflected in the sandy lowlands (Anderson & Hoffman, 2007). Most of the loss in biomass is derived from the highly palatable species – but with no evidence of competitive response from other perennial species. Some authors suggest that recovery is so slow that there is a need for active intervention in semi-arid regions (Todd & Hoffman, 2009). Studies have recorded a consistent directional change in vegetation compositional following rest from heavy grazing over a long period of time (e.g. Rahlao et al., 2008) but the time-frame is much longer than many management schemes.

Plant composition is different on rocky upland areas due to factors such as greater soil moisture (from run-on because of higher rock cover) and higher nutrient status i.e. more available micro-habitats, with many of the limited tree species of Namaqualand found only on the uplands. Although there seems to be a greater difference in biomass between upland and lowland sites rather than between different vegetation types (e.g. Heuweltjieveld, klipkloppe and Renosterveld) indicating a high degree of variability in this landscape. The rocky uplands are generally less heavily grazed due to inaccessibility for people and livestock (Anderson, Hoffman & Farrell, 2010). Some authors have suggested that the lowlands (lower slopes) are the more impacted and the rocky uplands are "buffered" from the effects of heavy grazing (Todd & Hoffman, 2009). Largely unknown for the succulent karoo is the rate of recovery following rest and basic demographic data e.g. rates of mortality and recruitment for key foraging species.

People using the land and working in the region need a better understanding of this ecosystem so as to be better equipped to deal with the demands from the land, for the land and the ominous implications of global climate change for the area (Desmet, 2007). Range managers and researchers are not only concerned with the impact of heavy grazing on rangeland diversity and composition but also with post-disturbance recovery of vegetation following rest from grazing (Rahlao et al., 2008). In view of this, short-term vegetation changes of perennial species occurring around an area used for grazing will be very useful. This study will test the hypothesis that increasing rockiness buffers arid rangelands from some of the impacts of heavy grazing and promotes faster recovery of the vegetation, especially palatable versus unpalatable species. Thus four questions are focussed on;

1. How has species composition changed over time in grazed and ungrazed plots?
2. How do the population dynamics of key species change over time in grazed and ungrazed plots?
3. How does the volume of key species change over time in grazed and ungrazed plots?
4. What influence does the % rockiness play in composition, population change and plant volume?

Methods

Study site

The study was conducted at Kuile (30°23'40.8"S, 18°16'54.1"E) in the Paulshoek communal area which is part of the Leliefontein reserve, set in the Kamiesberg uplands in north western Namaqualand of the Northern Cape Province, South Africa (Fig.1).

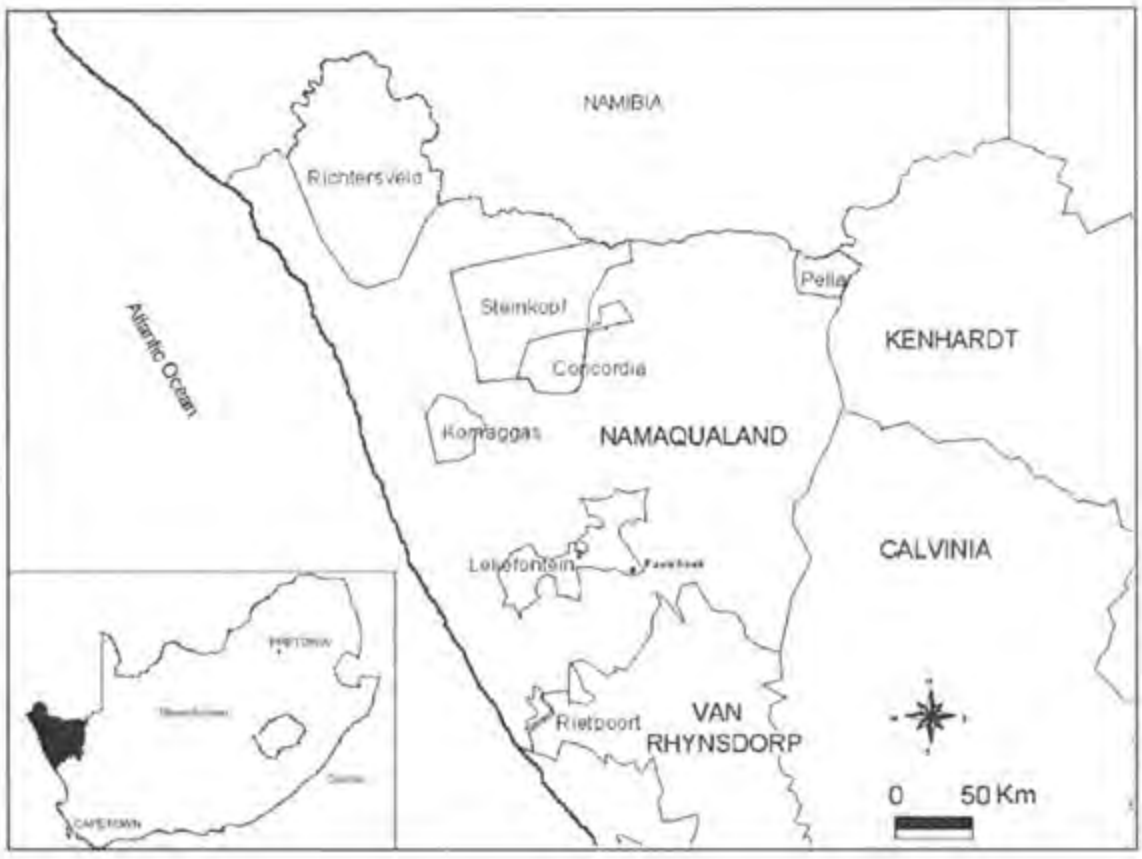

Fig.1: Map of southern Africa indicating the Leliefontein communal area in Namaqualand. (Anderson & Hoffman, 2007).

The climate is Mediterranean, characterized by a mean annual rainfall of 170 mm (Fig.2), which falls mainly in winter frontal systems (April-September) moving in from the Atlantic Ocean (Desmet, 2007). A CV of 32.6% indicates quite a high amount of variability in the rainfall received.

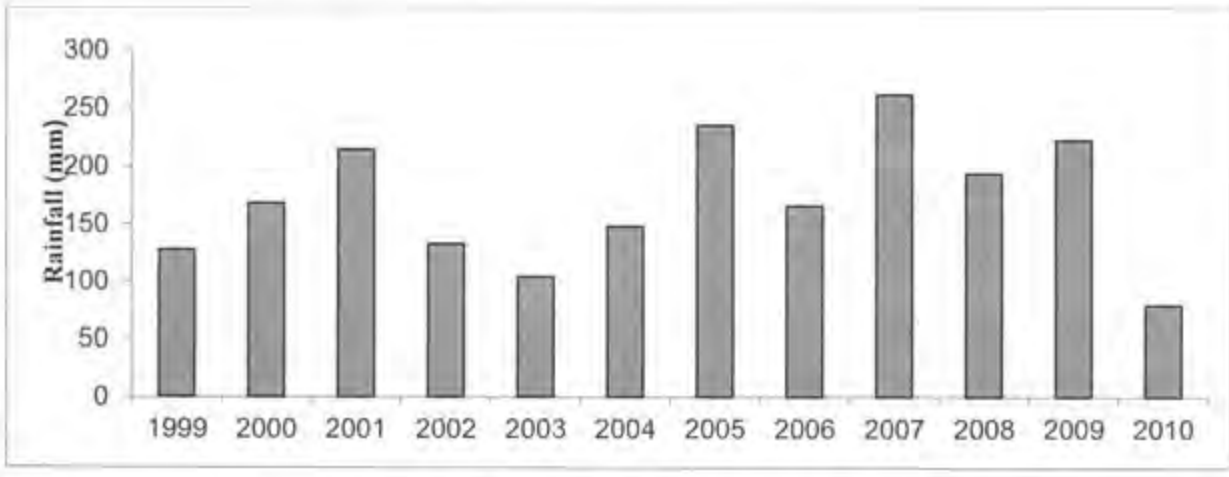

Fig.2: Mean annual rainfall for Kuile (S30 23 40.8, E18 16 54.1), near Paulshoek for the period 1999-2010. (μ= 170.3mm, CV= 32.6%)

The vegetation of the area is quite varied due to the topographic and orographic gradients associated with the Kamiesberg massif. The dominant vegetation types in the study area include Namaqualand Klipkoppe Shrubland which consists of the rocky hills and domes characteristic of the area as well as the sandy pediments separating these areas; the rocky upland areas consist primarily of Namaqualand Granite Renosterveld and the low-lying areas Namaqualand Blomveld (Todd & Hoffman, 2009). Many geophytes, succulents, some grasses and both deciduous and evergreen low shrubs occur within these types. The plains and slopes of the mountains are used as a general grazing area by the local farmers. On the communal rangeland, livestock are corralled each night at a central stock post and actively herded on grazing orbits across the communal rangeland during the day, the entire area is, in effect, continuously grazed (Todd & Hoffman, 2009). In disturbed and overgrazed areas, the unpalatable shrub *Galenia africana* has become dominant, and is a conspicuous feature of large portions of the communal area, particularly on the lowlands (Todd & Hoffman, 2009).

A 100x100 m permanently fenced area (SW to NE) was set-up on a slight slope containing a gradient of rockiness, and eight paired 5x5 m plots were staked out with metal rods (one inside the fence and one outside – total of 16) roughly equal distances from each other in November 2005 as part of the Biodiversity Monitoring Transect Analysis (BIOTA) project in the area (Jürgens et al., 2011). The paired plots were matched as closely as possibly in terms of slope and proximity to each other.

Data collection

Within each 5x5 m plot, a 1x1 m grid was created and all perennial plants were identified and mapped on graph paper at the start of the monitoring exercise in January 2006. The height and breadth measurements were recorded for each individual at each sampling period between 2006 and 2011. All measurements were taken by the same observer for all 6 years. The volume (V) of each shrub was calculated as if the shrub were an oblate spheroid (an ellipse rotated about its minor axis) using the following formula:

$$V = (\pi a^2 b)/6$$

where a is the minor axis (either height or the average diameter, whichever is smaller), and b is the major axis (height or average diameter, whichever is greater) (Phillips & MacMahon, 1981). Surface area (SA) and percentage cover for the plot (%C) was calculated for each individual for the plot as follows:

$$SA = (h/2)^2 * \pi$$

$$\%C = (SA/(500*500))*100$$

where h is the height of the individual plant.

Mortality, recruitment and population change for the seven most dominant species were calculated using the number of individuals present in 2006 (No) compared to the number of individuals present in 2011 (Nt) over (y) years, noting the number of new individuals (Nn), all within a single plot;

percent mortality [(Nt-Nn/No)^1/y – 1]*100

percent recruitment; [(Nn+No/No)^1/y – 1]*100

and percent population change; [(Nt/No)^1/y -1]*100.

Palatability for species was scored from a range of 0.1 to 5 (least palatable to most), based on local knowledge and expert opinion.

Statistical analysis

Only perennial species of four growth forms (leaf succulent, stem succulent, deciduous shrub and evergreen shrub) were used in the data analysis. Non-metric multidimensional scaling (NMS) was done in PC-ord 5.0 using Sørensons similarity to assess the direction and consistency of changes in plant community composition between 2006 and 2011. Ordinations were done using species percentage cover calculated from surface area, and volume, and all rare species were removed. Ordination of the plant community data (species) from 2006 was carried out to determine how the paired plots were arranged in multivariate space and all plots in relation to percent rockiness. Further ordinations were run for the period 2006-2011 to determine how each plot changed over the survey period. Multiple runs and stress criteria were used for the ordinations based on previous semi-arid studies (McCune & Grace, 2002; Rahlao et al., 2008).

Correlations between rainfall, volume, number individuals, % mortality and % recruitment were used to determine if rainfall had any influence at the short-term scale. Student T-tests were carried out to determine differences in plant volume, number of individuals, percent (%) mortality, percent (%) recruitment and percent (%) population change from 2006-2011 to assess the differences between ungrazed (inside) and grazed (outside) plots. Only those species with the highest frequencies (*Galenia africana* (Ga), *Eriocephalus ericoides* (Ee), *Hirpicium alienatum* (Ha), *Pentzia incana* (Pi), *Ruschia fredericii* (Rf), *Hermannia cuneifolia* (Hc), and *Chrysocoma ciliata* (Cc)) were used in the detailed analyses. T-tests were used to establish if there were significant relationships between total volume, numbers of individuals and % rockiness.

Results

Rainfall for the years preceding sampling times (2005-2010) did not have any significant correlation to responses in the vegetation even though it had a slightly higher average of 192.7 mm compared to 170.3 mm (Fig.2, 1999-2010) (e.g. rainfall compared to numbers of individuals for plots inside and outside, r = ±0.1). Table.1 below shows all perennial species which were present over all plots between 2006 and 2011, indicating their palatability scores and growth forms. Of the seven main species, three are unpalatable and the other four, palatable.

Composition

Table 1: List of all perennial species found within the plots, their abbreviations and palatability scores. Those highlighted are the seven most abundant species present in both 2006 and 2011.

Scientific Name	Abbreviation	Family	Growth Form	Palatability
Aridaria noctiflora	An	Aizoaceae	Deciduous shrub	2.6
Antimima sp.	Ant	Aizoaceae	Leaf succulent	2.0
Aptosimium spinescens	As	Scrophulariaceae	Deciduous shrub	1.0
Asparagus capensis	Asp	Asparagaceae	Evergreen shrub	1.0
Chrysocoma ciliata	Cc	Asteraceae	Evergreen shrub	0.7
Cotyledon orbiculata	Co	Crassulaceae	Leaf succulent	0.1
Crassula brevifolia	Cras	Crassulaceae	Leaf succulent	0.2
Euphorbia decussata	Ed	Euphorbiaceae	Stem succulent	2.2
Eriocephalus ericoides	Ee	Asteraceae	Deciduous shrub	4.1
Euphorbia pyramidalis	Ep	Euphorbiaceae	Stem succulent	0.1
Felicia muricata	Fel	Asteraceae	Evergreen shrub	4.8
Galenia africana	Ga	Aizoaceae	Evergreen shrub	0.3
Plinthus karooicus	Gg	Aizoaceae	Evergreen shrub	2.7
Hirpicium alienatum	Ha	Asteraceae	Evergreen shrub	4.8
Hermannia cuneifolia	Hc	Sterculiaceae	Evergreen shrub	4.8
Lycium cinereum	Lc	Solanaceae	Deciduous shrub	3.0
Mesembryanthemum sp 1	M1	Aizoaceae	Leaf succulent	2.0
Pteronia divaericata	Pd	Asteraceae	Deciduous shrub	2.5
Pelargonium alternans	Pel	Geraniaceae	Stem succulent	4.4
Pentzia incana	Pi	Asteraceae	Deciduous shrub	4.8
Pteronia incana	Pti	Asteraceae	Evergreen shrub	4.1
Ruschia fredericii	Rf	Aizoaceae	Evergreen shrub	2.8
Stoeberia sp	Stm	Aizoaceae	Leaf succulent	3.0
Tetragonia fruticosa	Tf	Aizoaceae	Deciduous shrub	3.7
Tripteris sinuata	Ts	Asteraceae	Deciduous shrub	4.8
Zygophyllum microphyllum	Zm	Zygophyllaceae	Leaf succulent	3.1

It is interesting to note that the seven main perennial species selected were all dwarf shrubs, with most being evergreen except Ee and Pi, which are deciduous (Table 1).

Analysis on percentage (%) cover of all species collected in 2006 (Fig.3) shows that two groups of the plots separate out relative to % rockiness. One group has high % rockiness (>50%) ["rocky" - inside plots 10 and 24 and outside plots 11 and 25], while the other has low (<30%) ["sandy"- inside plots 12,14,16,18,20,22 and outside plots 13,15,17,19,21,23]. Figs 4 and 5 below show how the plots in these two groups [rocky and sandy] change over the six years when using total plant volume. Interestingly, outside plots 11 and 25 (relative to the enclosure) (Fig.4) became more similar in 2011 to their starting position in 2006 and were similar to each other. Whereas, inside plots 10 and 24 had a definite direction over the course of the years and were relatively dissimilar. These trends were not seen clearly in the "sandy" plots (Fig.5), with only some (e.g. plots 13, 19 and 22) turning back on themselves from 2006 to 2011 and the rest with some indication of directionality, but no general pattern. But between 2007 and 2008 the greatest change was seen in many of the "sandy" plots being only slightly evident in the "rocky" plots.

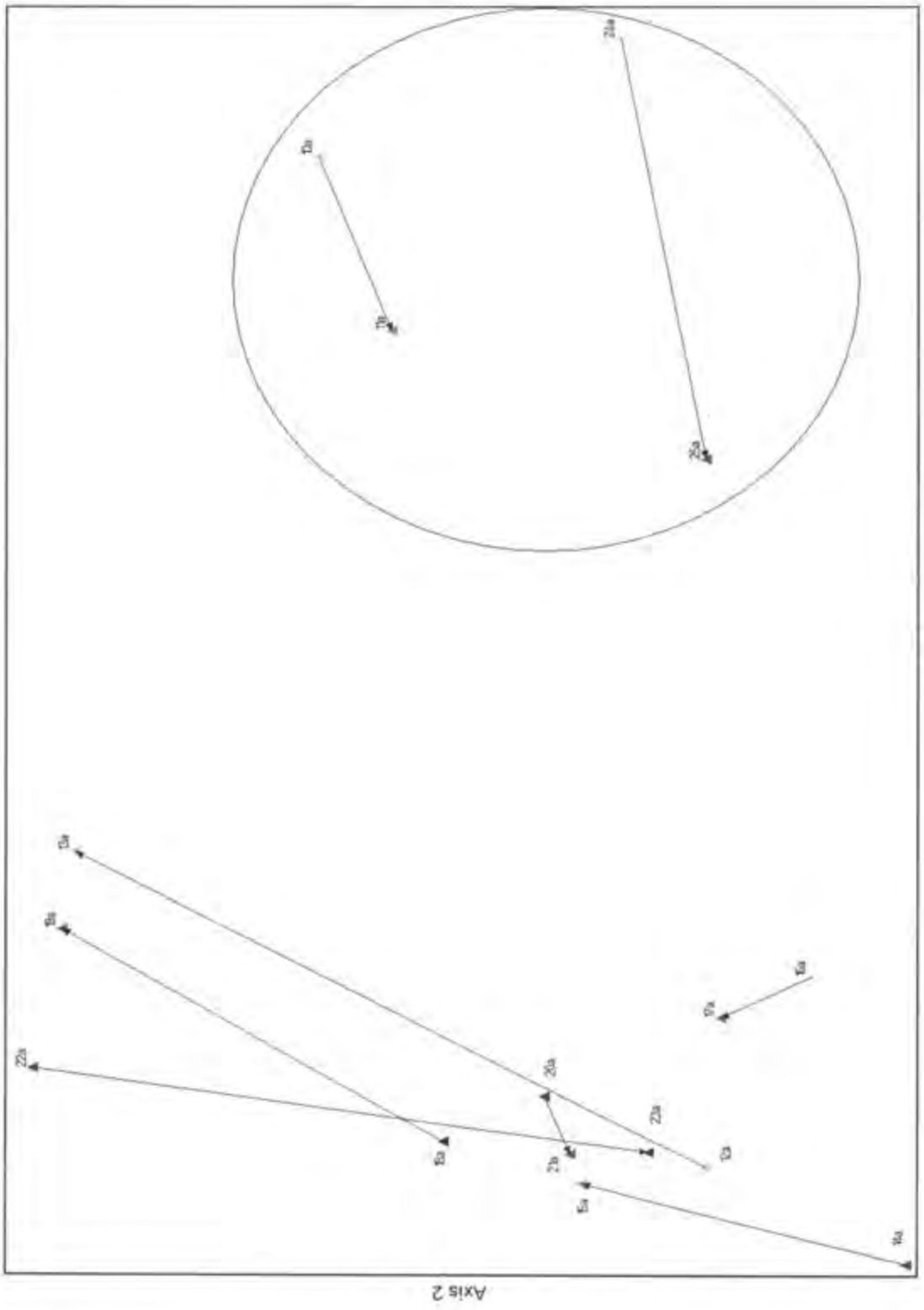

Fig. 3: NMS ordination plot of percentage (%) cover of all species in all 16 plots sampled in 2006. Two groups are separated out according to percentage (%) rockiness. High % rockiness (>50%) are circled, and low % rockiness (<30%) (16 plots, 38 species, stress value = 7.37, p = 0.02, 51 iterations).

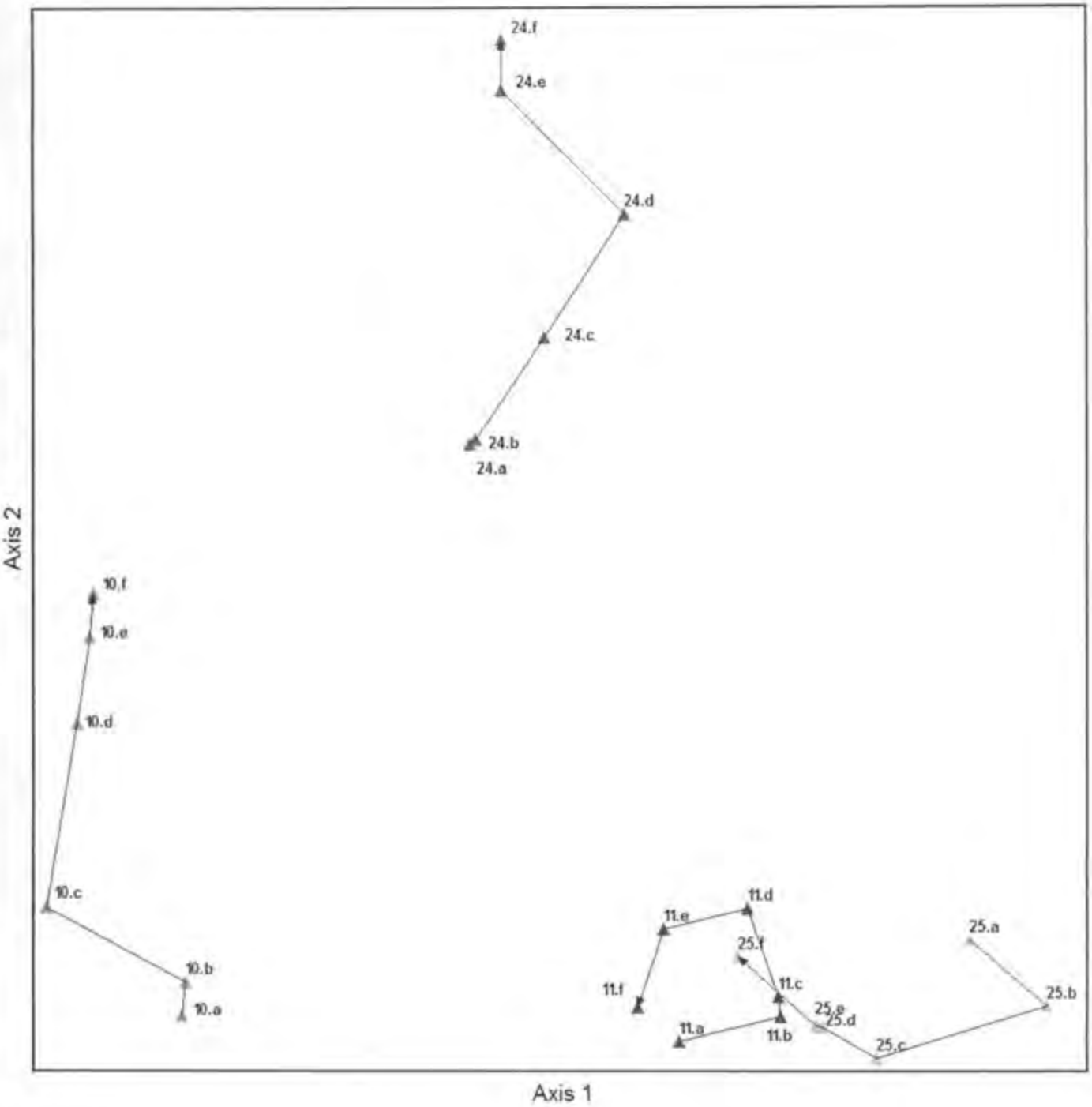

Fig. 4: NMS ordination showing how the "rocky" plots vary in plant volume over the six years (the letters after the plot number indicate; a=2006, b=2007, c=2008, d=2009, e=2010 and f= 2011). (24 plots, 25 species, stress value = 1.84, p = 0.004, 71 iterations)

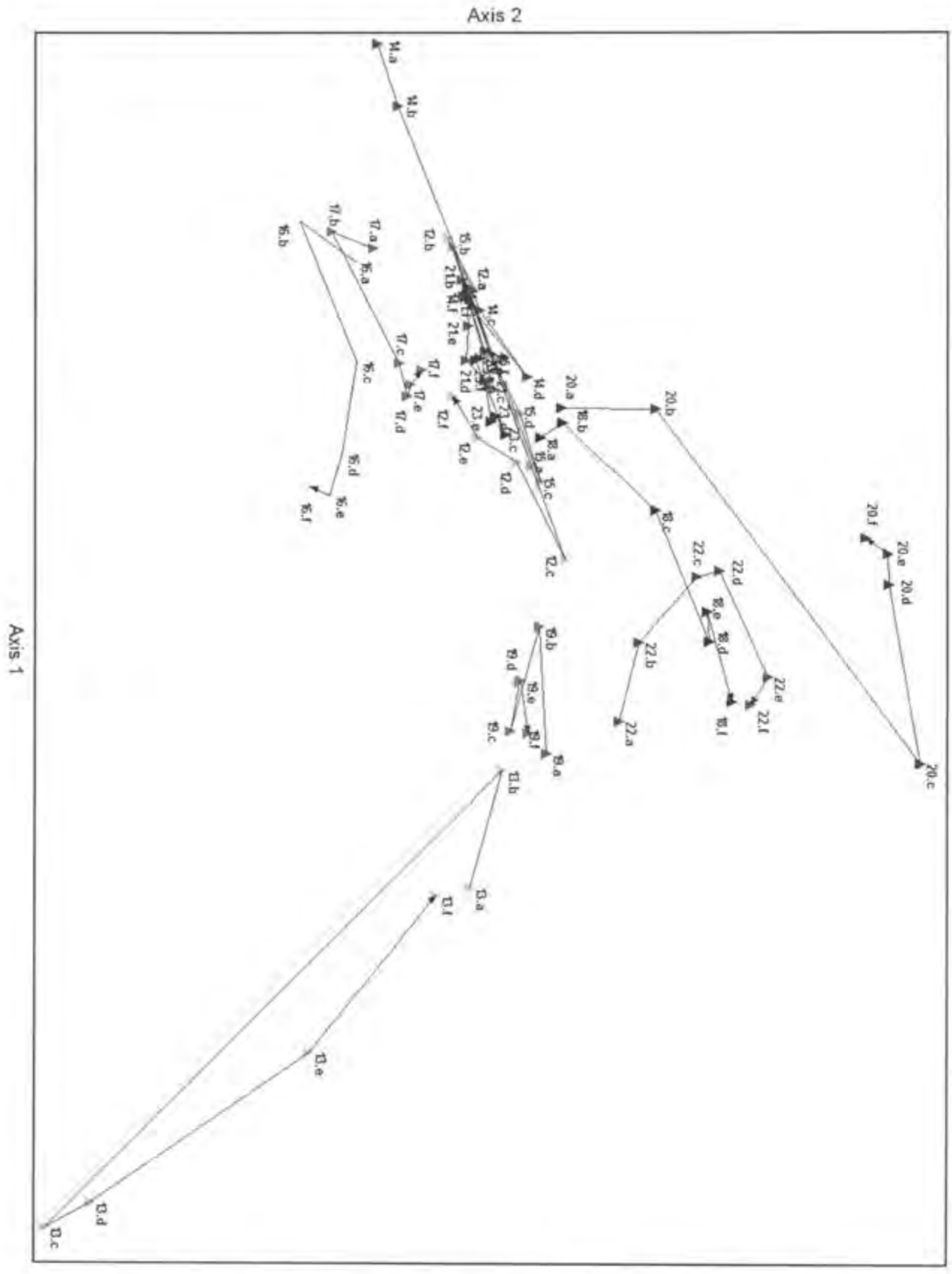

Fig. 5: NMS ordination showing how the "sandy" plots vary in plant volume over the six years (the letters after the plot number indicate; a=2006, b=2007, c=2008, d=2009, e=2010 and f= 2011). (72 plots, 16 species, stress value = 7.66, p = 0.008, 174 iterations).

Population dynamics and change

In general species numbers are higher inside than outside (Fig.6) with a large difference between the sets of plots in 2007. Both inside and outside numbers decrease to ~350 plants between 2007- 2008, which gradually increased after that and levelling off at slightly below their original population numbers (~500 individuals).

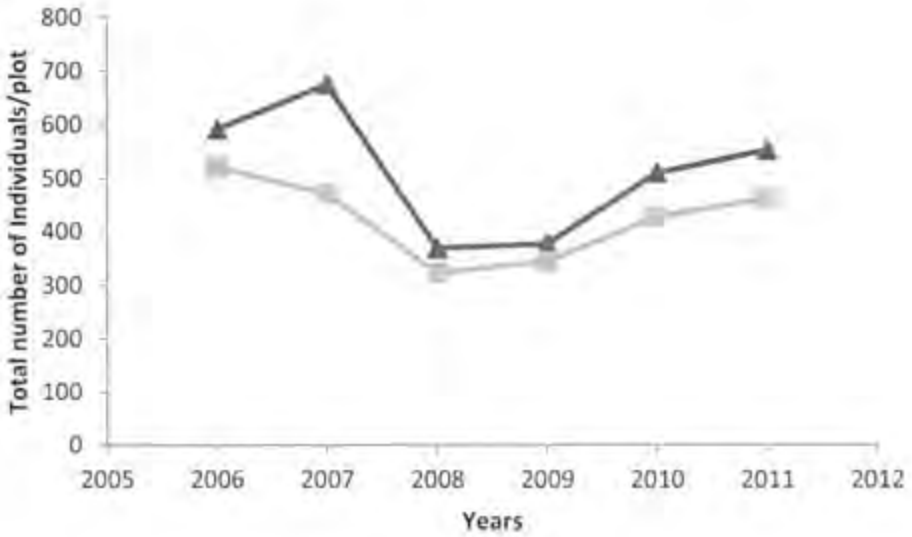

Fig.6: Change in number of individuals over 6 year period (2006-2011) for all species present inside (triangles) and outside (squares) of the fence (r^2 = 0.09 and r^2 =0.08, respectively).

In terms of the number of individuals over the years, Ga (Fig.7a) was the most unusual as both inside and outside plots had the same pattern. The abundance for Ga started at ~300 plants in 2006, dropped quite rapidly in 2009 to 110 plants and then stabilized at that level until 2011. The inside plots had just slightly fewer individuals every year. Ee, Ha (significantly, t =3.78, df=10, p= 0.003) and Rf show similar increases in the inside plots in 2009 while Pi (significantly, t =6.08, df=10, p<0.001) (Fig.7d) remained constant over the years. Hc (significantly, t =9.76, df=10, p<0.001) had both inside and outside plots constant in abundance until a drop from 80 to 60 individuals on the inside plots in 2010. Ha, Pi and Cc have increasing numbers of plants outside from 2008-2011, which were greater than inside only for Cc. Other than Ha, Pi and Hc, none of the other species were significant (p> 0.05) when comparing inside and outside.

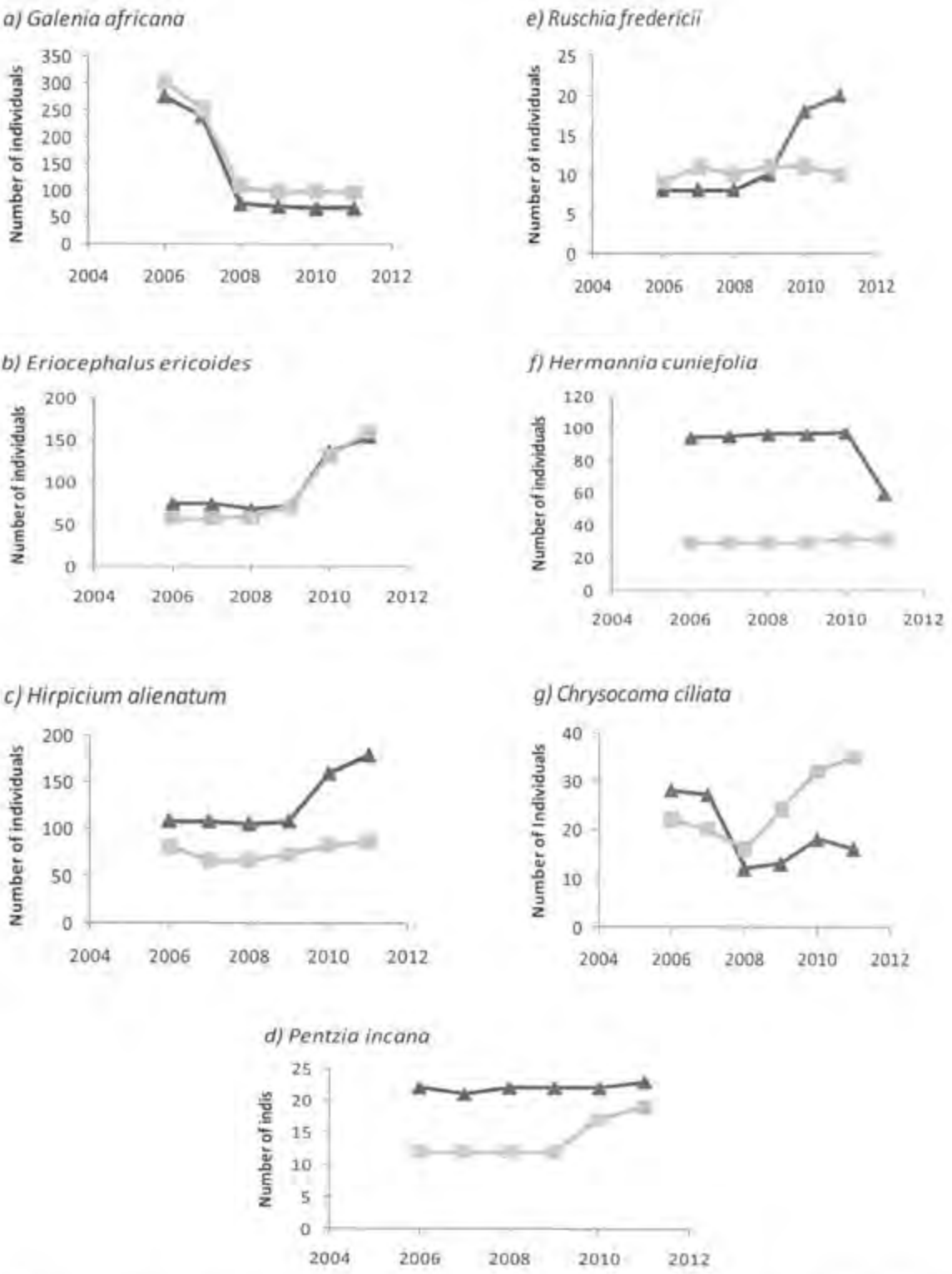

Fig.7: Number of individuals of the seven main species for inside plots (triangles) and outside plots (squares) a) Ga, b) Ee, c) Ha, d) Pi, e) Rf, f) Hc, g) Cc. a) to g) is in order from the most abundant (Ga) to the least (Cc). The number of individuals is totalled from all plots occurring inside, and all occurring outside. None of the trends were significant.

Table 3: Mean (SD) % recruitment from 2006-2011 for the seven main species occurring on plots inside and outside. Those which are significantly different between inside and outside are marked with*.

Species	Inside % Recruitment	Outside % Recruitment	T-stat	df	p-value
Galenia africana	0.80 (0.8)	1.10 (1.61)	-0.48	14	0.64
Eriocephalus ericoides	27.92 (18.8)	23.22 (15.5)	0.51	12	0.62
Hirpicium alienatum	10.40 (10.5)	6.35 (5.1)	0.92	12	0.38
Pentzia incana	0.78 (0)	8.55 (0)	1.20	1	0.44
Ruschia fredericii	13.46 (9.2)	23.22 (0)	-0.92	2	0.46
Hermannia cuneifolia	1.74 (2.4)	4.01 (4.5)	-1.00	9	0.34
Chrysocoma ciliata	3.70 (2.9)	13.09 (2.68)	*-4.39	*5	*0.01
All spp.	5.53 (3.1)	4.82 (4.2)	0.38	14	0.71

The % recruitment (Table 3), % mortality (Table 4) and % population change (Table 5) between 2006 and 2011, were compared for all plots occurring inside the fence and all plots occurring outside. Except for Cc which had a significant % recruitment and thus % population change for outside plots compared to inside (t= -4.39, df =5, p = 0.01), none of the others were significantly different when comparing inside and outside. Most of the dominant species, except Ee and Ha, generally had higher % recruitment in outside plots (Table 3). Pi and Rf experienced no mortality and some of the highest % recruitment between 2006 and 2011. The three most abundant species (Ga, Ee and Ha) had higher % mortality in the protected plots (Table 4). However, when all species were considered together, the % mortality was greater outside the protected plots. Most species, except Pi, Rf and Hc, had greater % population changes inside the fence than outside (Table 5).

Table 4: Mean (SD) % mortality from 2006-2011 for the seven main species occurring on plots inside and outside.

Species	Inside % Mortality	Outside % Mortality	T-stat	df	p-value
Galenia africana	-24.12 (6.1)	-19.63 (8.6)	-1.20	14	0.25
Eriocephalus ericoides	-16.36 (37.1)	-0.15 (0.4)	-1.16	12	0.27
Hirpicium alienatum	-0.72 (0.8)	-0.55 (1.5)	-0.27	12	0.79
Pentzia incana	0 (0)	0 (0)	0.00	0	0.00
Ruschia fredericii	0 (0)	0 (0)	0.00	0	0.00
Hermannia cuneifolia	0 (0)	-2.45 (3.8)	1.42	9	0.19
Chrysocoma ciliata	-15.53 (6.6)	-17.69 (4.09)	0.50	5	0.64
All spp.	-11.94 (9.4)	-13.54 (8.2)	0.37	14	0.72

Table 5: Mean (SD) % population change from 2006-2011 for the seven main species occurring on plots inside and outside.

Species	Inside % Population change	Outside % Population change	T-stat	df	p-value
Galenia africana	-21.09 (5.6)	-16.66 (8.1)	-1.27	14	0.22
Eriocephalus ericoides	27.00 (18.7)	23.08 (15.7)	0.43	12	0.68
Hirpicium alienatum	9.86 (10.8)	5.83 (5.9)	0.87	12	0.40
Pentzia incana	0.78 (0)	8.55 (0)	1.20	1	0.44
Ruschia fredericii	13.46 (9.2)	23.22 (0)	-0.92	2	0.46
Hermannia cuneifolia	1.74 (2.4)	1.83 (6.7)	-0.03	9	0.98
Chrysocoma ciliata	-8.81 (9.4)	5.68 (4.9)	-2.39	5	0.06
All spp.	-3.34 (10.3)	-5.81 (10.87)	0.47	14	0.65

Overall, using all perennial species found within the plots, there is higher % recruitment inside, higher % mortality outside and a greater % population change outside. None of the trends are significant.

Generally there are more plants present as % rockiness increases both inside and outside (Fig.8). Between 10- 50% rockiness, the inside has higher abundance, but <50% rockiness, the outside plots contain more individuals.

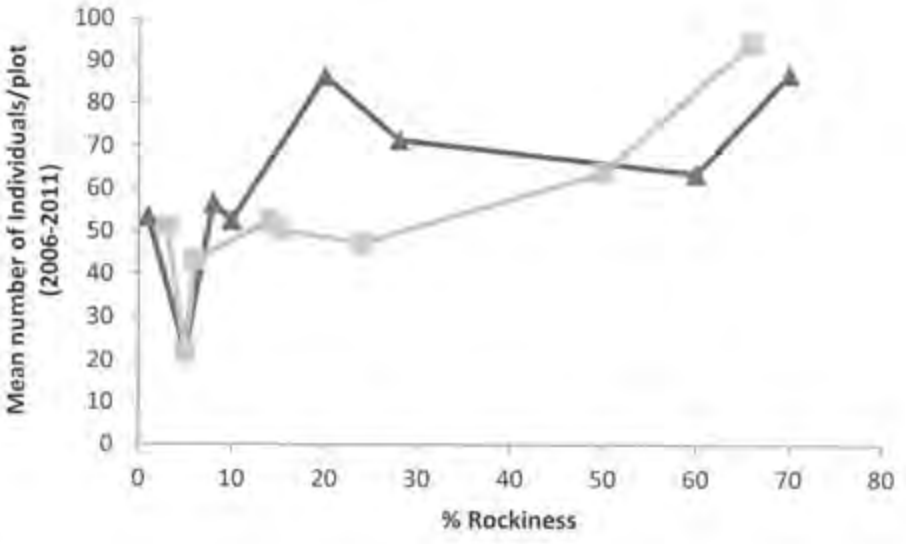

Fig.8: Abundance of all species individuals in relation to a gradient of rockiness for plots inside (triangles) and outside (squares) ($r^2 = 0.36$ and $r^2 = 0.74$ respectively).

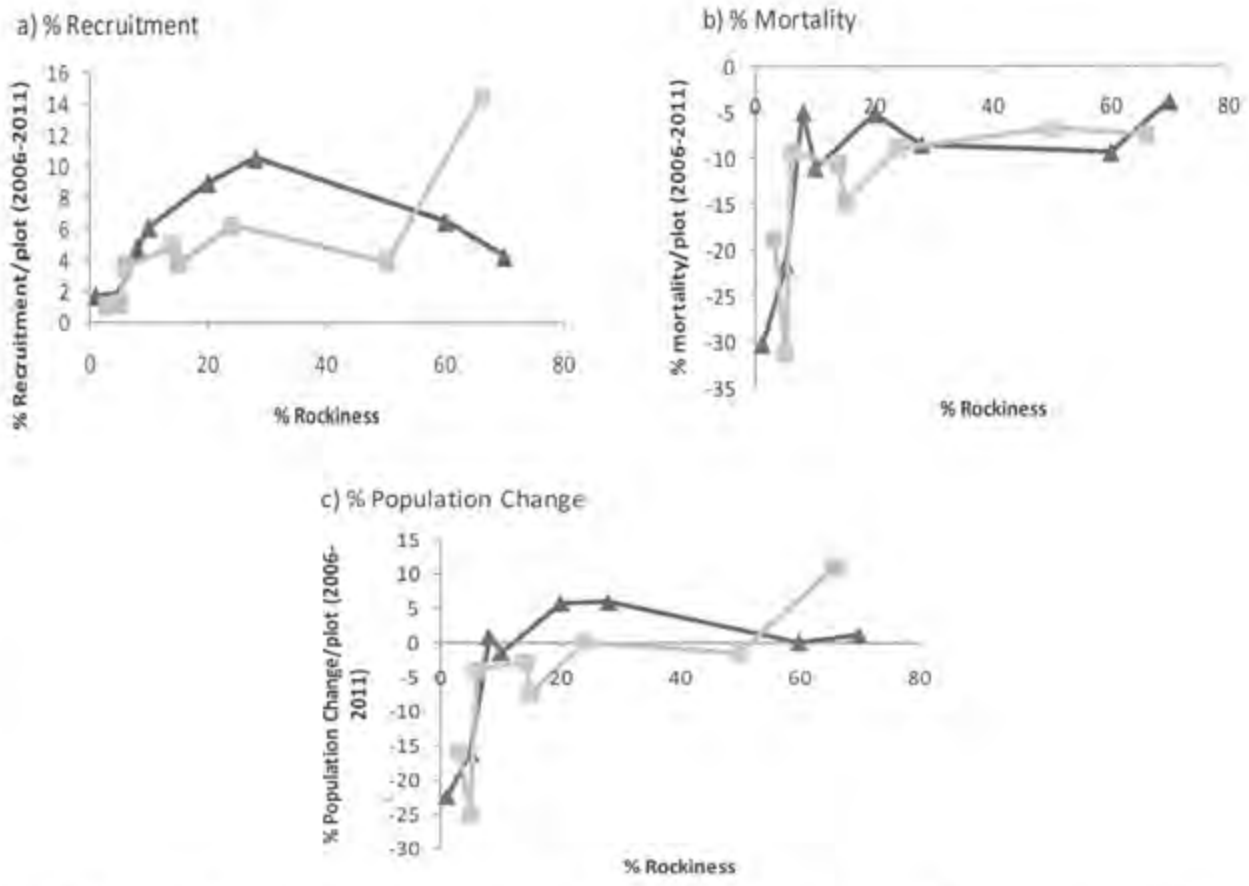

Fig.9: a) Percent (%) recruitment, b) Percent (%) mortality and c) percent (%) population change from 2006-2011 in relation to percent rockiness for plots inside (triangles) and outside (squares). Only % recruitment and % population change in outside plots have a strong relationship to % rockiness (r^2 =0.67 and r^2 =0.59 respectively).

As rockiness increases, recruitment over the 6-year period (Fig.9) increases gradually for inside plots reaching a peak of 10% at ~25% rockiness (Fig.9a). Mortality rapidly declines from -30% to -5% at ~20% rockiness, thereafter oscillating between -10% and -5% as rockiness increases further (Fig.9b). Recruitment in outside plots (Fig.9a) increases gradually from 1% to 4-6% until dramatically increasing to 14% (much higher than inside) at 50% rockiness. Mortality for the outside plots follows the same pattern as the inside plots (Fig.9b). The % population change between 2006 and 2011 for both inside and outside (Fig.9c) becomes more positive as rockiness increases due to increase in recruitment and decrease in mortality.

Response in volume

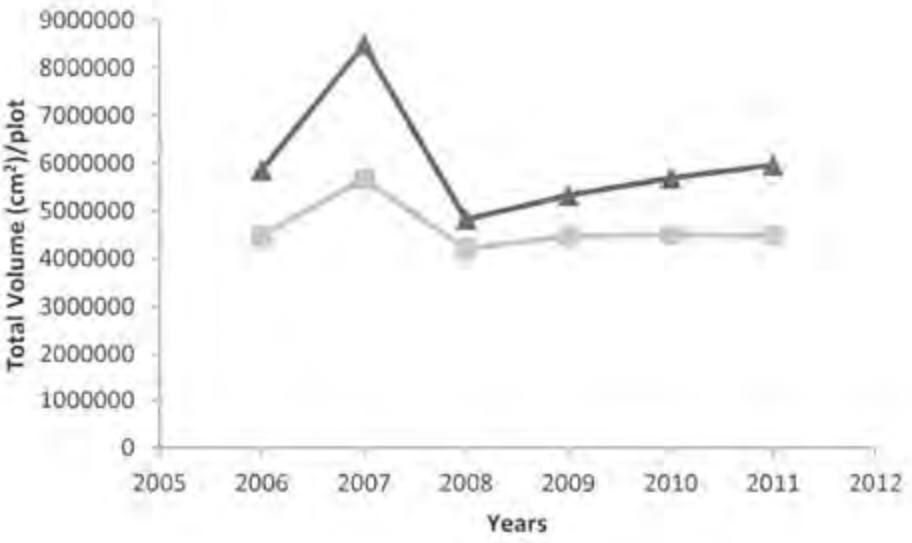

Fig.10: Total volume (of all species) over the 6 year period for plots inside (triangles) and outside (squares). (r^2= 0.10 and r^2= 0.11 respectively).

Total volume for both inside and outside (Fig.10), shows a rapid increase (6000 000 cm^2 to 8000 000 cm^2 and 4500 000 cm^2 to 5500 000 cm^2 respectively) from 2006-2007, but decreases again to the starting values in the following year, thereafter gradually increasing in small increments. Inside and outside plots are significantly different from each other over the 6-year period in terms of total volume (t stat= 2.38, df =10, p =0.04).

Growth responses to grazing and rest over time varied within the seven main species (Fig.11). Ee, Hc, Pi, Rf and Hc (the more palatable species; see Table 1) generally increased over the years while volumes in the outside plots remained at their initial low levels. However, Ga and Cc, the less palatable species, show a more complicated progression. Ga (Fig.11a) plants in the outside plots increased in volume to match those occurring on inside plots, then both inside and outside plots decreased in volume in 2008 and stabilized with outside plots having higher volumes from 2008-2011 than the inside plots. For Cc (Fig.11g), outside plots initially contained a higher volume than inside plots, but this reversed over the next two years with inside plots having a higher volume than outside plots. In 2011 the volumes for Cc declined and outside plots were once again greater in volume than inside plots. None of these trends in comparing inside and outside plots were significant (p>0.05).

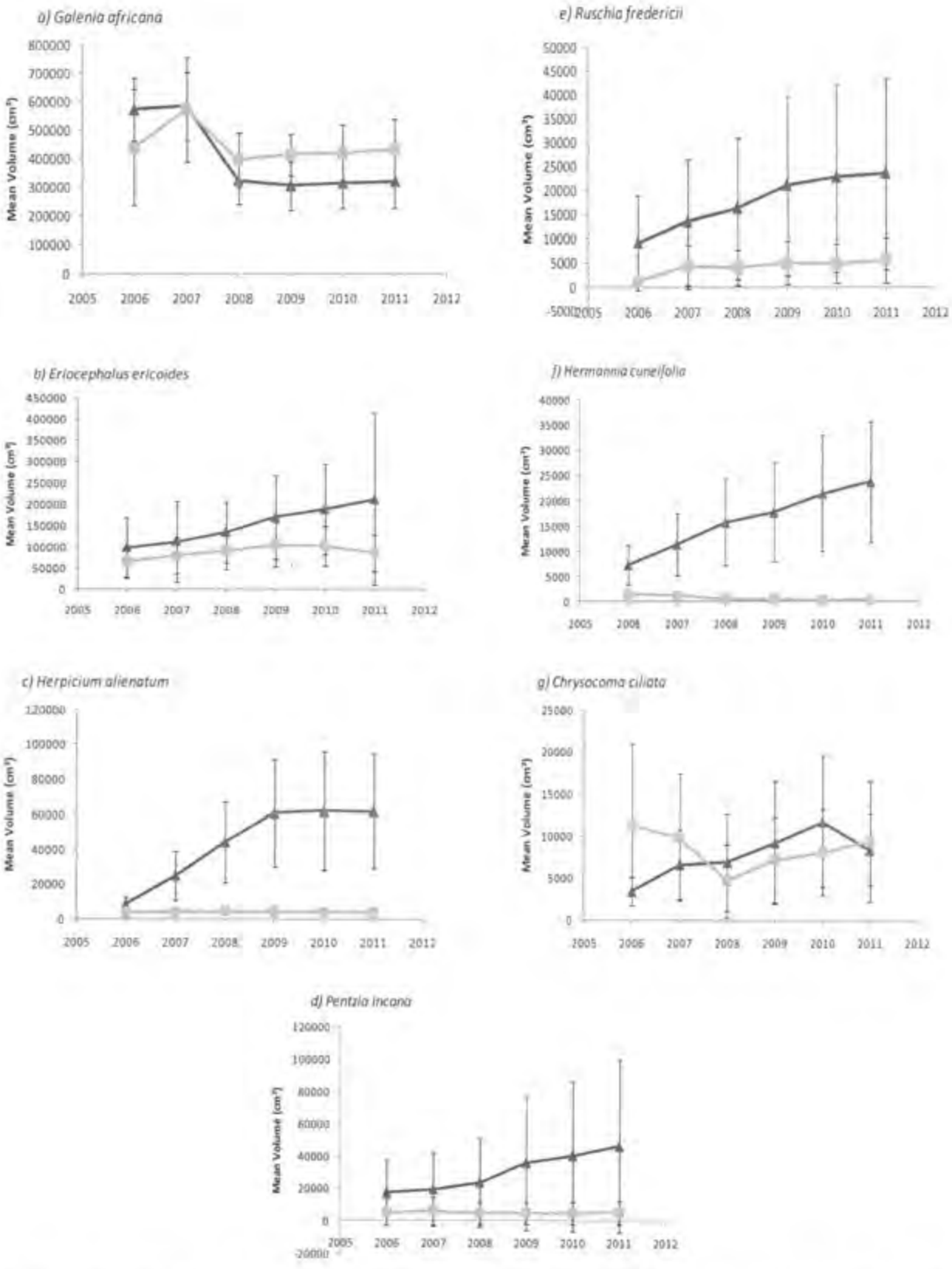

Fig.11: Growth (change in volume) of the seven main species for plots inside (triangles) and outside (squares). a) Ga, b) Ee, c) Ha, d) Pi, e) Rf, f) Hc, g) Cc. a) to g) is in order from the most abundant (Ga) to the least (Cc). Volume is averaged between all plots occurring inside, and all occurring outside.

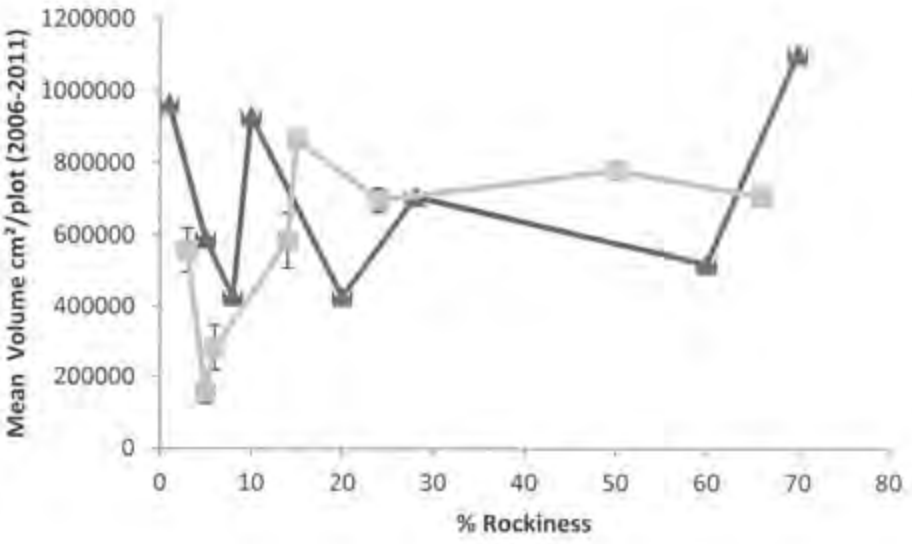

Fig.12: Mean volume of all species in relation to the percent rockiness for plots inside (triangles) and outside (squares). Inside, $r^2 = 0.04$ and outside, $r^2 = 0.30$.

In general, volume of all perennial species present (Fig.12) shows a decrease from 0-8% rockiness for both inside (950 000 cm^2 to 430 000 cm^2) and outside plots (570 000 cm^2 to 180 000 cm^2). There was a steep increase in plant volume between 8-15% for inside (430 000 cm^2 to 920 000 cm^2) and outside plots (180 000 cm^2 to 900 000 cm^2). This decreased for both thereafter (less dramatically for outside plots) until the rapid rise in volume for inside plots at 70% rockiness (580 000 cm^2 to 1050 000 cm^2). Overall there is a distinct increase in % volume change for inside plots (-800 000 cm^2 to 500 000 cm^2); whereas outside plots show very little change ($r^2 = 0.02$) despite an increase in the % rockiness.

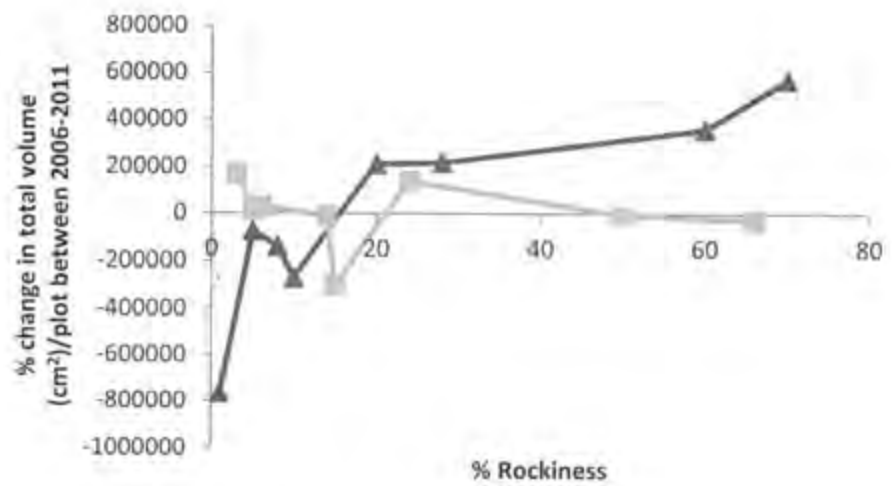

Fig.13: Percent (%) change in volume occurs along a gradient of rockiness for plots inside (triangles) and outside (squares). Inside ($r^2 = 0.70$) and outside ($r^2 = 0.02$).

Discussion

The results from this detailed short-term study indicate that there is indeed a long-temporal aspect to the Succulent Karoo, as has been noted by other authors (Anderson & Hoffman, 2007; Todd & Hoffman, 2009; Anderson, Hoffman, & O'Farrell, 2010; Dreber & Esler, 2011). How the species composition, population dynamics and volume changed over time, and what influence % rockiness had on these three categories, revealed some interesting points.

Rainfall

Observed temporal pattern in previous studies indicate that both condition and sequence of preceding rainfall seasons are likely to have a profound effect on plant dynamics (Todd & Hoffman, 2009) and soil seed banks of subsequent years (Dreber & Esler, 2011). However, in this study, higher than normal rainfall (2005-2010) had no significant correlation to numbers of individuals (all species) or population dynamics of the dominant species for 2006-2011. Even though 2007 had more rainfall compared to normal which may have enabled higher growth rates as per expected (Watson, Westoby, & Holm, 1997) there was little change in the number of individual plants and population dynamics of all species both inside the fence and out, despite other research indicating that semi-arid vegetation responds favourably to episodic wet events (Watson, Westoby, & Holm, 1997). Perhaps sampling on a monthly basis instead of annually would shed more light on this, as recruitment was high in 2011 even after the low precipitation of 2010. Alternatively, the episodic events may need to be more drastic i.e. complete drought for longer to affect % mortality, and as well as water accumulation from previous years culminating in a big enough rainfall event, to affect recruitment (i.e. store enough water to put out more branches and grow many flowers, producing enough seed for germination to be likely) (Dreber & Esler, 2011). Six years is not long enough to see the relationship between rainfall and vegetation in the Succulent Karoo.

Composition

The results of this study confirm a difference in the response of palatable and unpalatable plants to rest from grazing as previous studies have determined (Anderson & Hoffman, 2007; Todd & Hoffman, 2009; Anderson, Hoffman, & O'Farrell, 2010; Dreber & Esler, 2011). Less palatable species such as *Galenia africana* and *Chrysocoma ciliata* show more recruitment under grazing compared to rest from grazing because of the removal of competing adult plants (Todd & Hoffman, 2009). The shift in composition from large and succulent woody shrubs to dwarf shrubs and an herbaceous perennial component noted by

Anderson & Hoffman, (2009) could not be determined. Both inside and outside of the fence had been grazed and the time period was not long enough to see any shift to woody species as might be expected from range succession models (Westoby, Walker, & Noy-Meir, 1989). The long life-spans of the dominant shrub species and intergenerational transfer of relative abundance can be downplayed by recruitment being proportional to seed input (Todd & Hoffman, 2009). Species composition of some of the perennial species started to show a directional trend over 6 years; whereas annual species composition was dictated more by the timing and the amount of rainfall in a growing season (Schmiedel et al., 2010).

Compositional shifts towards smaller and more ephemeral species in the communal area are indicative of a system more closely dependent on rainfall (Anderson & Hoffman, 2007) which has only be seen over longer time scales. The selective pressure of grazing had not resulted in a great loss of heterogeneity (Anderson & Hoffman, 2007) although there was dominance of a few species which were both palatable and unpalatable. The beginnings of directional change towards more varied composition containing more succulents on the protected plots (Rahlao et al., 2008) were noted (Fig.4 & 5), but may not show in 6 years of protection due to the lag phase or compositional inertia characteristic of the Succulent Karoo and other semi-arid to arid regions (Todd & Hoffman, 2009). This propositioned compositional change may be due to micro-sites provided by those plots with higher % rockiness. These trap soil and seeds, especially the abundantly produced small seeds of most annual species (Dreber & Esler, 2011) allowing for many more favourable germination sites (Barbera, Navarro-Cano & Castillo, 2006).

Population dynamics and change

Due to the longevity of woody shrubs (e.g. time for establishment of some shrubs is <40 years, Hendricks et al., 2005), short-term vegetation shifts are small, limiting the potential for the recovery of overgrazed shrublands during periods of low grazing pressure (Todd & Hoffman, 2009). Though many studies focus on the short-term responses of the plants in the Succulent Karoo, often it has been put forward that long-term studies are needed in order to better understand these notoriously slow vegetation changes in semi-arid areas (Rahlao et al., 2008). But in the Succulent Karoo, change can be both slow and incremental, and unpredictably short and rapid (Watson, Westoby & Holm, 1997). Due to the longevity of the seed banks, after good rainfall there may be many new individuals especially of annual species which are prolific seeders (Dreber & Esler, 2011). Having said that, over the short-medium time period, there was little significant difference between % mortality, % recruitment and ultimately % population change between protected and grazed areas. That there was recruitment of palatable species in the grazed areas which indicates that these species will not die out as might be expected due to grazing (Todd & Hoffman, 2009).

This in itself shows that over the short to medium term (6 years) there was little change from perennial to annual because of grazing pressure and in the recovery from grazing pressure as based on abundance (Anderson & Hoffman, 2007; Rahlao et al., 2008; Todd & Hoffman, 2009; Anderson, Hoffman, & O'Farrell, 2010). This may be due to only one site in one type of vegetation, as previous studies noted the change of dominance from perennial species to annual species over longer time periods and from a larger sample size (Anderson & Hoffman, 2007; Todd & Hoffman, 2009). The increase in natural competition between the various plant growth forms on the ungrazed plots (Anderson et al., 2010) may explain the similarities in % mortality between the grazed and ungrazed plots.

% rockiness separated the plots in multivariate space (Fig.3) into two main categories – 'rocky' and 'sandy'. Those with a high percentage of rock cover >50% and those with low (<30%). Where there was a higher percentage of rock cover, higher recruitment and lower mortality rates for all species were noted, with larger numbers of plants as well. Seeds were better trapped on higher percent rock cover (% rockiness) than on sandy soil, affecting seed-bank locations (Dreber & Esler, 2011) due to properties and higher numbers of micro-habitats (Barbera et al., 2006) of the 'rocky' areas. This may account for the higher numbers of plants on grazed and protected plots and similarity in % recruitment between grazed and protected plots. This can be scaled up to the "buffering" of more rocky slopes noted by other authors (Anderson & Hoffman, 2007; Todd & Hoffman, 2009; Dreber & Esler, 2011).

Response in Volume

All the main species are dwarf-shrubs which show that over a 6-year period, responses are only measureable for those species which have a long-term perennial aspect. There were no significant differences between the grazed and protected plots after 6 years, the volume of unpalatable species *Galenia africana* and *Chrysocoma ciliata* showing a complicated progression, while the volume of palatable species generally increased in the protected plots but was sufficient in the grazed plots to down-weight any differences between the protected and grazed plots. The presence of palatable species in the grazed plots indicates a certain resilience of the ecosystem to grazing pressure (Anderson & Hoffman, 2007). The increase in shorter shrubs and low prostrate growth forms has been a renowned response to grazing (Anderson & Hoffman, 2007) while protected plants remained tall and erect (Noy-meir, Gutman, & Kaplan, 1989). This selection in growth form may account for the insignificant differences in volume between protected and grazed plots. A better quantity of measurement would have been above-ground biomass calculated through a non-destructive method (regression equations with some measure of weight) (Flombaum & Sala, 2007; Flombaum & Sala, 2009). This could then be expanded to aspects such as aboveground net primary production (ANPP), and forage availability (Flombaum & Sala, 2007).

The increase in % rockiness correlated with an increase in number of individuals and volume of all species and within the seven dominant species. Differences in response in protected and grazed plots showed that there could be a distinct separation in future. This supports the theory that rocky uplands (i.e. more micro-sites/habitats) are important in accelerating vegetation recovery from grazing and in maintaining the high compositional variability found in the Succulent Karoo (Dreber & Esler, 2011; Hendricks et al., 2005; Todd & Hoffman, 2009). Overall, the non-significance of most of the results indicates that 6 years is not long enough to see considerable responses in Succulent Karoo vegetation. This implies that decadal times-scales are the shortest period to consider in conservation and range management as this will be when climatic/episodic events may prompt responses in vegetation. It is important to consider different functional types when studying succession especially after a change in land-use (e.g. after 60 years in Spain, (Bonet & Pausas, 2004)). In view of plant conservation as well, certain management practices are more relevant than others (Assaeed, 2003) with some like the close association of rainfall and vegetation over long time scales from previous studies (Anderson & Hoffman, 2007; Anderson, Hoffman, & O'Farrell, 2010; Rahlao et al., 2008; Todd & Hoffman, 2009) implicating people's livelihoods in the region, particularly in light of predicted climate change (Anderson & Hoffman, 2007).

Conclusions

In general, other studies indicate a variable annual and geophyte component fluctuating in response to annual rainfall sequences within a relatively stable matrix of perennial shrub species fluctuating on decadal time scales in response to rare climatic events (Todd & Hoffman, 2009). High % rockiness (i.e. more micro-habitats) was important in accelerating vegetation recovery from grazing and in maintaining the high compositional variability found in the Succulent Karoo (Dreber & Esler, 2011; Hendricks et al., 2005; Todd & Hoffman, 2009).That the vegetation had minimal positive response over 6 years, indicates that in ranges, the long-term effect and impact of grazing should enforce to all those who manage or work with the land to know that their decisions last for decades at the minimum. Climatic/episodic events (Watson, Westoby, & Holm, 1997) will only prompt responses in Succulent Karoo vegetation after decades rather than annually as was found in other ecosystems such as savanna. In these semi-arid systems, micro-sites (increase in % rockiness) were very important as they allowed for soil and seeds to accumulate, providing a sufficient medium for growth (Dreber & Esler, 2011).

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