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**PLANT ECOLOGY OF THE NAMAQUALAND STRANDVELD:
COMMUNITY STRUCTURE AND DYNAMICS IN A WINTER-
RAINFALL DESERT**

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TABLE OF CONTENTS

Chapter 1:	pp. 1
General introduction and study site description.	
Chapter 2:	pp. 15
Spatial pattern analysis in Strandveld communities: evidence for general positive interactions.	
Chapter 3:	pp. 35
Within-clump species associations as a qualitative guide to the relative importance of deterministic interactions vs. chance in Strandveld communities.	
Chapter 4:	pp. 49
High turnover rates and weak apparent interspecific interactions: further evidence for non-equilibrium dynamics in Strandveld communities	
Chapter 5:	pp. 63
The relative performance of clumped vs. experimentally isolated plants in the Medium Strandveld	
Chapter 6:	pp. 77
The horizontal distribution of root biomass in Strandveld communities	
Chapter 7:	pp. 85
General conclusions	
Appendix 1:	pp. 89
Derivation of the C -function.	

ABSTRACT

The Strandveld forms the western coastal margin of the arid Namaqualand system. As a whole, Namaqualand has a very unusual diversity of plant life. Firstly it is unusually diverse in the most basic sense - there are lots of species, and many of them are endemic. Secondly, the ratio of species diversity to functional diversity is very high (i.e. there appears to be a great deal of functional overlap). Thirdly, in the specific case of the Strandveld, this diversity exists in a very homogeneous abiotic context. This leads to a challenging theoretical question: how does this diversity persist at a local scale? Although fundamental in nature, the answer to this question has many applied implications in terms of how we might manage the system, and how we might rehabilitate areas that have been damaged by activities such as mining. In order to begin to address this question, I set out to explore the spatial and temporal structure of selected Strandveld communities. This strategy has proved fruitful in many other systems and was in keeping with prevailing conceptual model for Namaqualand.

My earliest observation in these communities was that the majority of perennial plants assemble into cosmopolitan vegetation clumps. This led me to postulate that communities are shaped by a positive feedback between seed dispersal strategies that promote the recruitment into clumps and general physical benefits associated with microhabitat modification and mutual protection. Aspects of this postulate were tested with a combination of manipulative and sampling experiments. The results from a removal experiment suggested that interactions between individuals and their neighbors in clumps are in fact more complex than initially thought. Both negative and positive interactions were evident when different variates were considered, indicating that a balance between positive and negative interactions exists. This result was further supported by the observation that the spatial distribution of below-ground biomass does not mirror the highly clumped above ground pattern, suggesting that competition for water is a likely possibility.

Despite this evidence that interactions between individuals may shape the spatial structure of these communities, I could find little evidence that the interactions between individuals of particular species result in any deterministic outcome. There was certainly no evidence for any deterministic competitive exclusion. The species make-up of the vegetation clumps suggests that a large element of chance is involved in the assembly of clumps, and the lack of any strong relationships in populations between the size of individuals and their biotic neighborhoods further supports this suggestion. The implication of this is that these Strandveld communities may be examples of communities with stochastic domination where species coexistence occurs, not in spite of, but because they are functionally equivalent generalists.

Together, this understanding of the forces shaping the spatial structure of Strandveld communities, and the suggestion that Strandveld communities may be characterized by stochastic domination constitutes a very valuable contribution to the conceptual framework that has emerged to explain Namaqualand's unique plant diversity.

ACKNOWLEDGEMENTS

When all is said and done, this thesis represents a series of collaborative studies around a general theme. The vegetation survey described in Chapter 1 was conducted in collaboration with Tilla Raimondo and Phil Desmet. The spatial pattern analysis (Chapter 2), the interpretation of clump membership (Chapter 3), the description of Standveld dynamics (Chapter 4), and the preliminary study of below ground patterns (Chapter 6) have been written up as papers by myself and my two supervisors Richard Cowling and Karen Esler. The experimental study on plant interactions (Chapter 5) was a collaborative experiment conducted by Byron and Heather Lamont, Karen Esler and myself.

In addition to thanking these principle collaborators, I'd like to thank Wendy Paisley for the unending administrative support that she gave. I'd also like to thank Taffy Johnson, Jessica Kemper, Angela Mbatha and Terry Wilson for their assistance with fieldwork at various stages of the thesis. William Bond provided valuable comments on drafts of Chapter 2 while Sue Milton provided comments on the work presented in Chapter 6.

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CHAPTER 1:

GENERAL INTRODUCTION AND STUDY SITE DESCRIPTION.

Introduction

Aside from the aesthetic splendor of Namaqualand, and the charismatic nature of many of the plant species that are unique to this system, what really sets it apart botanically is something of an oxymoron: it is an astoundingly diverse desert. In an area of about 50 000 km² at least 2750 species of vascular plants occur (Cowling *et al.* 1999a). Approximately half of these are endemic. This translates to levels of both local and regional plant species richness that are higher than any other desert system in the world. For example, there are four times the number of species as equivalent sized areas of the North American winter rainfall deserts (Cowling *et al.* 1999b). Add to this the fact that the ratio of functional diversity to species diversity in Namaqualand communities is generally relatively low (Cowling *et al.* 1994), and one gets a challenging conundrum: how has this diversity come about and how does it persists (particularly at a local level). With this in mind, Cowling *et al.* (1999c) proposed a conceptual model (Figure 1) that integrates what is known about the selective regime and environmental constraints common in Namaqualand, with plant adaptations (both functional and behavioral), to explain community structure and ultimately the unique species richness of the system. While the model suggests a number of novel interpretations of community structure in arid systems, it is far from complete and much of what it proposes is highly speculative. For this reason, it provides a very rewarding platform from which to launch this detailed study of the community structure and plant behavioral adaptations in the Strandveld - the coastal vegetation strip of Namaqualand. Two suggestions in particular form a thread that runs throughout this thesis, tying together chapters that are otherwise written as stand-alone conceptual units. The first is that while many contemporary models have emphasized the role of competition in structuring desert plant communities (e.g. Beals 1968, Fonteyn & Mahall 1981, Fowler 1986) the Cowling *et al.* (1999c) model explicitly plays down competition while emphasizing the role of positive interactions. The second suggestion is more subtle. The model suggests that the high levels of determinism that have been described in several other desert systems (Yeaton & Manzanares 1986, Yeaton & Esler 1990, Valiente-Banuet & Ezcurra 1991, Aguiar & Sala 1999) may be overshadowed by the structural homogeneity of the species and uncertainty resulting from the sensitivity of the species to drought and hence rapid population turnover. I believe that the analyses presented in this thesis go a long way towards addressing certain

difficulties surrounding these two suggestions, and cementing them into a powerful explanatory tool.

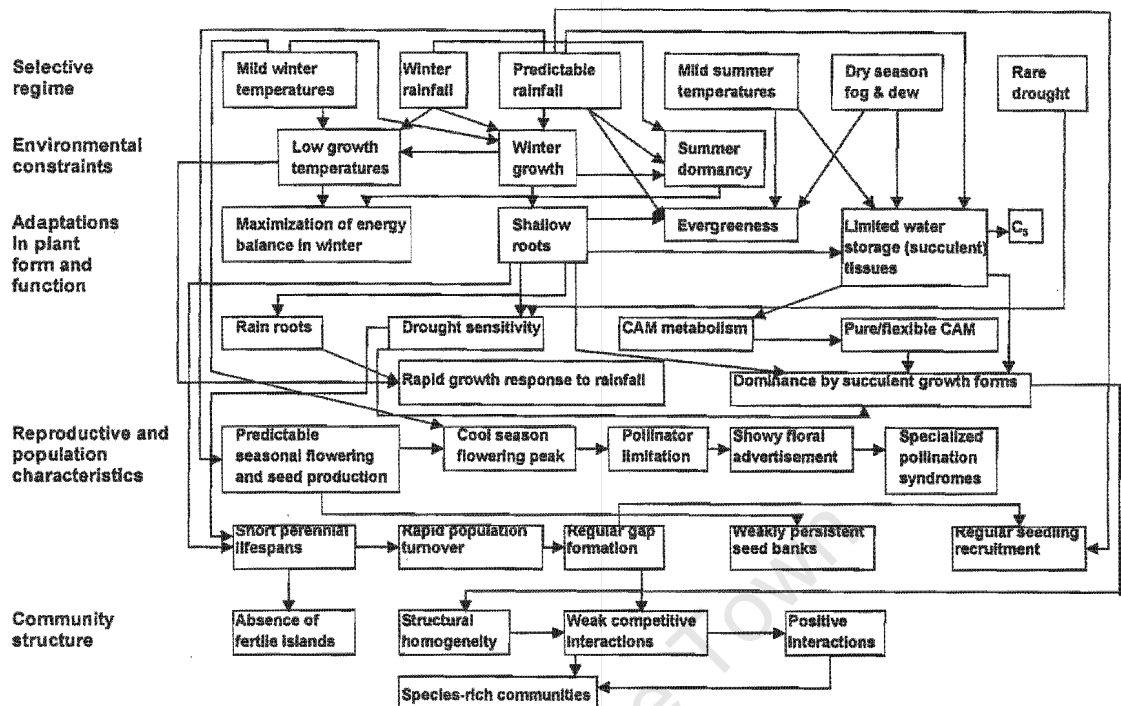


Figure 1. Namaqualand conceptual model integrating selective regime and environmental constraints with plant adaptations (both functional and behavioral), community structure and ultimately species richness (From Cowling et al. 1999c).

Thesis overview

Following on from this thesis overview, the remainder of Chapter 1 is dedicated to describing the Groen River study site and placing it in a broader regional context. I then present a description of the spatial distribution of plants in selected Strandveld communities (Chapter 2). In terms of the model presented in Figure 1, this step provides a formal, empirical description of the spatial structure of these communities, which in turn provides a basis for speculation on possible processes responsible for this structure. The overwhelming trend that emerged was the tendency for most perennial species to assemble into multi-species vegetation clumps (Plate 1). In Chapter 3, I build on this observation by providing a description of species membership in vegetation clumps and use this as a basis to argue that chance plays a larger than generally recognized role in the structuring of Strandveld communities. In Chapter 4, I add to this argument regarding the role of chance. I combine a more detailed analysis of certain aspects of data from the first census of the mapped plots described in Chapter 2, with



Plate 1. Clumped vegetation patterns near the Groen River mouth. Top: Short Strandveld community. Bottom: Medium Strandveld community

selected results from a second census of the mapped plots. Taken together Chapters 3 and 4 lend a great deal of support to the suggestion that dynamics in Namaqualand communities may be anything but highly deterministic.

They do not, however, provide any clue as to why most perennial plants favour associating into clumps. While I speculate on possible mechanisms (including positive interactions) in Chapter 2, in Chapter 5, I begin to address this question explicitly, using results from an experiment in which adult individuals were isolated from their clumps and compared with matched plants that were not. I follow this up with a study of the relative spatial arrangement of root and shoot biomass in Chapter 6 and speculate on how this may contribute to the perpetuation of clumped above ground vegetation patterns. Finally, in Chapter 7, my concluding chapter, I revisit the conceptual model in Figure 1 armed with the major findings of this thesis. In addition to updating the model, I also discuss some interesting questions raised by the thesis and present possible directions for future research.

Groen River - the study site

The Strandveld - The Strandveld forms the western coastal margin of Namaqualand (Cowling *et al.* 1999c) which is in turn one of two domains in the Succulent Karoo biome (Rutherford & Westfall 1986, Jürgens 1991, Rutherford 1997). This simple definition, however, belies a great deal of uncertainty as to the exact extent of the vegetation type, particularly in a north/south direction (Figure 2). Definitions range from the conservative (Port Nolloth in the north to the Olifants in the south) to the generous (from 20°S in the north to Cape Point in the south) (Le Roux & Schelpe's 1988, Jürgens 1991, Boucher & Le Roux's 1993, Low & Rebelo 1996, Williamson 1997). The uncertainty surrounding the northern boundary essentially stems from the fact that access to the coastal strip north of the Orange River has been highly restricted due to diamond mining in the area and as a result botanical exploration has been limited. In the case of the southern boundary on the other hand, there is no clear vegetation disjunction to indicate the end of the Strandveld. Historically, it was thought that the boundary between the Palaeotropical and the Cape Floral Kingdoms occurred somewhere between the Berg and Olifants Rivers (Moll *et al.* 1984). However, this view has become obsolete with the suggested inclusion of the Succulent Karoo into the Greater Capensis Kingdom by Jürgens (1991). Environmentally, there is a strong but continuous gradient of decreasing precipitation from the hyper-arid regions of southern Namibia (0-20 mm/year) to the more than 500mm/yr at Cape Point which also supports the view that placing a southern boundary on the Strandveld is likely to be arbitrary.

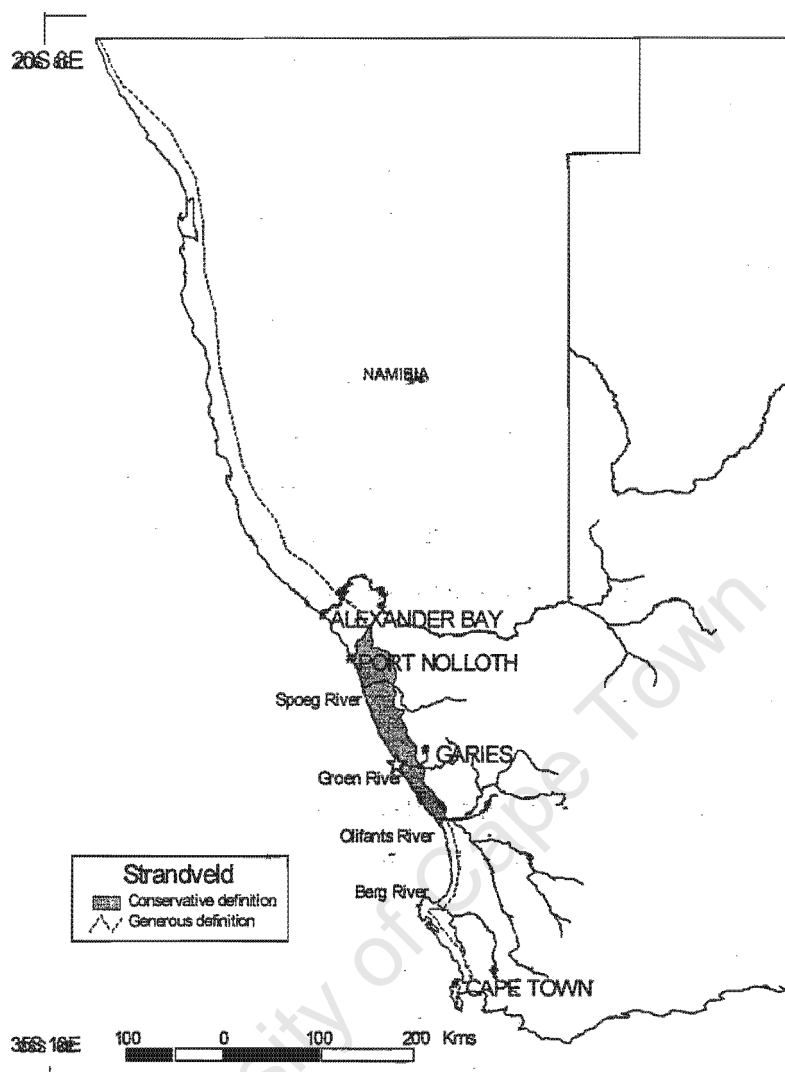


Figure 2. Map of the west coast of southern Africa showing the position of the Groen River study site as well as various interpretations of the extent of the Strandveld.

Physiography – Irrespective of how the Strandveld is defined though, the Groen River (30°51'S 17°34'E) is situated in the mid- to southern section. The area receives an average annual rainfall of around 140 mm which is close to the median for the arid coastal zone. In terms of the particular study period covered by this thesis (July 1997 to August 1999), following unusually high rainfall in June 1997, both the July 1997 - July 1998 and the July 1998 - August 1999 periods were relatively dry (111 mm and 123mm respectively [interpolated data]). As is generally the case in Namaqualand most of this falls in winter. Fog and dew are a regular occurrence and may contribute significantly to the total precipitation (Cowling *et al.* 1999c). Temperatures in the area are generally moderate. The average

maximum temperature in January (the hottest month) is about 20°C, while the average minimum temperature in June (the coolest month) is about 9°C. Frosts do not occur. Wind is a very important feature of the climatic regime (Desmet & Cowling 1999). In summer, steep pressure gradients associated with a cold ocean and a warm hinterland account for the high winds. In winter, the seawards tumble of unstable air from the high altitude interior plateau towards advancing low-pressure systems is the cause of the föhn-like hot berg winds. These winds result in high evaporative demands; may have profound effects on seed dispersal; and may result in physical damage to plants directly through wind throw or through sand blasting (von Willert *et al.* 1992, Jürgens 1996). In addition to this source of disturbance, the area is also subject to grazing. Currently this is mainly in the form of grazing by sheep. Prior to widespread human settlement though, indigenous antelope such as springbok, gemsbok, black Wildebeest, blesbok, quagga and red hartebeest would have had much the same impact (Klein & Cruz-Urbe 1987). Springbok in particular were reported to have moved in large aggregations in Namaqualand (Skinner 1993). The soils in the area are red or white sands that may be of either terrestrial or marine origin. They are generally characterized by three horizons: a relatively shallow indistinct sandy orthic A horizon; a sandy, apedal B horizon of variable depth (20-150 cm); and an underlying impenetrable "dorbank" (silcrete) or calcrete sub-soil. The combination of a B horizon of variable depth and an impenetrable sub-soil results in the range of potential plant rooting depths.

Vegetation - Prior to this study, there have been only two reports that present detailed descriptions of the west-coast Strandveld communities. In the first of these, Desmet (1996) formally described the plant communities between the towns of Port Nolloth and Alexander Bay some 170 km North of the Groen River in the hyper-arid fringes of the Strandveld. The second, by Boucher & Le Roux (1989), is perhaps the more relevant in terms of this thesis in that it describes the communities (including the Strandveld communities) in the coastal strip between the Olifants and Spoeg Rivers, an area that includes the study site. They defined five main vegetation sub-types: 1) strand communities; 2) Strandveld communities; 3) Succulent Karoo; 4) sand plain fynbos; and 5) river and estuarine vegetation. Within the Strandveld sub-type they recognized three broad "communities" based largely on the height of the vegetation. They characterized a Short Strandveld community with an average shrub height between 10 and 35 cm and vegetation cover of perennial species of less than 50%. They suggest that this community is associated with shallower soils where there is very little ground storage of moisture. The second Strandveld community that they identified was the Medium Strandveld which is characterized by a greater dominance of larger shrubs (> 50 cm) and which they suggest has a

perennial cover of between 50 and 60 %. Finally, they identified a tall Strandveld found on deep calcareous sands, which is dominated by shrubs of 1 - 2 m tall with a canopy cover of 60-75%. Because of the large scale focus and preliminary nature of this study by Boucher & Le Roux (1989), I decided to conduct a formal survey of the vegetation present in the immediate vicinity of the Groen River mouth.

Vegetation Survey: sampling methods – The vegetation was sampled along three major transects perpendicular to the coast. The sample “plots” comprised smaller sub-transects laid out parallel to the coast within areas of homogeneous vegetation. For each sub-transect a tape measure was laid out over the vegetation, and the beginning and end points of each plant were recorded. Annuals and geophytes were not included in the sampling because of their ephemeral nature. A total of 19 sub-transects were sampled along the three major transects. This sub-transect approach was used in preference to a more conventional plot approach so that plant cover and cover abundances of species could be calculated rather than estimated.

Environmental variates recorded at each sub-transect included general features such as distance from the sea, slope and aspect, as well as specific soil physical and chemical characteristics. Soil samples collected from 5 cm below the surface were assayed for texture, pH, resistance, macro elements (sodium, calcium, magnesium, phosphorus and nitrogen) and trace elements (boron, copper, manganese and zinc). Soil depth (depth to an impenetrable subsoil horizon) was also recorded. In addition, the nature of the sub-soils was characterized on the basis of a crude estimate of the calcium carbonate (CaCO_3) content (high in calcretes and lower in dorbanks). Average root depth (depth to which the majority of the roots extended) and maximum depth for the roots, (roots which extended the deepest into the soil) were also recorded as were the average and emerging heights of the sampled vegetation.

For each species in every sub-transect, an importance value based on both relative density and relative dominance was calculated. Relative densities were calculated as the ratios of the number of individuals of the species to the total number of individuals expressed as a percentage. Species dominance values were calculated as the proportion of the transect occupied by a particular species relative to the proportion of the transect occupied by all of the species, again expressed as a percentage. The importance value for each species in a sub-transect was then calculated as the sum of the relative density and relative dominance values.

Vegetation survey: analysis – The choice of analysis used for multivariate data sets such as this is a

tricky one. Traditionally in ecology, a combination of classification using especially Two-Way Indicator Species Analysis (Hill 1979), and Detrended Correspondence Analysis (Ter Braak 1987) have been used. However, both of these approaches have been strongly criticized (van Groenewoud 1992, McCune 1997 respectively). To a large extent these critiques stem from the fact that it is easy to forget that these techniques are exploratory rather than definitive. For this reason I selected the simplest and most explicitly exploratory approach that I could. I first divided the sub-transects into groups (communities) on the basis of the species importance values using a simple non-hierarchical classification approach (Genstat Committee 1993). The optimization criterion used was to maximize the total Euclidean distance between the classes. This criterion does not rely on the assumptions of multi-normality or equal within-class dispersion. I then examined the environmental properties associated with these groups using box and whisker diagrams.

Table 1. The classification of plots into Medium Strandveld (MSV), Short Strandveld (SSV) and strand communities and the associated soil depths and vegetation heights.

Plot	Community	Ave. Soil depth (cm)	Average height (m)	Emerging height (m)
1B	MSV	120	1.2	2
1D	MSV	135	1.2	2
1G	MSV	1.22	1.3	1.8
2E	MSV	200	1.2	2.85
2F	MSV	220	1.5	2
2G	MSV	190	1	1.5
3A	MSV	110	1.25	2
1A	SSV	44.2	0.2	0.5
1C	SSV	62	0.6	1
1E	SSV	73	0.3	0.75
2B	SSV	100	0.5	1.5
2C	SSV	74.3	0.3	1
2D	SSV	80	0.19	0.5
3B	SSV	66.6	0.6	0.8
3C	SSV	48.25	0.2	0.4
3E	SSV	121	0.45	0.8
1F	strand 1	220	0.25	0.5
2A	strand 1	200	0.2	0.5
3D	strand 2	37	0.2	0.35

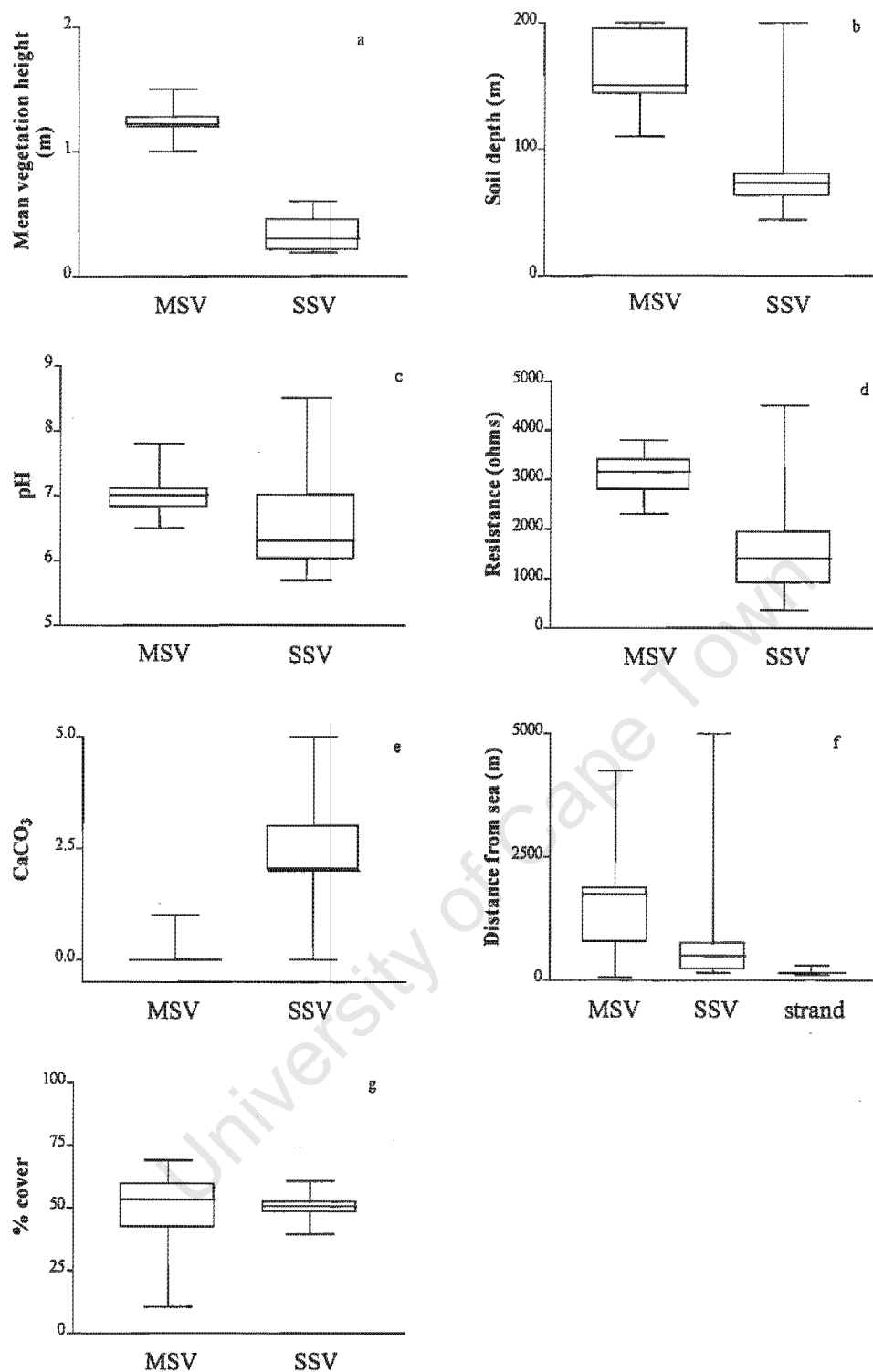


Figure 3. Box and whisker diagrams for a number of community characteristics in Strandveld communities. In all graphs, the first box and whisker is the Medium Strandveld (MSV) and the second represents the Short Strandveld (SSV). In the case of 'f', the third box and whisker represents the strand communities.

Vegetation survey: results – The classification algorithm divided the majority of sub-transects (16 out of the 19) into two groups that correspond more-or-less with Boucher & Le Roux's (1989) Short and Medium Strandveld communities (Table 1, Plate 1). There is no evidence in the data to suggest that an additional Tall Strandveld community described by Boucher & Le Roux is warranted. In addition, it would appear from Figure 3g, that Boucher & Le Roux's suggestion that vegetation cover may be a distinguishing feature of different Strandveld communities is erroneous. The three sub-transects that did not fall within the two main groups, probably represent communities from the strand vegetation sub-type (Boucher & Le Roux 1989) since all three occur within 300m of the sea (Figure 3f). However, the classification used here suggests that these communities were not sampled adequately to allow any real interpretation of the group and so they are excluded from Figure 3 with the exception of Figure 3f.

In terms of abiotic affinities, it would appear that the Short Strandveld generally occurs on shallower soils, although the soil depth range does overlap with the Medium Strandveld (Figure 3b). In addition to this distinction, Short Strandveld communities were often associated with higher levels of calcium carbonate in the sub-soil (suggesting an affinity with calcrete sub-soils) and lower resistances (possibly due to a stronger coastal influence) (Figure 3 d, e and f respectively). The lower resistances generally corresponded with higher concentrations of elemental sodium and calcium. Levels of copper appeared to be slightly higher in the Medium Strandveld, while the other elements assayed were more or less the same in both communities. Surprisingly there were no consistent pH differences between the sub-transects (Figure 3c).

Conclusions - Two important results emerge from this introductory chapter. The first is that the vegetation at the Groen River study site is very likely to be representative of much of the coastal vegetation (certainly from Port Nolloth in the north to the Olifants river in the south, and perhaps even beyond this range). The second is that at this site two communities (the Short and Medium Strandveld) dominate and that any study of the ecology of the Strandveld communities must include both of these. For this reason most of the work described in the remainder of this thesis was replicated in representative patches of these two communities.

References

- Aguilar, M.R. & Sala, O.E. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14(7):273-277.

- Beals, E.W. 1968. Spatial patterns of shrubs in a desert plain in Ethiopia. *Ecology*. 49:744-746.
- Boucher, C & 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. & Le Roux, A. 1993. Dry coastal ecosystems of the South African west coast. In: van der Maarel, E. (ed) *Dry coastal Ecosystems. Africa, America, Asia and Oceania*. Elsevier, Amsterdam. pp 75-88.
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments* 27:141-158.
- Cowling, R.M., Esler, K.J. & Rundel, P.W. 1999a. Special Issue Editorial: The plant ecology of Namaqualand, South Africa. *Plant Ecology* 142(1-2):1-2.
- Cowling, R.M., Esler, K.J. & Rundel, P.W. 1999c. Namaqualand, South Africa- an overview of a unique winter rainfall desert ecosystem. *Plant Ecology* 142(1-2):3-21.
- Cowling, R.M., Rundel, P.W., Desmet, P.G. & Esler, K.J. 1999b. Extraordinarily high regional-scale diversity in southern African arid lands: subcontinental and global comparisons. *Diversity and Distributions*. 4:27-36
- 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. & Cowling, R.M. 1999. The Climate of the Karoo- A functional approach. In: Dean, W.R.J. & Milton, S.J. (eds), *The Karoo: ecological patterns and processes*. Cambridge University press, Cambridge. pp. 3-16.
- Fonteyn, P.J. & Mahall, B.E. 1981. An experimental analysis of structure in a desert plant community. *Journal of Ecology*. 69: 883-896.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid systems. *Annual Review of Ecology and Systematics*. 17:89-110.
- Genstat 5 Committee 1993. *Genstat 5 Release 3 Reference Manual*. Oxford Science Publications, Oxford.
- 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.
- Jürgens, N. 1996. Psammophorous plants and other adaptations to desert ecosystems with high

- incidence of sand storms. *Feddes Repertorium* 107(3/4).
- Klein, R.G. & Cruz-Urbe, K. 1987. Large mammal and tortoise bones from Eland's Bay Cave and nearby sites, Western Cape Province, South Africa. In: Parkington, J. & Hall, M. (ed) *Papers in the Prehistory of the Western Cape, South Africa*. BAR International Series, Oxford. pp. 132-163.
- Le Roux, A. & Schelpe, T. 1988. *Namaqualand*. Botanical Society of South Africa, Kirstenbosch.
- Low, A.B. & Rebelo, A.G. 1986. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria.
- McCune, B. 1997. Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78(8): 2617-2623
- Moll, E.J., Campbell, B.M., Bossi, L., Jarman, M.L. & Boucher, C. 1984. A description of the major vegetation categories in and adjacent to the Fynbos biome. *South African National Science Progress Report CSIR* 83:1-29.
- Rutherford, M.C. & Westfall, R.H. 1986. Biomes of southern Africa: an objective categorization, 1st ed. *Memoirs of the Botanical Survey of South Africa*, 54:1-98.
- Rutherford, M.C. 1997. Categorization of biomes. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge. pp 91-98.
- Skinner, J.D. 1993. Springbok treks. *Transactions of the Royal Society of South Africa*. 48:291-305.
- 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.
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán valley, Mexico. *Journal of Ecology*. 79:961-971.
- van Groenewoud, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSpan Analysis. *Journal of Vegetation Science* 3: 239-246.
- Von Willert, D.J., Eller, B.M., Werger, M.J.A., Brinckmann, E. & Ihlenfeldt, H-D. 1992. *Life Strategies of Succulents in Deserts with Special Reference to the Namib Desert*. Cambridge University Press, Cambridge.
- Williamson, G. 1997. Preliminary account of the floristic zones of the Sperrgebiet (Protected Diamond Area) in southwest Namibia. *Dintera* 25:1-68.
- Yeaton, R.I. & Esler, K.J. 1990. The dynamics of a succulent karoo vegetation. A study of species

association and recruitment. *Vegetatio*. 88:103-113.

Yeaton, R.I. & Manzanares, A.R. 1986. Organization of vegetation mosaics in the *Acacia schaffneri* – *Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology*. 74:211-217.

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Chapter 2:

SPATIAL PATTERN ANALYSIS IN STRANDVELD COMMUNITIES: EVIDENCE FOR GENERAL POSITIVE INTERACTIONS.

Abstract

In this chapter I describe of the spatial arrangement of individual plants in mapped plots in the Short and Medium Strandveld communities. In both communities there was a very strong tendency towards clumped patterns when all plants were considered together. There was also a predominance of clumped patterns when the most abundant species in both communities were considered individually. When the arrangement of the most abundant species was considered relative to the arrangement of all other individuals at the within-clump scale, there was a high frequency of positive associations in both communities (62% and 65%). As an opening hypothesis I speculate that these patterns represent a combination of seed dispersal strategies that favor clumped patterns and a predominance of positive spatial associations between plants in both of the communities. When specific pairwise associations between the most abundant species were considered at the within-clump scale, differences were apparent between the two communities. In the Short Strandveld neutral associations predominated, while in the Medium Strandveld, neutral and positive association accounted for equal proportions of the associations. This between-plot difference was also apparent when the volumes of plants were related to an index of neighborhood competitiveness. In the Short Strandveld there were no significant relationships while in the Medium Strandveld there were some weak (but significant) relationships. These differences were not altogether unexpected. If we assume that plants in the Medium Strandveld are generally longer-lived, then spatial associations between plants are likely to develop over a longer time and, therefore, are likely to be stronger.

Key words

Coexistence, community spatial structure, dispersal, diversity, hypotheses, mutualism

Introduction

In Chapter 1, I introduced the question: how is the species diversity, with its apparent redundancy, maintained in Namaqualand (and more specifically Strandveld) plant communities? The answer to this is particularly elusive in the context of Strandveld communities that occur on the coastal sand plains where small-scale environmental heterogeneity is very limited. As such, the potential for diverse "habitat niches" (Hubbell & Foster 1990) is also limited. The Namaqualand

conceptual model (Cowling *et al.* 1999) introduced in Chapter 1 (Chapter 1 - Figure 1), suggests that the immediate answer to this question may lie in the temporal and spatial structure of these communities. Certainly the key to the persistence of species once they have evolved lies at the level of community structure. Studies from in the Southern Karoo Domain (Namaqualand's southeastern neighbor in the Succulent Karoo) have suggested cyclical succession as a good general model for within-community temporal and spatial structure (Yeaton & Esler 1990). According to this model, several species of small-seeded Mesembryanthemaceae (the dominant leaf succulent shrubs) germinate and establish in open areas between existing plants. This guild of pioneers then act as seed traps for wind-dispersed seeds and serve as facilitators during the establishment phase of the secondary colonizers. Once established, the colonizers out-compete the pioneer succulents and persist until they die. This type of behavior is not unique to this desert system (e.g. Valiente-Banuet & Ezcurra 1991) and is essentially analogous to an assembly of loose or facultative host-parasitoid like relationships (Wilson & Nisbet 1997). Given this analogy it is possible to borrow (at least conceptually) the theoretical work described in Hassel *et al.* (1991) in order to explain the stability of the two guilds in such systems. These authors suggest that spatial heterogeneity in the distributions of the interacting species is a key stabilizing factor. However, while this explains the stable coexistence of the two guilds (the pioneer guild and the successor guild) within this system, it does not explain the stable coexistence of several species within each guild. This is perhaps reflected in the simulation model of this cyclical succession dynamic in the eastern Succulent Karoo region proposed by Wiegand *et al.* (1995) which relies on the inclusion of small-scale disturbances in order to achieve coexistence of the five main species.

The Southern Karoo Domain is, however, characterized by far greater structural and functional diversity than the strictly winter rainfall Namaqualand Domain (Cowling *et al.* 1994, Milton *et al.* 1997). In addition, evidence for the competitive interactions which are crucial to this cyclical succession model, and which abound in the form of simple nearest neighbor relationships in the Southern Karoo Domain (e.g. Esler & Cowling 1993) do not appear to be a common feature in Namaqualand communities (R.M.Cowling & J.J. Midgley unpublished data). It would thus seem that there is an additional dimension to plant interactions (or stochasticity) that is important in the structuring of these Namaqualand communities. My objective in this chapter was thus to formally quantify the static spatial structure of individuals in the Short and Medium Strandveld communities, and then to use this as a basis for formulating hypotheses about other aspects of community structure and function.

Materials and Methods

Nomenclature – Nomenclature used throughout this thesis was according to Arnold & DeWet (1993) for all taxa except the Mesembryanthemaceae (Mesembryanthema, Aizoaceae *sensu*

Bitterich & Hartmann 1988) where it was according to the Bolus Herbarium (BOL). Families for all species mentioned are listed in Table 1.

Table 1. Summary of the associations between species with more than 10 individuals and all the other individuals in the two communities. SSV = Short Strandveld, MSV = Medium Strandveld.

Species	SSV	MSV	Family
Dead	0	+	
<i>Cephalophyllum spongiosum</i> (L.Bolus) L.Bolus	+		Mesembryanthemaceae
<i>Pteronia onobromoides</i> DC.	+	+	Asteraceae
<i>Didelta carnosa</i> (L.f.) Aiton var. <i>tomentosa</i> (Less.) Roessler	+		Asteraceae
<i>Osteospermum oppositifolium</i> (Ait.) T.Norl.	+	+	Asteraceae
<i>Helichrysum trichostatum</i> (Thunb.) Less.	+		Asteraceae
<i>Ruschia fugitans</i> L.Bolus	0		Mesembryanthemaceae
<i>Othonna cylindrica</i> (Lam.) DC.	0	+	Asteraceae
<i>Euphorbia burmannii</i> E.Mey. ex Boiss.	+		Euphorbiaceae
<i>Galenia crystallina</i> (Eckl. & Zeyh.) Fenzl.	-		Aizoaceae
<i>Zygophyllum spinosum</i> L.	+		Zygophyllaceae
<i>Arctotis merxmuelleri</i> (Harv.) P.Beauv.	+	0	Asteraceae
<i>Vanzijlia annulata</i> (Aberger) L.Bolus	+		Mesembryanthemaceae
<i>Hermannia amoena</i> Dinter ex Friedr.-Holzh.	+		Sterculiaceae
<i>Asparagus capensis</i> L.	0		Asparagaceae
<i>Ficinia nigrescens</i> (Schrud.) J.Raynal	+		Cyperaceae
<i>Lessertia rigida</i> E.Mey	+		Fabaceae
<i>Limonium perigrinum</i> (P.J.Bergius) R.A.Dyer	+		Plumbaginaceae
<i>Hermannia cuneifolia</i> Jacq.	0		Sterculiaceae
<i>Ehrharta calycina</i> J.E.Sm.	-		Poaceae
<i>Crassula subaphylla</i> L.	+		Crassulaceae
<i>Trachyandra falcata</i> (L.f.) Kunth	-		Liliaceae
<i>Lampranthus multiseriatus</i> (Lbolus) N.E.Br.	0		Mesembryanthemaceae
<i>Lycium ferocissimum</i> Meirs	0	0	Solanaceae
<i>Zygophyllum morganii</i> L.	+	+	Zygophyllaceae
<i>Eriocarpus africanus</i> L.	-	+	Asteraceae
<i>Stoeberia utilis</i> (L.Bolus) Van Jaarsv.	+	+	Mesembryanthemaceae
<i>Chrysanthemoides incana</i> (Burn.f.) Norl.		+	Asteraceae
<i>Pharnaceum lanatum</i> Berl.	+	-	Aizoaceae
<i>Tetragonia fruticosa</i> L.	+	+	Aizoaceae
<i>Manochlamys albicans</i> (Aiton) Allen		0	Chenopodiaceae
<i>Ruschia</i> sp.		0	Mesembryanthemaceae
<i>Pteronia divaricata</i> (P.J. Bergius) Less.		0	Asteraceae
<i>Euphorbia mauritanica</i> L.		+	Euphorbiaceae
<i>Asparagus lignosus</i> Burn.f.		+	Asparagaceae
<i>Senecio sarcoides</i> (DC.) Sch.Bip.		+	Asteraceae
<i>Salvia lanceolata</i> Lam.		+	Lamiaceae

Community analysis -- A 12.5 x 25 m plot was laid out in a representative area of the Short Strandveld community (30°51'15"S, 17°34'49"E) and another of 30 x 50 m was laid out in the Medium Strandveld (30°52'15"S, 17°35'21"E). In each of these, species, size (height and two crown diameters) and location of all individuals with at least one dimension greater than 10 cm were recorded. In addition, the location and size of dead individuals were recorded. In the Short Strandveld plot, 1567 individuals representing 40 species were mapped while in the Medium Strandveld, 1534 individuals representing 36 species were mapped. These data were used to investigate several aspects of spatial pattern in each community. Firstly, I investigated the overall dispersion of individuals ignoring species. Secondly, I investigated the point patterns for individual species with more than 40 measured individuals. Thirdly, I considered all pairwise relationships between the species in this restricted subset of the data. Finally, I considered the distributions for

each species with more than 10 individuals relative to all the other individuals in the community.

These four aspects of pattern were investigated using the density functions of point-to-point distances for appropriate subsets of data. Ripley's univariate and bivariate K -functions were used for this (Diggle 1983, Ripley 1987). A weighting approach was used to correct for edge effects (Diggle 1983). This approach yields unbiased results for distances up to half the shortest side of the plot (Haase 1995). In order to make interpretation easier, the K -functions were transformed to $L(t)$ -functions (Prentice & Werger 1985, Rebertus *et al.* 1989). This transformation has the effect of stabilizing the variance and under complete spatial randomness the expectation for $L(t)$ is zero. For the univariate cases, 95% confidence limits of the $L(t)$ -functions for complete spatial randomness were estimated using random permutations of the plants in the plots. These were based on 100 simulations each. Departures of the empirical function below the lower confidence limit indicate significant regularity while positive values above the upper confidence limit indicate aggregation (Prentice & Werger 1985). For the bivariate analyses, confidence intervals were once again estimated using a randomization approach. In this case, however, the primary structure of each of the individual point patterns was retained and only their relative locations were randomized using toroidal shifts. Positive values above the confidence limits indicate significant "attraction" between the subsets of points while negative values below the confidence limits indicate significant "repulsion".

In the case of the pairwise species comparisons where positive spatial associations were suggested, I also calculated an index of asymmetry. In order to do this I defined a C -function for each species in the pair (See Appendix 1):

$$C_{12}(t) = \frac{100 \cdot A \cdot \left(\left(\sum_{i=1}^{n_1} \left(\sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 \right) - \left(\sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 / n_1 \right)}{n_2}$$

where n_1 and n_2 are the number of individuals in each of the two subsets being compared; t is the distance from the focal individual which defines the scale at which pattern is being considered; A is the area of the mapped plot divided by the area of the circle with radius t ; u_{ij} is the distance between the i th and the j th plants; $I_t(u)$ is defined to be 1 if $t \geq u$ or 0 otherwise (i.e. a counter variable); and w_{ij} is the weighting factor to correct for edge effects (the proportion of the circumference of the circle with radius u_{ij} and centered on the point i and passing through j that lies within the plot boundaries).

Unlike the K -functions that are in essence the average of the density functions for all individuals in a population (and therefore symmetrical), the C -functions are based on the coefficients of variation between density distribution for the individuals in each of the populations. For a species that is obligately associated with another, the variation should be low since all the

individuals will be closely associated with the other species. In contrast, where the species is less obligately dependent on the association, the values for C will be greater since individuals will not always be associated with the other species. The index of asymmetry (cv ratio) between two species is then simply the ratio of the C -functions for each of the species. When this index is close to one, the relationship can be said to be symmetrical. As it moves away from one (either greater or less than one), the symmetry becomes weaker. Whether the index becomes less than one or greater depends on which of the two species is less obligately dependent on the association. The interpretation of these asymmetry indices is not without its difficulties. From a purely statistical point of view, nothing is known about the sampling distribution of this statistic and it is even difficult to conceive of randomization approaches that might resolve this. For this reason I made no attempt to perform any significance tests on the values calculated. From a biological perspective, asymmetry may reflect a spatial association that is tending towards commensalism (+/0) or it may simply be a result of demographic imbalances where one of the species is much less abundant than the other and its mutualism potential therefore becomes "saturated". Nonetheless, I felt that calculating this index was a valuable exercise since it provided a means for detecting any "extreme" deviation from symmetry which might suggest that the observed positive spatial association is in fact commensal (+/0) or even an exploitation (+/-) spatial association.

Finally, in the absence of any time series data for mortality I was forced to make use of an indirect approach to assess the likelihood that thinning was an important aspect of within-clump dynamics. I assumed that if thinning were occurring, there should be a significant relationship between the size of individuals and an index of their neighborhood "competitiveness". As an index of neighborhood competitiveness, I used angular competition index described in Randall & Rejmánek (1993). This involves the calculation of the sum of the angles subtended by the crowns of competitors within a certain radius of the focal individual (1.25m in the case of the Short Strandveld, and 2.5m in the case of the Mediums Strandveld). The relationship between this index and the focal plant volumes was then investigated by means of regression. This analysis was carried out on the entire communities regardless of species as well as on the subsets of species that had more than 40 individuals.

Results

The Short Strandveld - When all individuals in this community were considered together, the overwhelming pattern was significant clumping apparent at all scales up to 6 m (Figure 1). The majority of plants occur in dense clumps with a mean diameter of 2.5 m (sem=0.11 based on a subsample of 20 clumps), and which are surrounded by open ground. A greater diversity of patterns emerged when species with more than 40 individuals were considered on their own (Figure 2). In the case of dead plants, as well as *Cephalophyllum spongiosum* individuals, the

distributions were clearly random over the entire range of scales investigated. The remainder of species all showed some degree of intraspecific clumping at assorted scales. For example, *Arctotis merxmuelieri* and *Vanzijlia annulata* showed clumping at almost all scales except less than about 0.5 m where they did not depart significantly from complete spatial randomness. In contrast, clumping in *Galenia crystallina* and *Euphorbia burmannii* was restricted to less than 2 m and less than 0.5 m respectively. Significant clumping at intermediate scales was evident in the case of *Ruschia fugitans* and *Othonna cylindrica*. Significant regularity was noticeably absent in all instances.

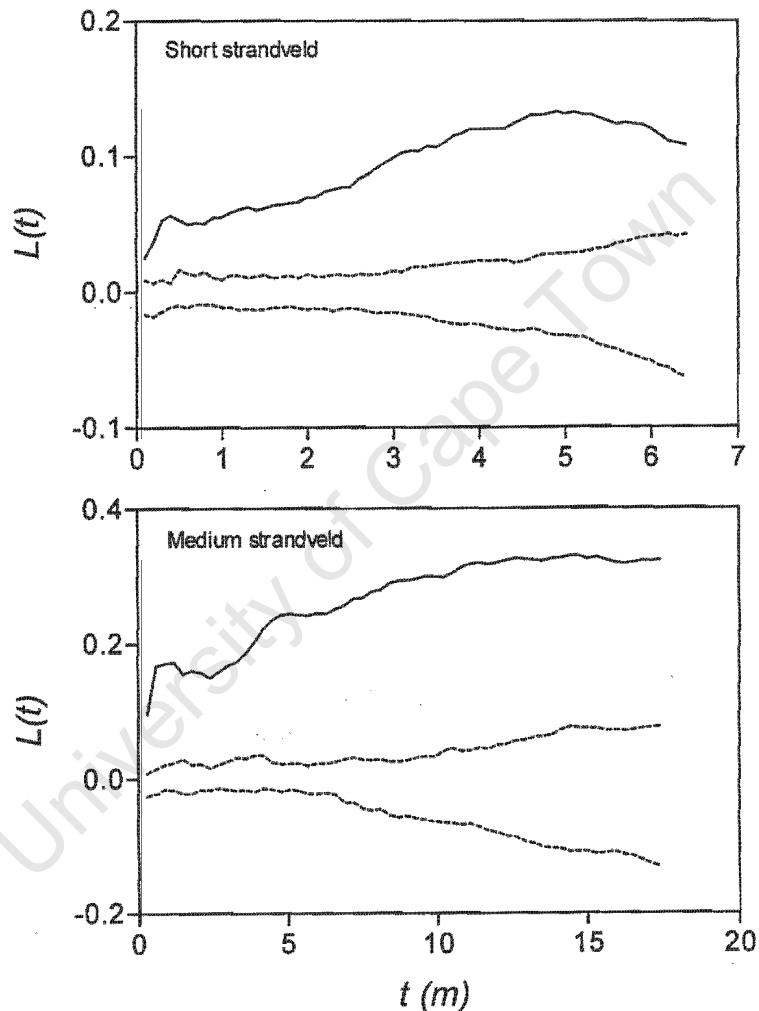


Figure 1. The overall dispersion patterns of individuals in two Namaqualand communities: a. Short Strandveld; b. Medium Strandveld. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits.

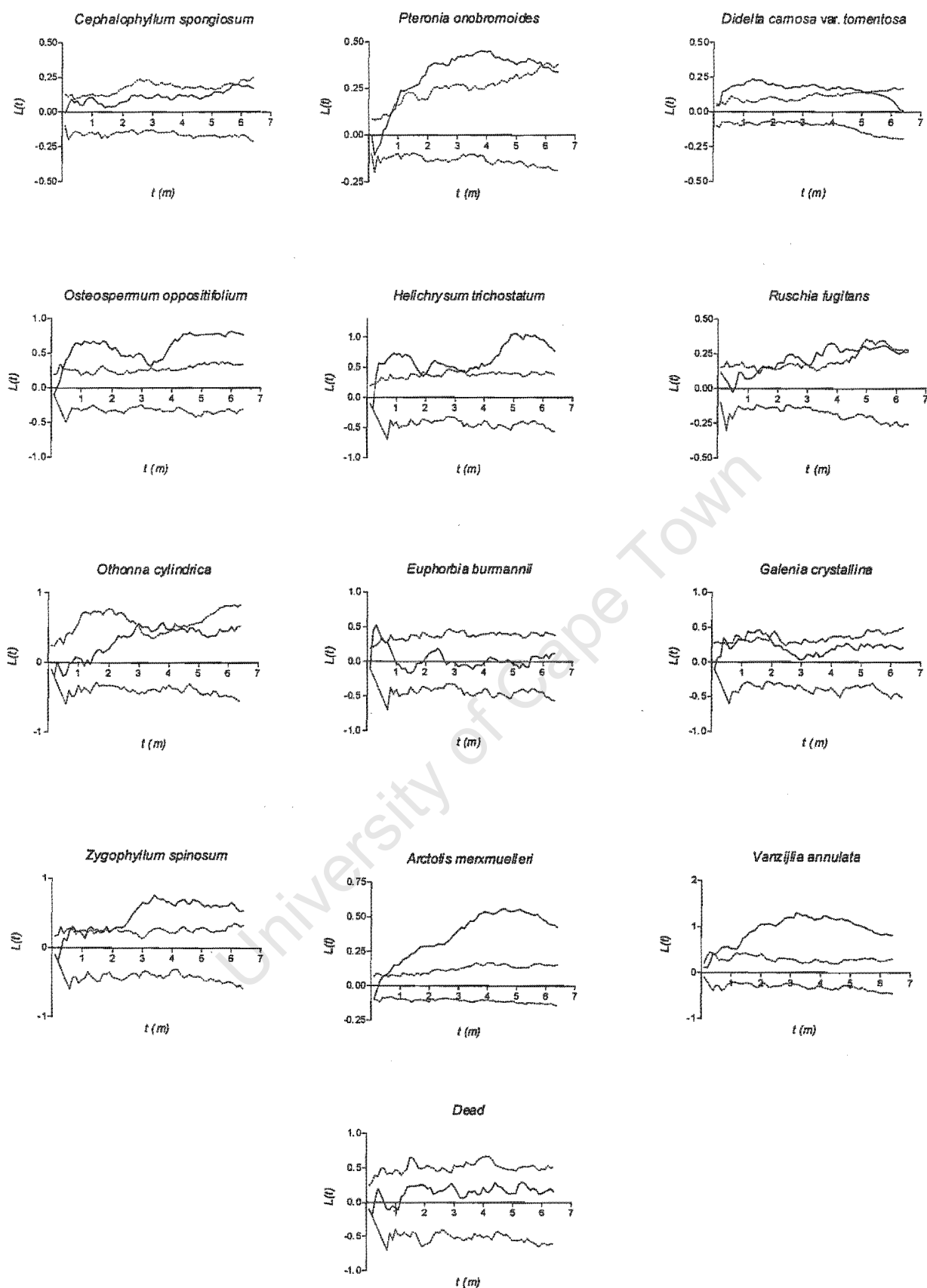


Figure 2. Dispersion patterns for species with more than 40 individuals in the Short Strandveld community. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits.

In order to simplify the interpretation of the pairwise patterns, I made use of the observed strong first-order clumping and restricted my attention to within-clump patterns (i.e. patterns which were apparent at scales less than a maximum of 4.0 m). Clumps were defined on the basis of the maximum clump size (4.0 m) rather than the mean of 2.5 m. At this scale, 71% of the spatial associations were not significantly different from randomness, 23% were positive and only 6% were negative (Table 2). This general trend of random spatial associations being most abundant followed by positive spatial associations and with negative spatial associations being the least abundant was consistent in all but two species. In the case of *Galenia crystallina*, negative associations accounted for 33% of the total while there were no positive spatial associations recorded. In *Pteronia onobromoides*, seven out of the 12 spatial associations were positive, four were random and one was negative. For the 18 positive spatial associations, the indices of asymmetry suggested that, in general, asymmetry was weak (Figure 3). In no instances were there any order of magnitude differences (i.e. cv ratios less than 0.1 or greater than 10). Where asymmetry was apparent, this was usually associated with large differences in the number of individuals in the two populations.

Table 2. Summary of pairwise associations between individuals of species with more than 40 individuals in the Short Strandveld plot. The codes used are: De – dead plants; Cs – *Cephalophyllum spongiosum*; Po – *Pteronia onobromoides*; Dc – *Didelta carnosus* var. *tomentosa*; Oo – *Osteospermum oppositifolium*; Ht – *Helichrysum trichostatum*; Rf – *Ruschia fugitans*; Oc – *Othonna cylindrica*; Eb – *Euphorbia burmannii*; Gc – *Galenia crystallina*; Zs – *Zygophyllum spinosum*; Am – *Arctotis merxmuelieri*; Vs – *Vanzijlia annulata*.

	De	Cs	Po	Dc	Oo	Ht	Rf	Oc	Eb	Gc	Zs	Am	Vs
De	0	0	0	+	+	0	0	0	+	0	0	0	0
Cs		0	+	+	0	0	0	0	0	0	0	0	0
Po			0	+	0	0	+	0	+	-	+	+	+
Dc				0	0	0	0	+	0	0	0	+	0
Oo					0	+	0	0	0	0	0	+	0
Ht						0	0	0	0	0	0	0	0
Rf							0	0	0	-	0	0	0
Oc								0	+	0	0	0	+
Eb									0	0	0	0	0
Gc										0	-	-	0
Zs											0	+	0
Am												0	-
Vs													0

In contrast to the dominance of neutral associations within-clumps when specific species pairs were considered, pairwise analyses between individual species and the rest of the community were characterized by a predominance of positive associations (62%) over either random (22%) or negative (15%) associations (Table 1). Finally, there were no significant relationships between the size of individuals and the competition index within-clumps at the 5% level.

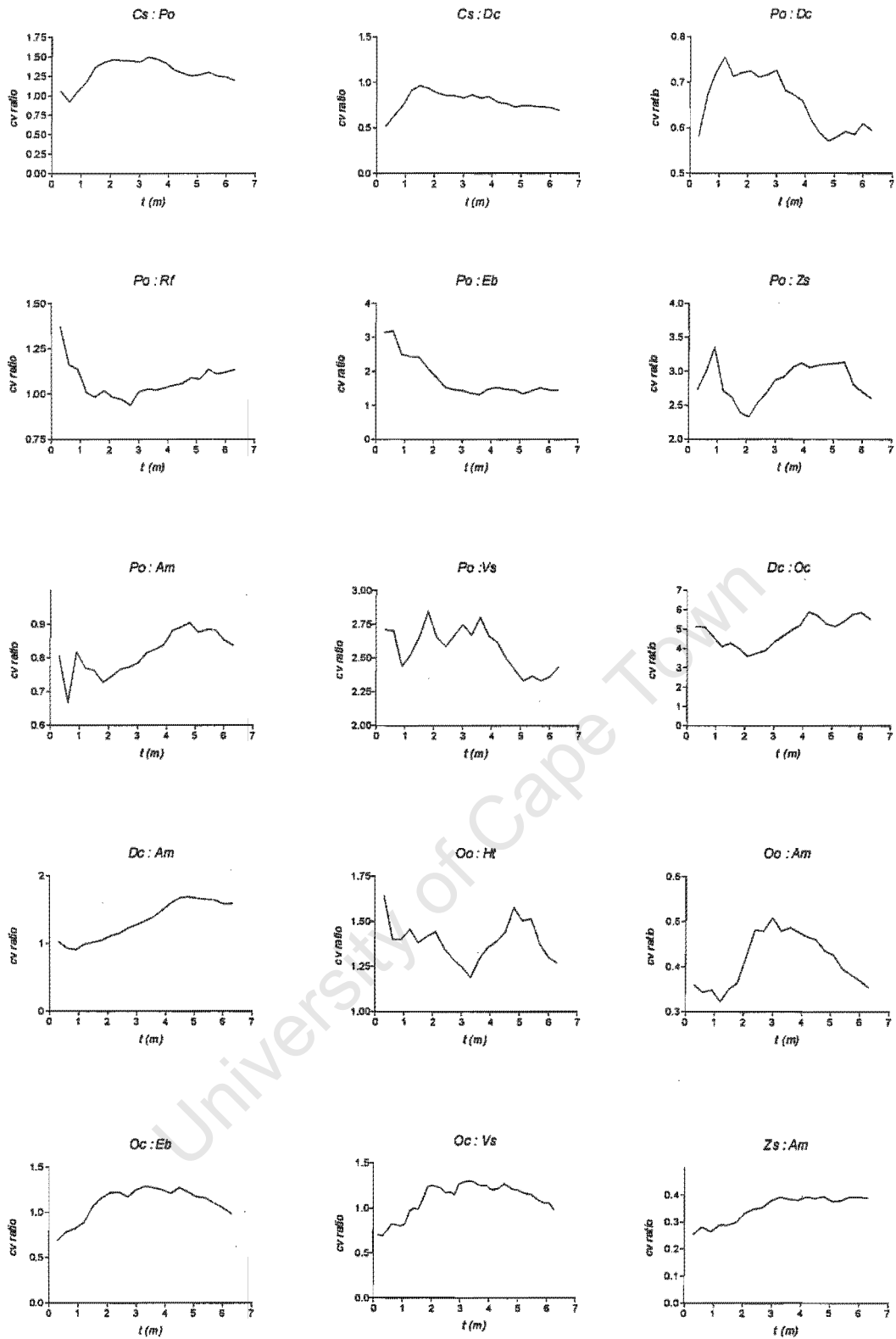


Figure 3. Asymmetry indices (cv ratio) for positive pairwise associations in the Short Strandveld community. Species codes are: *Cs* - *Cephalophyllum spongiosum*; *Po* - *Pteronia onobromoides*; *Dc* - *Didelta carnosus* var. *tomentosa*; *Rf* - *Ruschia fugitans*; *Eb* - *Euphorbia burmanii*; *Zs* - *Zygophyllum spinosum*; *Am* - *Arctotis merxmuelleri*; *Vs* - *Vanzijlia annulata*; *Oc* - *Othonna cylindrica*; *Oo* - *Osteospermum oppositifolium*.

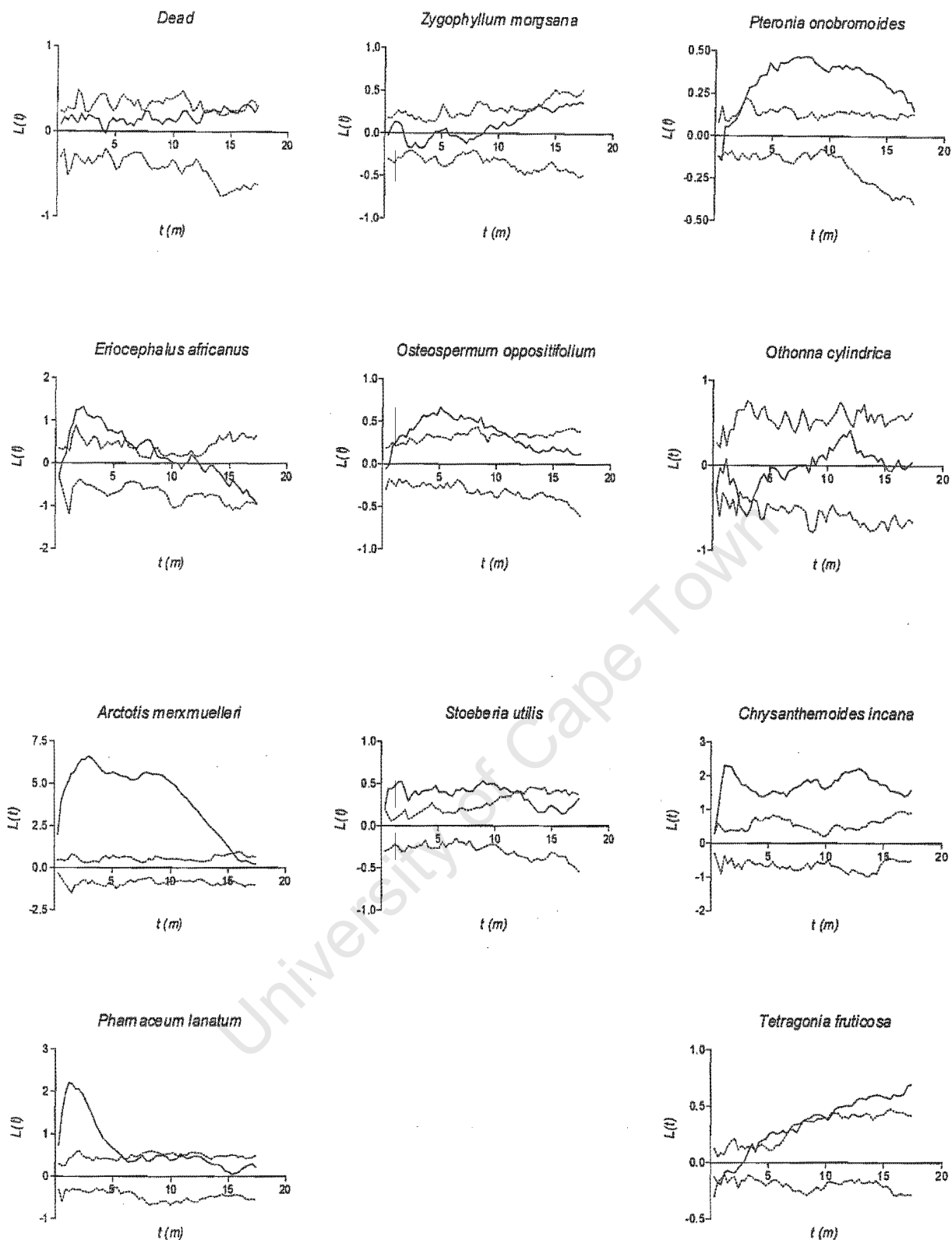


Figure 4. Dispersion patterns for species with more than 40 individuals in the Medium Strandveld community. The solid line represents the actual calculated L values while the broken lines represent the 95% confidence limits.

The Medium Strandveld - As with the Short Strandveld, the overall pattern of dispersion in this community was towards clumping at all scales considered (Figure 1). In this community, the clumps tended to be larger than in the Short Strandveld (mean=5.17 m, sem=0.34, n=20) which is not surprising given the larger overall size of the individuals. In terms of the patterns in univariate density functions for the 11 species that had more than 40 individuals (Figure 4), there were no species that were completely randomly distributed over the entire range of scales investigated. Only *Othonna cylindrica* showed any significant regularity and the rest of the species showed significant aggregation at some spatial scale, although this was fairly "weak" in the case of the dead plants and *Zygophyllum morganiana*.

Table 3. Summary of pairwise associations between individuals of species with more than 40 individuals in the Medium Strandveld plot. The codes used are: De – dead plants; Zm – *Zygophyllum morganiana*, Po – *Pteronia onobromoides*; Ea - *Eriocephalus africanus*; Oo - *Osteospermum oppositifolium*; Oc - *Othonna cylindrica*; Am – *Arctotis merxmulleri*; Su – *Stoeberia utilis*; Ci - *Chrysanthemoides incana*; Pl – *Pharnaceum lanatum*; Tf – *Tetragonia fruticosa*.

	De	Zm	Po	Ea	Oo	Oc	Am	Su	Ci	Pl	Tf
De	0	+	+	-	+	0	0	+	+	0	+
Zm		0	+	0	+	0	0	0	+	+	+
Po			0	+	+	+	0	0	+	-	+
Ea				0	0	0	0	0	0	-	-
Oo					0	0	0	0	+	-	+
Oc						0	0	0	0	0	0
Am							0	0	+	0	0
Su								0	-	0	+
Ci									0	0	+
Pl										0	-
Tf											0

For the bivariate patterns, I once again restricted my attention to within-clump patterns, in this case patterns which were apparent at scales less than 7m (Table 3). In this community, a much lower percentage of the spatial associations were random (49% as opposed to 71%). Positive spatial associations accounted for 38% of the remaining spatial associations while negative spatial associations made up 13%. The higher percentage of negative spatial associations in this community can largely be attributed to one species (*Pharnaceum lanatum*) which accounted for 55% of the negative spatial associations (7% of the total). This finding is interesting in light of the fact that in the Short Strandveld, *P.lanatum* was positively associated with several other species (Table 1). The most likely explanation for this anomaly is that in the Medium Strandveld, *P.lanatum* is structurally much smaller than the surrounding vegetation, while this is not the case in the Short Strandveld. Removing this species from the calculation yielded 49% random spatial associations, 44% positive spatial associations and 7% negative spatial associations. Once again, there were generally no extreme asymmetries detected at the within-clump scale (Figure 5). In terms of the pairwise analyses between individual species and the rest of the individuals in the

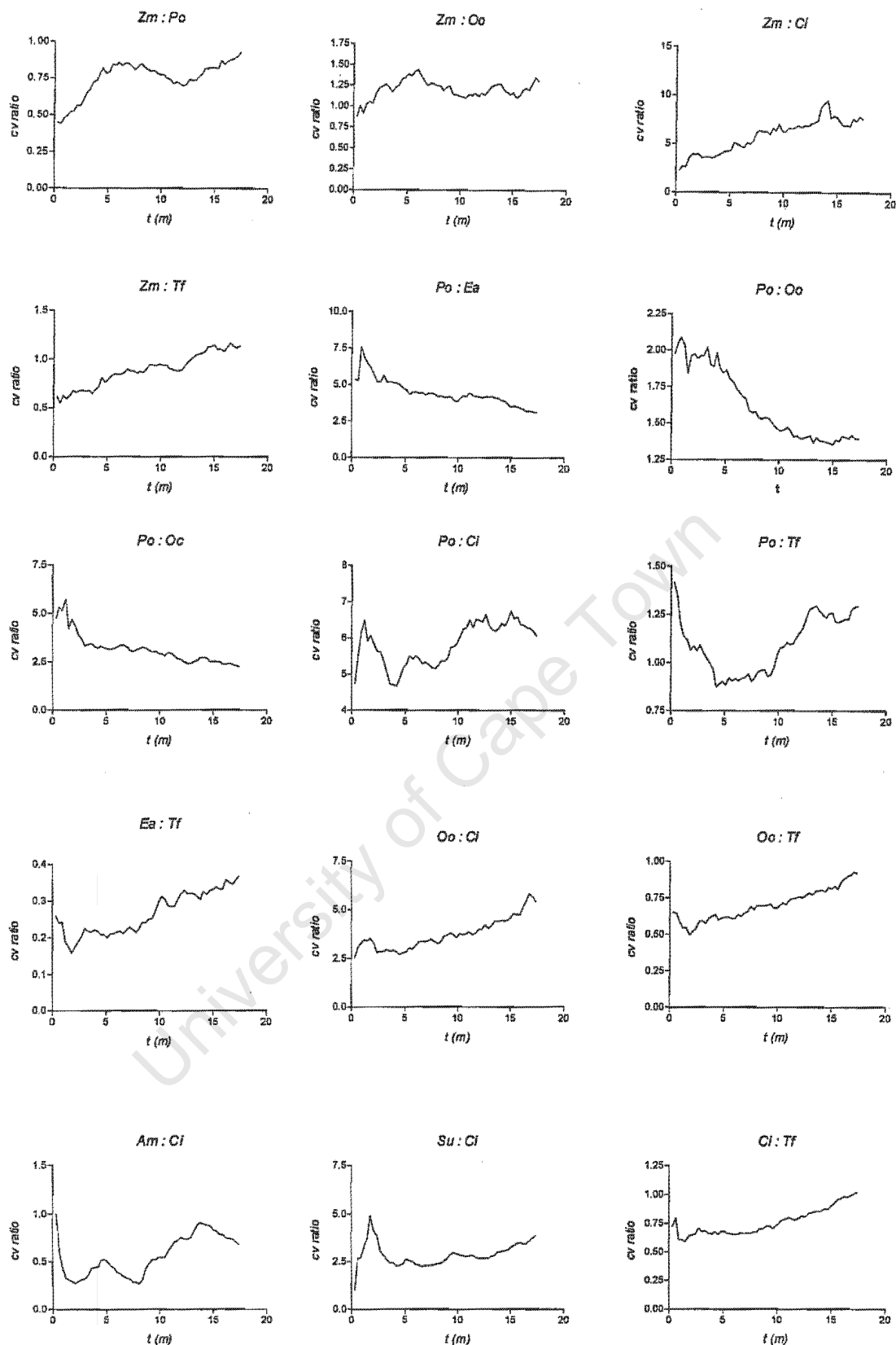


Figure 5. Asymmetry indices (cv ratio) for positive pairwise associations in the Medium Strandveld community. Species codes are: Zm – *Zygophyllum morgsana*; Po – *Pteronia onobromoides*; Oo – *Osteospermum oppositifolium*; Ci – *Chrysanthemoides incana*; Tf – *Tetragonia fruticosa*; Ea – *Eriocephalus africanus*; Oc – *Othonna cylindrica*; Am – *Arctotis merxmuelieri*; Su – *Stoeberia utilis*.

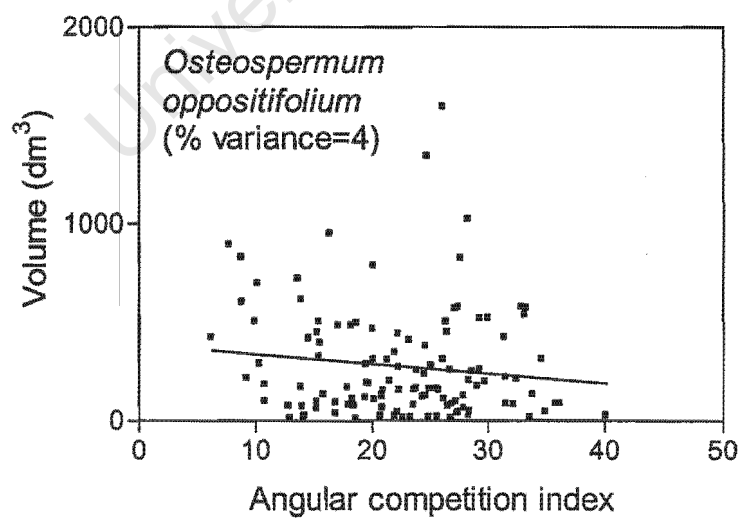
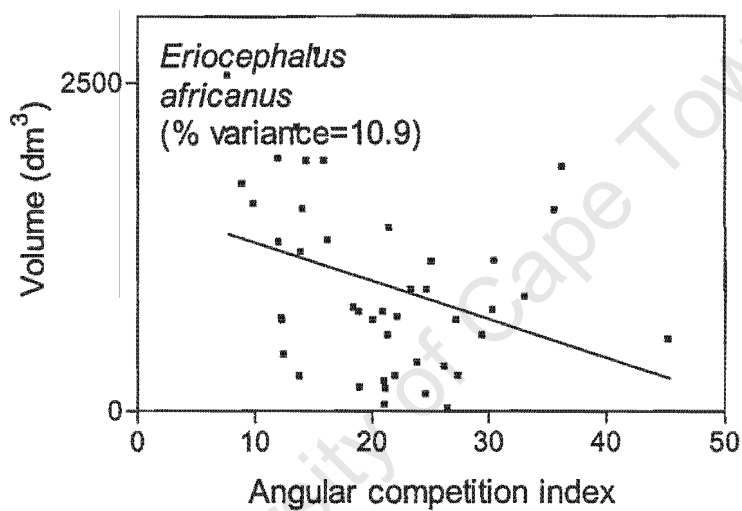
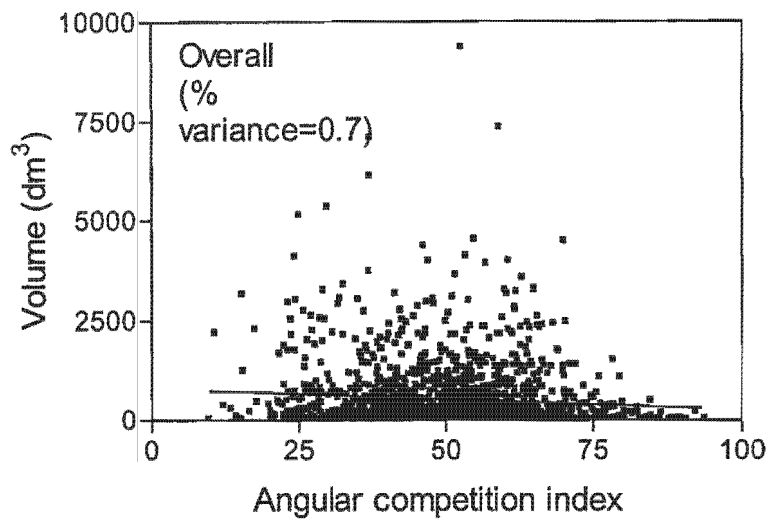


Figure 6. Scatter plots for the statistically significant regressions of plant volume against the angular competition index.

community, the ratios were similar to those in the Short Strandveld. Positive associations dominated (65%), followed by neutral associations (30%) while there was only one species (5%) which was negatively associated with all the rest (Table 1).

In the regression analyses of the relationship between individual volumes and their associated competition indices there was overall a statistically significant relationship at the 5% level. However, the biological significance of this is difficult to assess. The regression only accounted for 0.7% of the variation and no clear trend is evident from the scatter plot (Figure 6a). In addition to this, overall "trend", there were statistically significant relationships in *Eriocephalus africanus* and *Osteospermum oppositifolium* (F. prob=0.017 and 0.046 respectively). In the case of *Osteospermum oppositifolium*, the biological significance of this relationship was dubious as the variance accounted for by the regression was very low (Figure 6c). In *Eriocephalus africanus* (Figure 6b) the relationship was more meaningful with nearly 11% of the variance accounted for by the regression. In addition, the biological significance of this relationship is supported by the fact that *E. africanus* is negatively associated with *Tetragonia fruticosa* (Table 3). Despite the general weakness of these relationships, there are additional lines of evidence that suggest that competition may play a larger role in this community than in the Short Strandveld. The most important of these is the fairly high frequency of positive associations between dead plants and selected species (60%, Table 3). One possible explanation for this difference between the two communities is that plants in this Medium Strandveld community may be generally longer lived. If this difference in longevity can be assumed, it seems reasonable to hypothesize that the Medium Strandveld community should be the more "structured" of the two communities. Because individuals are more persistent, it is likely that certain spatial associations (particularly competition) will have longer to develop and should therefore be more apparent.

Discussion

The general patterns that emerge from this study are very provocative. This is not because they are necessarily unusual, but rather because they are probably fairly common (e.g. Couteron & Kokou 1997, Prentice & Werger 1985), and I feel that they have been frequently misinterpreted. I argue that the most parsimonious interpretation of the multi-species clumping that characterizes both communities, is that a dominant form of interaction between individuals is direct facultative mutualism (Boucher *et al.* 1982). Clearly, this is not the only possible explanation. For one, clumping in communities could result from a patchy physical environment (Couteron & Kokou 1997, Ludwig & Reynolds 1988). In the case of this system, however, this does not seem to be the most likely possibility. There is no obvious macroscopic heterogeneity that corresponds with the vegetation clumps: there are no rocks which force pattern; no dramatic soil differences that correspond with the vegetation clumps; and very little topographic variation.

Since it seems unlikely that the observed patterns can be attributed to abiotic heterogeneity, it is necessary to consider potential biotic causes. One possibility is that the patterns are a result of contagious biotic process such as vegetative reproduction or limited seed dispersal (Ludwig & Reynolds 1988). In this system where wind plays a key role in seed dispersal of many species (Milton *et al.* 1997), there can be no doubt that the seed trapping effect of existing vegetation does play a role in the maintenance of the clumped structure. In other species, seed dispersal is very limited and seeds simply fall below the parent plant where they germinate and grow. Both of these common seed dispersal patterns would promote clumps. However, are they enough to explain the clumping observed and what are the implications of these clumps in terms of plant interactions?

When considering plant interactions, it is useful to distinguish between immediate and net interactions (Callaway & Walker 1997, Holmgren *et al.* 1997). Three net behavioral models have been invoked in the literature on desert vegetation to explain clumped patterns. The first is the process of maturation thinning (Phillips & MacMahon 1981, Prentice & Werger 1985). According to this model, seedlings and small individuals tend to be highly clumped as a result of dispersal characteristics. However, as the individuals mature, competition occurs, and with it thinning occurs. There is, therefore, a trend in patterns of dispersion from clumped through random and finally, if the system is left for long enough, to regularity (Phillips & MacMahon 1981). Here the clumping structure apparent in spatial analyses is largely an artifact of contagious dispersal phenomena already described, along with the demographic patterns in populations. In short, if large numbers of seedlings and juveniles occur in clumps, these will create a statistical critical mass that will confer an overall clumped pattern to the population. Such sequences have commonly been used as a *post hoc* explanation for why static patterns of individual dispersion do not unequivocally suggest competition i.e. for why plants are not regularly dispersed (e.g. Phillips & MacMahon 1981, Prentice & Werger 1985). They have also been used as a basis for a critique of classical nearest neighbor analyses (Wright & Howe 1986). However, in terms of the analysis presented here, the important feature of such behavior is that there should be evidence of competition within-clumps. The lack of any statistically significant relationships between the volumes of individuals and their within-clump angular competition indices in the Short Strandveld plot, and the general lack of any biologically interpretable relationships (with one exception) in the Medium Strandveld plot, make this possibility an unlikely general model.

The second behavioral category commonly described in desert systems and which could in theory produce clumped patterns is cyclical succession (Valiente-Banuet & Ezcurra 1991, Yeaton & Esler 1990, Yeaton & Manzanares 1986). As already mentioned above, cyclical succession is a net +/- interaction that is analogous to a host-parasitoid type relationship. Once again, this proposed behavioral model poses a serious challenge to pattern analysis, in this case because it is very difficult to resolve asymmetric spatial associations, let alone spatial associations which are

completely opposite. However, we can break down the cyclical succession model into immediate interactions and by doing this it is clear that competition is again a very important sub-model (as found by Yeaton & Esler 1990 and Esler & Cowling 1993). There should, once again, be evidence for competition within-clumps and as I have already discussed this does not appear to be the case. In addition, the asymmetry indices that I calculated do not suggest any extreme asymmetries in the spatial associations tested. However, the high frequency of positive associations between dead plants and various species in the Medium Strandveld could well indicate that cyclical succession is occurring.

The third common behavioral category reported in desert systems is the nurse-plant effect (Silvertown & Wilson 1994). This behavioral pattern is often used synonymously with the cyclical succession (e.g. Valiente-Banuet & Ezcurra 1991). However, I prefer to treat the two as separate models. Accordingly, the nurse-plant effect relies on the structural differentiation of the members of the association into different niches throughout their lives. The relationship is therefore not a +/- pseudo host-parasitoid relationship but rather a +/- commensal relationship. Species that become nurse plants are usually structurally large and long-lived. I feel that this behavior is unlikely to play a dominant role in these Strandveld communities since it relies on structural diversity that does not exist. In addition, it is difficult to identify consistent clump dominants (although I present no data or rigorous analysis to demonstrate this observation). Such systems should also be characterized by a great deal of asymmetry in terms of the positive spatial associations. As mentioned, this is not apparent from the asymmetry indices. Finally, there should also be traces of competition at spatial scales greater than the primary clumping as a result of competition between-clump dominants (Silvertown & Wilson 1994). However, the low frequency of negative interactions within species (univariate patterns) and the lack of evidence for negative spatial associations at between-clump spatial scales suggests that this is not the case.

Having identified possible inconsistencies between the patterns that I observed and the three most commonly invoked models of desert community behavior, I return now to my initial speculation that interactions between plants in these communities are dominated by direct facultative mutualisms. This has important implications. Clearly, the first implication is that this hypothesis must be tested. Also, the nature of the mutualisms, if they in fact exist, should be characterized. There are several possible mechanisms that could lead to positive interactions (Callaway 1995). Occurrence in clumps may favorably modify the water relations of members of the clump through mutual shading or through boundary layer changes (Monteith & Unsworth 1990). Clumping may also afford protection against grazing or trampling. Finally, there may be a certain amount of soil enrichment with organic carbon and nutrients immediately under plant canopies (but see Stock *et al.* 1999). These mechanisms all fall within the "ecosystem engineer" concept coined by Jones *et al.* (1997). An "ecosystem engineer" is defined as an organism that physically modifies, maintains and creates habitats.

In terms of community processes, it is important to establish that these interactions can in fact be stable. Early theoretical models suggested that mutualisms should be inherently unstable (May 1982). However, more recent work has suggested that the juxtaposition of positive and negative interactions is important in constraining these mutualisms, and in this way stabilizing them. Once again, the concept of “net” interaction is relevant and the balance between positive and negative interactions will dictate the stability of interactions (Callaway & Walker 1997, Holmgren *et al.* 1997). It will also play a central role in determining the spatial patterns that emerge in communities. Dominance of positive interactions would result in clumping structure being favored even though this would, in theory, increase the potential for competition. Positive and negative interactions may be separated spatially (e.g. above and below ground – Bertness & Leonard 1997) or they may be separated temporally. The latter case can be viewed as an extension of the thesis proposed by Goldberg and Novoplansky (1997) for competitive interactions.

Finally, I return to the second question that I set out to address: how the proposed interactions could contribute to the maintenance of the species diversity in these systems. Until recently, the conclusion that any community was dominated by mutualisms would necessarily have been interpreted as suggesting that the system should be unstable (May 1982). However, it has recently been suggested that mutualisms may in fact stabilize diversity, not only between different trophic levels (as suggested by Levine 1980), but also within a trophic level. Hacker & Gaines (1997) proposed a graphical extension of the “intermediate disturbance” hypothesis to demonstrate how positive interactions could significantly contribute to maintenance of diversity in physically harsh environments. Wilson & Nisbet (1997) used a spatially explicit cellular automata model to investigate the effect of “cooperation” (positive interactions) between species in defining boundaries between these species distributions. Their simulations showed that increased cooperation resulted in more gradual boundaries (i.e. coexistence) between species. Thus by allowing a combination of more gradual boundaries between species, and reduced the exposure to disturbance and stress, positive interactions in the Strandveld communities may contribute significantly to the maintenance of species diversity.

In conclusion, the two Strandveld communities represent assemblages of vegetation clumps or micro-communities. I speculate that this clumping is the result of a positive feedback between physical benefits associated with microhabitat modification (“ecosystem engineering”) and mutual protection and the dominant seed dispersal strategies.

References

- Arnold, T.H. & DeWet, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* 62:1-825.
- Bertness, M.D. & Leonard, G.H. 1997. The role of positive interactions in communities: lessons

- from intertidal habitats. *Ecology* 78(7):1976-1989.
- Bitterich, V. & Hartmann, H. 1988. The Aizoaceae – a new approach. *Botanical Journal of the Linnean Society* 97:239-254.
- Boucher, D.H., James, S. & Keeler, K.H. 1982. The ecology of mutualisms. *Annual Review of Ecology and Systematics* 13: 315-347.
- Callaway, R.M. 1995. Positive interactions among plants. *The Botanical Review* 61(4):306-348
- Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78(7):1958-1965.
- Couteron, P. & Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology* 132:211-227.
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments* 27:141-158.
- Cowling, R.M., Esler, K.J. & Rundel, P.W. 1999c. Namaqualand, South Africa- an overview of a unique winter rainfall desert ecosystem. *Plant Ecology* 142(1-2):3-21.
- Diggle, P.J. 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London.
- Esler, K.J. & Cowling, R.M. 1993. Edaphic factors and competition as determinants of pattern in South African karoo vegetation. *South African Journal of Botany* 58:461-468.
- Goldberg, D. & Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409-418.
- Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction. *Journal of Vegetation Science* 6:575-582.
- Hacker, S.D. & Gaines, S.D. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78(7):1990-2003.
- Hassell, M.P., May, R.M., Pacala, S.W. & Chesson, P.L. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. *The American Naturalist* 138(3):568-583.
- Hilton-Taylor, C. 1996. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In: van der Maesen, L.J.E., van der Burgt, X.M. & van Medenbach de Rooy, J.M. *The Biodiversity of African Plants*. Pp 58-72. Kluwer, Dordrecht.
- Holmgren, M., Scheffer, M. & Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78(7):1966-1975.
- Hubbell, S.P. & Foster, R.B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. In: Bawa, K.S. & Hadley, M. *Reproductive Ecology of Tropical Forest Plants*. Pp 325-349. UNESCO/International Union of Biological Sciences, Paris.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1997. Positive and negative effects of organisms as

- physical ecosystem engineers. *Ecology* 78(7):1946-1957.
- Jürgens, N. 1991. A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegatatio* 97:21-38.
- Levine, S. 1980. Indirect mutualism: Variations on a theme. *The American Naturalist* 116:441-448.
- Ludwig, J.A. & Reynolds, J.F. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley & Sons, New York.
- May, R.M. 1982. Mutualistic interactions among species. *Nature* 296:803-804.
- Milton, S.J., Yeaton, R.I., Dean, W.R.J. & Vlok, J.H.J. 1997. Succulent Karoo. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Monteith, J.L. & Unsworth, M.H. 1990. *Principles of Environmental Physics*. 2nd Ed. Edward Arnold, London.
- Prentice, I.C. & Werger, M.J.A. 1985. Clump spacing in a dwarf desert shrub community. *Vegetatio* 63:133-139.
- Phillips, D.L. & MacMahon, J.A. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69:97-115.
- Randall, J.M. & Rejmánek, M. 1993. Interference of bull thistle (*Cirsium vulgare*) with growth of ponderosa pine (*Pinus ponderosa*) seedlings in a forest plantation. *Canadian Journal of Forest Research* 23:1507-1513.
- Rebertus, A.J., Williamson, G.B. & Moser, E.B. 1989. Fire-induces changes in *Quercus laevis* spatial pattern in Florida sandhills. *Journal of Ecology* 77:638-650.
- Ripley, B.D. 1987. Spatial point pattern analysis in ecology. In: Legendre, P. & Legendre, L. (eds), *Developments in Numerical Ecology* pp. 407-431. Springer Verlag, Berlin.
- Silvertown, J. & Wilson, J.B. 1994. Community structure in a desert perennial community. *Ecology* 75(2):409-417.
- Stock, W.D., Dlamini, T. & Cowling, R.M. 1999. Plant-induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecology*
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán valley, Mexico. *Journal of Ecology* 79:961-971.
- Wiegand, T., Milton, S.J. & Wissel, C. 1995. A simulation model for a shrub ecosystem in the semiarid karoo, South Africa. *Ecology* 76(7):2205-2221.
- Wilson, W.G. & Nisbet, R.M. 1997. Cooperation and competition along smooth environmental gradients. *Ecology* 78(7):2004-2017.
- Wright, S.J. & Howe, H.F. 1987. Pattern and mortality in Colorado Desert plants. *Oecologia*

73:543-552.

- Yeaton, R.I. & Esler, K.J. 1990. The dynamics of a succulent karoo vegetation. A study of species association and recruitment. *Vegetatio* 88:103-113.
- Yeaton, R.I. & Manzanares, A.R. 1986. Organization of vegetation mosaics in the *Acacia schaffneri* – *Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology* 74:211-217.

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Chapter 3:

WITHIN-CLUMP SPECIES ASSOCIATIONS AS A QUALITATIVE GUIDE TO THE RELATIVE IMPORTANCE OF DETERMINISTIC INTERACTIONS VS. CHANCE IN STRANDVELD COMMUNITIES.

Abstract

In this chapter I set out to investigate the relative importance of deterministic species interactions vs. chance in structuring vegetation clumps in the Short and Medium Strandveld. My basic assumption was that deterministic patterns of species association into vegetation clumps must reflect underlying deterministic dynamics and vice versa. In each community I considered the statistical significance (using a supercritical chi-squared test) and the strength (using Jaccard Indices) of the associations between 16 species (120 species pairs) in 400 vegetation clumps. At the 5% level, only seven out of 120 associations in the Medium Strandveld and 13 out of 120 in the Short Strandveld were statistically significant. All of these associations were positive. Of the 16 species considered in the Medium Strandveld, nine were involved with at least one significant association while in the Short Strandveld, 12 were involved with at least one. The strength of these associations was generally stronger in the Medium Strandveld than in the Short Strandveld although in both communities they were generally weak (Jaccard Indices < 0.5). These results indicate that, while a certain degree of determinism is evident in the species associations in these two communities, the role of chance cannot be ignored when interpreting vegetation patterns or when proposing models describing within-patch dynamics.

Key words

Desert plant communities, Jaccard Index, supercritical chi-squared test, vegetation patches.

Introduction

Arid ecosystems are commonly characterised by a two-phase mosaic structure with vegetation clumps interspersed in a low cover matrix (Aguiar & Sala 1999). The Short and Medium Strandveld communities are no exception to this with both exhibiting irregularly shaped patches ('leopard' vegetation) characteristic of wind driven systems (Chapter 1). The recognition that such patterns prevail in arid systems has had a profound influence on our interpretation of these systems. While

many early theoretical works focused on the role of competition in arid systems (e.g. Beals 1968, Moore & Bhadresa 1978, Fonteyn & Mahall 1981, Fowler 1986), it is now necessary to embrace a far broader range of driving forces because competition on its own cannot explain clumped patterns (Chapter 1). At the very least, positive plant interaction must be considered. In their review on the subject, Aguiar & Sala (1999) lend weight to the potential importance of facilitation by presenting several possible examples of "ecosystem engineering" (Jones *et al.* 1997) activities that might lead to facilitation in vegetation patches.

Aguiar & Sala (1999) also present a deterministic patch dynamic model with particular functional types (shrubs vs tussock grasses) playing specific roles in the building and degradation of patches. Similar deterministic models are described in a number of earlier works (Yeaton & Manzanares 1986, Yeaton & Esler 1990, Valiente-Banuet & Ezcurra 1991). The Namaqualand Strandveld communities however, pose a challenge to this deterministic genre of model in that growth form diversity seems to be very low relative to species diversity (Cowling *et al.* 1994). One possible theoretical answer to this challenge is found in Cody (1986). He argues that in arid systems harsh above-ground abiotic conditions should drive species towards convergence while severe competition between species for below-ground resources should drive evolution towards differentiation of root growth forms. The implication is that functional differentiation need not be manifest in above-ground structural differences between species. It is, on the other hand, also possible that the Strandveld communities may be more compatible with stochastic community interpretations such as that of Hubbell & Foster (1986). While these authors do not entirely exclude the role of deterministic interactions in community processes, they argue that chance and history may play a substantial and often ignored role.

Unraveling the relative importance of these two community-structuring forces (deterministic interactions vs. chance) represents a major challenge. In theory, one way to resolve this would be to explore in detail the specific resource use of species in these communities - the "quantify everything" approach. Unfortunately, disputes over our ability to identify important resources; over the ability of our analytical methods to resolve resource levels as perceived by plants; and differences in opinion as to what constitutes a large enough structural difference, all contribute to the ultimate downfall of this approach (Shmida & Ellner 1984; Cody 1986; Hubbell & Foster 1986).

In this chapter I explore the relative importance of deterministic interactions and chance from a less conventional (although by no means new) angle using a description of patch membership patterns. This is based on the assumption that functional differentiation necessary for deterministic models should manifest itself in the form of within-patch structure and particularly in clump membership (as argued by Cody 1986). For example, if a pair of species have evolved in such a way

that they partition resources particularly well, then they should be predisposed to co-occur and this should be reflected in positive associations. Conversely, if they do not partition resources well (i.e. they fall within the same functional guild) they should be negatively associated. In short I assume that the more intricate the web of significant associations (positive and negative), and the stronger these associations are, the more important deterministic interactions must be and vice versa.

Methods

In representative areas of both Short and Medium Strandveld communities I surveyed the species composition of 400 vegetation clumps (50 clumps along each of eight transects). For the analysis of the patterns of association, I restricted my attention to species that were recorded more than 20 times in the 400 clumps. Thus 16 species in each of the two communities were considered. The analysis comprised two steps. I first assessed the significance of associations, and I then gauged the strength of these. I used the Bonferroni supercritical chi-square approach (Ludwig & Reynolds 1988, Silvertown & Wilson 1994) to assess the significance of associations between individual species pairs rather than a more powerful "overall" test such as that described by Schluter (1984). There were two reasons for this decision. Firstly, this supercritical approach focused attention on the significance of individual species associations. Secondly, the level of conservatism (lack of power) associated with the approach is appropriate given the obvious lack of complete independence of the samples, and the less obvious possibility that spatial autocorrelation may inflate the Type I error rate (Roxburgh & Chesson 1998). Having established the significance of associations (and whether the associations were positive or negative) I then calculated the Jaccard Index (JI) as an indication of interaction strength (Ludwig & Reynolds 1988, Genstat Committee 1993). Values of this index range from 0 (species never found together) to 1 (species always occur together). In order to better visualize the multitude of associations, I used principal coordinates analysis (Genstat Committee 1993) to produce biplots of relative species positions based on the symmetric matrix of Jaccard Indices.

Results

In the Medium Strandveld only seven out of 120 species pairs were significantly associated with each other at the 5% level (Table 1). In all seven the associations were positive. The strength of these associations, as indicated by their Jaccard Indices (JI's), ranged from 0.456 to 0.159 on a scale from 0 to 1 (Table 2). Of the sixteen species considered, nine were involved with these significant combinations. Five of these were involved in only one significant association, three were involved in

Table 1. Chi-squared values for the 120 associations between species in the medium strandveld. Values in bold indicate statistical significance at the 5% level when compared to the supercritical chi-squared criterion of 12.46. The sign indicates whether the association is positive or negative (only of interest where the association is significant). The species codes used are: Po - Pteronia onobromoides; Zm - Zygophyllum morgsana; Tf - Tetragonia fruticosa; Oo - Osteospermum oppositifolium; Su - Stoeberia utilis; Al - Asparagus lignosis; Oc - Othonna cylindrica; Ea - Erioccephalus africanus; Em - Euphorbia mauritanica; Pd - Pteronia divaricata; Lf - Lycium ferocissimum; Ht - Helichrysum trichostatum; Ac - Asparagus capensis; Se - Senecio sarcoides; Sl - Salvia lanceolata; Ma - Manochlamys albicans.

	Po	Zm	Tf	Oo	Su	Al	Oc	Ea	Em	Pd	Lf	Ht	Ac	Se	Sl
Zm	+ 4.73														
Tf	- 0	+ 4.041													
Oo	+ 7.017	+ 0.07	+ 14.315												
Su	+ 4.739	- 0.033	+ 17.129	+ 10.33											
Al	+ 11.327	+ 3.529	+ 0.613	+ 8.993	+ 0										
Oc	+ 13.442	+ 0.445	+ 1.374	+ 1.673	+ 20.873	+ 2.518									
Ea	+ 8.493	+ 0.602	+ 16.368	+ 10.574	+ 9.26	- 0.059	+ 2.632								
Em	+ 4.466	- 0.002	+ 0.869	+ 4.949	+ 0.28	+ 0.096	+ 2.001	+ 3.698							
Pd	- 9.501	+ 0.546	- 0.707	- 0.572	+ 0.28	- 0.915	+ 6.827	- 3.294	+ 0.051						
Lf	- 0.06	+ 4.214	+ 1.267	+ 2.026	- 3.916	+ 13.465	- 0.075	- 7.04	+ 0	+ 0.351					
Ht	- 1.683	+ 6.153	+ 1.566	+ 0.91	+ 0.033	+ 4.183	- 0.117	- 2.736	+ 0.709	+ 2.223	+ 15.876				
Ac	+ 0.229	+ 0.286	+ 0.037	+ 2.844	- 0.191	- 0.943	- 0.001	+ 0.853	+ 0.78	- 0.051	- 0.477	+ 0.254			
Se	+ 1.309	- 1.19	+ 0.024	+ 0.61	- 0.086	+ 1.442	- 5.011	- 0.111	- 0.315	- 0.247	- 1.106	- 2.163	+ 4.834		
Sl	+ 0	+ 1.666	- 0.083	+ 4.398	+ 1.045	+ 4.364	+ 3.15	- 0.612	+ 7.289	+ 2.226	+ 1.021	+ 2.806	- 0.18	- 0.041	
Ma	+ 0.149	- 0.896	+ 0.054	- 2.157	- 0.609	+ 0.518	- 0.313	- 0.836	+ 0.912	+ 0.12	+ 1.495	+ 3.58	- 0.102	+ 0.82	+ 0.82

Table 2. Jaccard Indices for the 120 species associations in the medium strandveld. Once again associations that are significant are indicated in boldface. The species codes are as for Table 1.

	Po	Zm	Tf	Oo	Su	Al	Oc	Ea	Em	Pd	Lf	Ht	Ac	Se	Sl	Ma
Po	1															
Zm	0.635	1														
Tf	0.509	0.499	1													
Oo	0.5	0.422	0.456	1												
Su	0.472	0.396	0.452	0.406	1											
Al	0.438	0.393	0.339	0.371	0.292	1										
Oc	0.431	0.36	0.34	0.324	0.398	0.301	1									
Ea	0.409	0.353	0.399	0.365	0.352	0.252	0.292	1								
Em	0.145	0.122	0.133	0.153	0.123	0.116	0.137	0.147	1							
Pd	0.096	0.127	0.102	0.1	0.119	0.09	0.157	0.072	0.074	1						
Lf	0.11	0.133	0.122	0.126	0.071	0.168	0.094	0.051	0.065	0.079	1					
Ht	0.074	0.106	0.095	0.092	0.081	0.109	0.07	0.049	0.075	0.091	0.159	1				
Ac	0.069	0.07	0.066	0.085	0.057	0.048	0.061	0.075	0.068	0.041	0.028	0.052	1			
Se	0.061	0.045	0.054	0.061	0.049	0.067	0.022	0.046	0.028	0.029	0.015	0	0.089	1		
Sl	0.054	0.064	0.05	0.076	0.064	0.079	0.075	0.04	0.104	0.075	0.063	0.077	0.021	0.023	1	
Ma	0.052	0.042	0.05	0.032	0.039	0.056	0.04	0.035	0.059	0.045	0.065	0.08	0.022	0.05	0.05	1

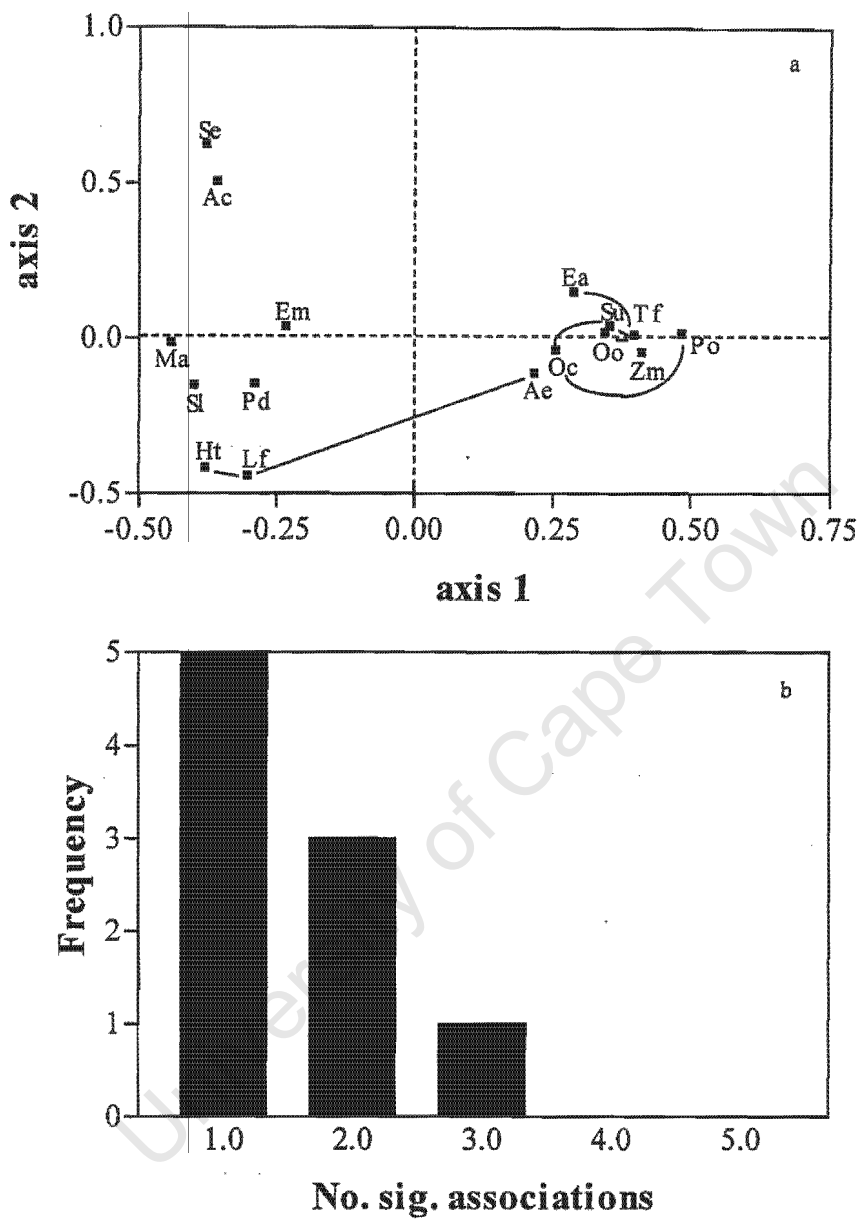


Figure 1. a) A biplot derived from the Jaccard Indices of association strength for species in the Medium Strandveld. Significant associations are indicated by lines joining the species. The species codes are as defined in Table 1. b) The frequency distribution of the number of significant associations that species in the Medium Strandveld participate in.

Table 3. Chi-squared values for the 120 associations between species in the short strandveld. Statistical significance at the 5% level is indicated by boldface. The supercritical chi-squared criterion is again 12.46. The sign indicates whether the association is positive or negative (only of interest where the association is significant). The species codes not already defined in Table 1 are: *Cs* - *Cephalophyllum spongiosum*; *Rf* - *Ruschia fugitans*; *Lp* - *Limonium perigrinum*; *Zs* - *Zygophyllum spinosum*; *Va* - *Vanzijlia annulata*; *Lm* - *Lampranthus multiseriatus*; *Eb* - *Euphorbia burmannii*; *Ha* - *Hermannia amoena*; *Gc* - *Galenia crystallina*.

	Po	Cs	Rf	Lp	Ht	Oo	Oc	Zm	Zs	Va	Tf	Lm	Eb	Ha	Ac
Cs	+ 10.3374														
Rf	+ 8.8679	- 0.203													
Lp	+ 29.391	+ 16.173	+ 15.963												
Ht	+ 1.136	+ 27.438	+ 8.347	+ 10.324											
Oo	+ 2.389	+ 7.21	+ 1.874	+ 4.022	+ 0										
Oc	+ 4.608	+ 15.917	+ 0.709	+ 11.436	+ 8.859	+ 0.213									
Zm	+ 5.2	+ 8.241	- 0.209	+ 10.003	+ 10.877	+ 5.822	+ 12.253								
Zs	+ 3.28	+ 6.916	+ 3.576	+ 17.628	+ 21.405	+ 4.765	+ 5.442	+ 1.492							
Va	+ 0.342	+ 4.877	- 0.29	+ 0.464	+ 1.194	+ 2.379	+ 6.787	+ 1.173	- 0.231						
Tf	+ 5.378	+ 7.656	- 2.825	+ 0.427	+ 4.374	+ 0.009	+ 3.409	+ 6.794	+ 0.005	+ 2.651					
Lm	+ 4.059	+ 1.501	+ 2.177	+ 13.561	+ 2.97	+ 3.133	+ 3.14	+ 0.43	+ 1.146	- 0.023	- 2.613				
Eb	+ 8.671	+ 9.383	+ 0.322	+ 1.65	+ 1.069	+ 1.128	+ 0.465	+ 1.972	+ 5.012	- 0.023	+ 17.478	- 0.013			
Ha	- 0.019	+ 2.627	+ 0.491	+ 5.842	+ 0.976	+ 0.877	+ 0.194	- 0.825	+ 1.245	- 0.098	+ 0.118	+ 0.254	+ 0		
Ac	+ 0.924	+ 12.094	+ 1.73	+ 2.231	+ 12.891	+ 5.383	+ 3.212	+ 4.473	- 0.452	- 0.167	+ 19.05	+ 0.112	+ 16.644	+ 0.087	
Gc	- 6.994	+ 0.725	- 0.69	+ 0.019	+ 0.412	- 0.783	+ 0.515	+ 8.364	+ 0.659	+ 2.633	- 0.23	- 0.133	+ 1.917	+ 0.004	+ 13.894

Table 4. Jaccard Indices for the 120 species associations in the short strandveld. Significant associations are again indicated in boldface. The species codes are as for Table 3.

	Po	Cs	Rf	Lp	Ht	Oo	Oc	Zm	Zs	Va	Tf	Lm	Eb	Ha	Ac	Gc
Po	1															
Cs	0.492	1														
Rf	0.457	0.37	1													
Lp	0.336	0.305	0.302	1												
Ht	0.243	0.328	0.272	0.235	1											
Oo	0.236	0.257	0.225	0.195	0.143	1										
Oc	0.233	0.269	0.202	0.226	0.214	0.142	1									
Zm	0.221	0.231	0.164	0.213	0.216	0.187	0.213	1								
Zs	0.195	0.209	0.194	0.233	0.245	0.172	0.173	0.139	1							
Va	0.16	0.187	0.136	0.131	0.14	0.148	0.173	0.129	0.085	1						
Tf	0.156	0.163	0.092	0.112	0.146	0.096	0.136	0.154	0.085	0.121	1					
Lm	0.144	0.133	0.136	0.182	0.132	0.132	0.13	0.1	0.107	0.073	0.03	1				
Eb	0.157	0.16	0.121	0.122	0.116	0.115	0.103	0.119	0.138	0.073	0.184	0.064	1			
Ha	0.092	0.115	0.102	0.132	0.099	0.097	0.084	0.052	0.096	0.059	0.069	0.071	0.059	1		
Ac	0.094	0.127	0.099	0.102	0.149	0.12	0.107	0.114	0.048	0.052	0.173	0.063	0.164	0.056	1	
Gc	0.042	0.079	0.058	0.063	0.073	0.042	0.073	0.121	0.073	0.091	0.038	0.039	0.082	0.045	0.143	1

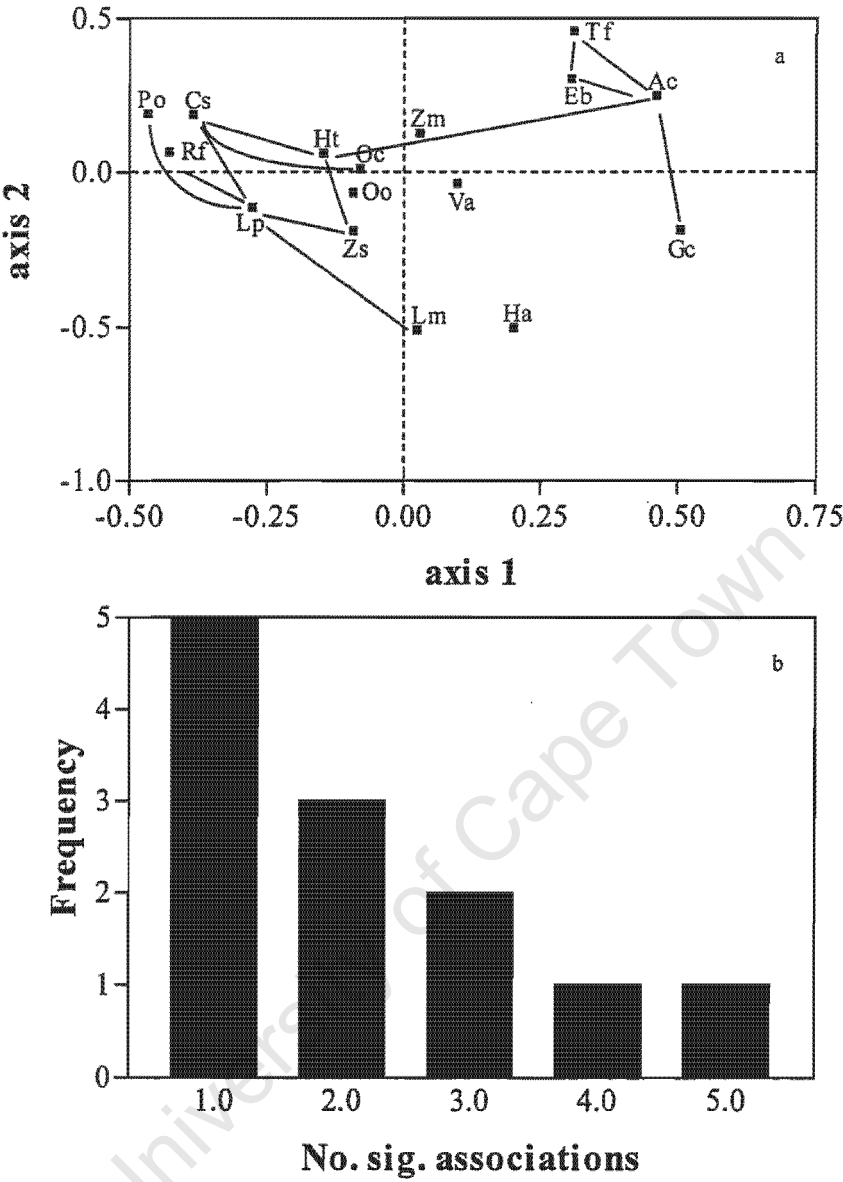


Figure 2. a) A biplot derived from the Jaccard Indices of association strength for species in the Short Strandveld. Significant associations are again indicated by lines joining the species. The species codes are as defined in Tables 1 and 3. b) The frequency distribution of the number of significant associations that species in the Short Strandveld participate in.

two and one (*Tetragonia fruticosa*) was involved in three significant associations (Figure 1). Associations involving this last mentioned species also appeared to be the strongest (JI's of 0.456, 0.452 and 0.399).

In the Short Strandveld 13 out of the 120 pairs of species were significantly associated at the 5% level (Table 3) and once again all of these associations were positive. Association strengths were generally lower than in the Medium Strandveld ranging from 0.336 in the case of *Pternoia onobromoides* and *Limonium perigrinum* to 0.143 in the case of *Asparagus capensis* and *Galenia crystallina* (Table 4). Twelve out of the sixteen species considered were involved in significant associations. Of these, five were involved in only a single significant association; three were involved with two significant associations; two were involved with three associations; one was involved with four significant associations; and finally one (*Limonium perigrinum*) was involved with five associations (Figure 2). Once again associations involving this last species were among the strongest (Table 4).

Discussion

In a similar study to this one, Silvertown & Wilson (1994) reported only a slightly higher proportion of significant associations (14 %) in a Chihuahuan desert system. Their overall conclusion was that "considerable structure" was evident. However, using this as a precedent for concluding that there is considerable structure in the Strandveld is not entirely appropriate. Their conclusion was based on a battery of tests mostly at the overall community level, and because of this, it applies most specifically to the overall community-wide level. The focus of my analysis was however, on species-specific associations within clumps only. And given the low number of significant associations (about 6% in the Medium Strandveld and 11% in the Short Strandveld), the results suggest that the Strandveld vegetation clumps show little structure compositionally.

A far more convincing argument in favor of structure (and thus of determinism) at this level is the fact that in both Strandveld communities, a large proportion of species were involved with at least one significant association. This is particularly clear in the biplots in Figures 1 and 2. In the Medium Strandveld, around 56% of species were involved with one or a few positive association while in the Short Strandveld this figure is around 75%. These positive associations might arise because one or both of the species exhibit some special synergy with the other, over and above the simple background positive interaction indicated by the presence of clumps (i.e. species-specific positive interactions [Callaway 1998]). Alternatively it may be that the species involved compete less (due, for example, to efficient resource partitioning) and therefore experience a greater net positive effect than the

background positive effect. Either way, these positive associations clearly represent structure and indicate an element of determinism in terms of patch dynamics.

Once again though, concluding that this deterministic element is the prevalent factor structuring these communities is premature. While most of the species are involved with at least one significant association, they are usually only involved with one or two (Figures 1 and 2). Exceptions to this include *Limonium perigrinum* and *Asparagus capensis* in the Short Strandveld and *Tetragonia fruticosa* in the Medium Strandveld which are involved with between three and five associations. Both *L.perigrenum* and *T.fruticosa* produce large winged seeds, which might explain this strong positive association with other species. These exceptions aside, when one considers that the average clump contains around five species (Figure 3) which translates into ten different species associations it stands to reason that many of these associations could arise purely by chance. In addition to this, most of the significant associations are in fact fairly weak (Jaccard Indices < 0.5). The implication is that even where determinism is apparent, this determinism is far from absolute. An element of chance is still present.

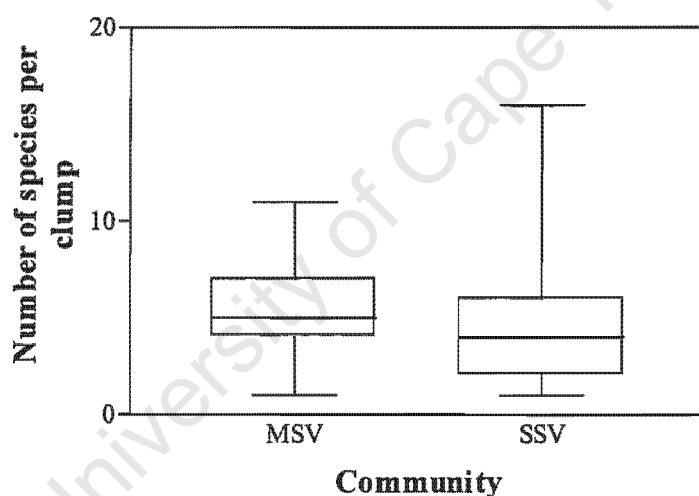


Figure 3. Box and whisker representation of the number of species that occur in vegetation clumps in the Short (ssv) and Medium Strandveld (msv) communities.

The picture that emerges from this study, therefore, is in stark contrast with the highly structured and deterministic interpretations of patch processes that have been advanced to date in other arid systems (Yeaton & Manzanares 1986, Yeaton & Esler 1990, Valiente-Banuet & Ezcurra 1991, Aguiar & Sala 1999). This may either be the result of genuinely unusual system characteristics in the Strandveld or alternatively may simply reflect a desire on the part of previous workers to emphasize

determinism rather than chance. Hubbell & Foster (1986) make the point that "theoreticians abhor unique events". The complete absence of significant negative associations however, which is one of the most astounding differences between these results and those described by Silvertown & Wilson (1994), could perhaps be taken as evidence for the former. In a circular fashion, it may also hold the key to why this system is unique. Directional competition between species (i.e. competition that leads to a deterministic outcome) is a fundamental precursor to the evolution of functional differentiation (Cody 1986). While the lack of evidence for such competition in communities today need not necessarily indicate that it was absent in the past, this may well have been the case. If so, this points to the dominance of abiotic evolutionary forces which should in turn lead to convergence and (as has been reported in the Namaqualand Strandveld) the low ratio of functional to species diversity (Cowling *et al.* 1994). This argument is however highly speculative and fraught with all the methodological difficulties associated with using descriptions of patterns as an explanation of these patterns (Cale *et al.* 1989).

Finally, a paradoxical result emerging from this analysis is that in terms of the number of significant associations; the proportion of species involved in these; and the number of interactions these species are involved in, it would appear that the Short Strandveld is the more structured of the two communities. However, it is also clear that the relative strength of the significant associations that were detected in the Short Strandveld were generally weaker than in the Medium Strandveld. Thus, what at first appears to be strongly contrary to the findings in Chapter 2 may in fact not be that contrary at all.

To conclude, while this analysis indicates that there is a certain element of determinism in the association of species into vegetation patches in the Short and Medium Strandveld communities, it also highlights the importance of pure chance. Whether this element of chance is unique to this system or whether it is a feature of many other arid systems that has been glossed over is a question that remains unanswered. Either way, this evidence that chance plays an important role in the Strandveld has profound implications in terms of understanding species diversity and the forces maintaining this diversity in this system.

References

- Aguiar, M.R. & Sala, O.E. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14(7):273-277.
- Beals, E.W. 1968. Spatial patterns of shrubs in a desert plain in Ethiopia. *Ecology*. 49:744-746.

- Cale, W.G., Henebry, G.M. & Yeakley, J.A. 1989. Inferring process from pattern in natural communities. Can we understand what we see? *Bioscience*. 39(9):600-605.
- Callaway, R.M. 1998. Are positive interactions species-specific? *Oikos*. 82(1):202-207.
- Cody, M.L. 1986. Structural niches in plant communities. In: Diamond, J. & Case, T.J. (eds), *Community Ecology*. Harper & Row Publications, New York. pp. 381-405
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments*. 27:141-158.
- Fonteyn, P.J. & Mahall, B.E. 1981. An experimental analysis of structure in a desert plant community. *Journal of Ecology*. 69: 883-896.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid systems. *Annual Review of Ecology and Systematics*. 17:89-110.
- Genstat 5 Committee 1993. *Genstat 5 Release 3 Reference Manual*. Oxford Science Publications, Oxford.
- Hubbell, S.P. & Foster R.B. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond, J. & Case, T.J. (eds), *Community Ecology*. Harper & Row Publications, New York. pp. 381-405.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*. 78(7):1946-1957.
- Ludwig, J.A. & Reynolds, J.F. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley and Sons, New York.
- Moore, P.D. & Bhadresa, R. 1978. Population structure, biomass and pattern in a semi-desert shrub, *Zygophyllum eurypterum*, in the Turan biosphere reserve of northeastern Iran. *Journal of Applied Ecology*. 15:837-846.
- Roxburgh, S.H. & Chesson, P. 1998. A new method for detecting species associations with spatially autocorrelated data. *Ecology*. 79(6):2180-2192.
- Schluter, D. 1984. A variance test for detecting species associations, with some example applications. *Ecology*. 65(3):998-1005.
- Shmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio*. 58:29-55.
- Silvertown, J. & Wilson, J.B. 1994. Community structure in a desert perennial community. *Ecology*. 75(2):409-417.
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán valley, Mexico. *Journal of Ecology*. 79:961-971.

- Yeaton, R.I. & Esler, K.J. 1990. The dynamics of a succulent karoo vegetation. A study of species association and recruitment. *Vegetatio*. 88:103-113.
- Yeaton, R.I. & Manzanares, A.R. 1986. Organization of vegetation mosaics in the *Acacia schaffneri* – *Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology*. 74:211-217.

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Chapter 4:

HIGH TURNOVER RATES AND WEAK APPARENT INTERSPECIFIC INTERACTIONS: FURTHER EVIDENCE FOR NON-EQUILIBRIUM DYNAMICS IN STRANDVELD COMMUNITIES.

Abstract

In this chapter I discuss a number of aspects of plant interactions and dynamics in the Short and Medium Strandveld. Firstly I explore in more depth the relationships between the sizes of individuals and an index of the collective size of the plants in their immediate surroundings (a neighborhood index). Secondly I present estimated rates of mortality and recruitment into the smallest observed size classes, and consider the possibility that mortality is related to the neighborhood indices that I calculated. In the Short Strandveld, four out of the twelve most abundant species showed statistically significant relationships between the size of individuals and their neighborhood indices. In the Medium Strandveld three out of the ten most abundant species showed statistically significant relationships between individual sizes and neighborhood indices. In all cases however, these relationships were relatively weak in terms of the variance accounted for by the regression models. In both communities, mortality and recruitment rates were surprisingly high for an arid system. The probability of dying was not related to neighborhood index in any of the species considered in either community. The lack of convincing evidence for strong interactions, together with observed levels of temporal and spatial heterogeneity lends additional support to the idea introduced in the previous chapter, that a relatively high degree of stochasticity may characterize the dynamics of these communities. In addition, I argue that intrinsic properties of the vegetation are central to the maintenance of the temporal and spatial heterogeneity necessary for such non-equilibrium dynamics to persist.

Key words

Neighborhood index, spatial heterogeneity, temporal heterogeneity

Introduction

Understanding the nature and strength of the demographic impacts of interactions between individuals and the communities within which they occur, is fundamental to understanding community processes. In Chapters 2 and 3 I reviewed the more common models that have been

used to explain patterns in desert communities. These ranged from the early works that focused on the role of competition in structuring populations and communities to the more recent models (including maturation thinning, nurse plant effects and cyclical succession) that were developed to account for aggregated patterns. The emphasis in most of these models has been on the deterministic aspects of species interactions. So for example, in the nurse plant model, certain species are consistently nurse plants, while others are consistently patient plants. In the cyclical succession model, certain species are consistently primary colonizers while others are consistently secondary colonizers.

The one exception to this is the maturation thinning model where density dependent competition (a deterministic process) is truncated by disturbance. The development of this model paralleled the development of one of the major avenues of debate in community ecology – the stress/disturbance vs. competition debate (Southwood 1988, Taylor *et al.* 1990, Reader *et al.* 1994), and to some extent brought desert plant community ecology into the arena of non-equilibrium theory. While there are some weaknesses with this maturation thinning model (see Chapter 5), the results that I presented in Chapter 3 certainly suggest that a strong element of chance is involved in the outcome of interactions between the individuals of different species in the Namaqualand Strandveld. In this chapter I consider two additional lines of data pertinent to this non-equilibrium hypothesis. I firstly examine evidence for relationships between the size of individuals and their plant “neighborhoods” based on static patterns. Strong evidence for interactions would suggest that these have played a major role in structuring populations despite stochastic events. Weak evidence on the other hand could suggest a dominant role of stochasticity. I then present evidence for high turnover rates within populations that I believe contribute a great deal to the uncertainty (stochasticity) associated with interactions.

Methods

The data used in this analysis combines the data that emerged from the first mapping of the two Strandveld plots described in Chapter 2, with the data from the second census of these same plots a year later in 1998. In 1998 fewer individuals were mapped in both of the two communities. This reflects that fact that although there were good early rains in the winter of 1997, the late season rains were lower than expected and 1998 was an unusually dry year (Chapter 1). As described in Chapter 2, I calculated a “neighborhood index” from the 1997 mapped plot data for each individual in the two communities using a modification of the “angular competition index” developed by Randall & Rejmánek (1993). In this chapter however, I extend this by calculating these neighborhood indices for a series of radii around each focal individual (see

Tables 1 and 3 for the range of distances considered in each plot) in order to consider the effect of spatial scale. I then explored the relationships between these neighborhood indices and the focal plant volumes for the most abundant species in each plot using simple linear regression.

From the recensus of the plots in 1998 I was able to estimate turnover (“recruitment” and mortality) rates for the most abundant species in the two communities. It is important to note that what I refer to as recruitment is in fact recruitment into the smallest measured size class rather than true recruitment from seed during the 1997 to 1998 period. It therefore represents true recruitment over the past two to three years. For species where there were adequate numbers of recruits, I calculated the proportion of recruits that occurred under existing vegetation clumps. Finally, using logistic regression, I was able to explore the possibility that death of individuals was related to the neighborhood index of those individuals in species where there was sufficient mortality (more than five deaths).

Results

In the Short Strandveld, a total of 12 species with more than 40 measured individuals were considered. These accounted for about 88% of the mapped individuals. Fifteen out of the 96 relationships between focal plant volumes and neighborhood indices (12 species at eight radii, Table 1) were significant at the 5% level. These significant relationships were restricted to four species: *Cephalophyllum spongiosum* and *Ruschia fugitans* (both leaf-succulent, creeping species in the Mesembryanthemaceae); *Galenia crystallina* (a perennial but weedy pioneer species in the Aizoaceae); and *Osteospermum oppositifolium* (a perennial Asteraceous shrub). In the case of *Cephalophyllum spongiosum*, the slopes of the significant fitted lines were all positive, while in all the other three species they were negative (Table 1, Figure 1). Despite being statistically significant, none of the regression models accounted for more than 10% of the variance (Table 2). In the case of the two mesembs, none of the models even accounted for 5% of the variation.

Mortality in the Short Strandveld ranged from a high of 33% (expressed as a percentage of the total mapped in 1997) in the case of *Didelta carnosus* a short-lived shrub, to a low of 9% in the case of *Ruschia fugitans* (Table 3). Averaged over all species, the total mortality was around 18%. In addition to this confirmed mortality, in all species certain individuals that were alive in 1997 were absent without trace in 1998 (the first “Unexplained” column in Table 3). While some of these undoubtedly represent measurement error, the fact that the percentage of unexplained individuals present in 1998 (second “Unexplained” column in Table 3) was substantially lower suggests that a fairly large proportion of these were in fact the result of mortality. This is particularly the case for *Didelta carnosus* (40% unexplained) that has non-persistent above-ground

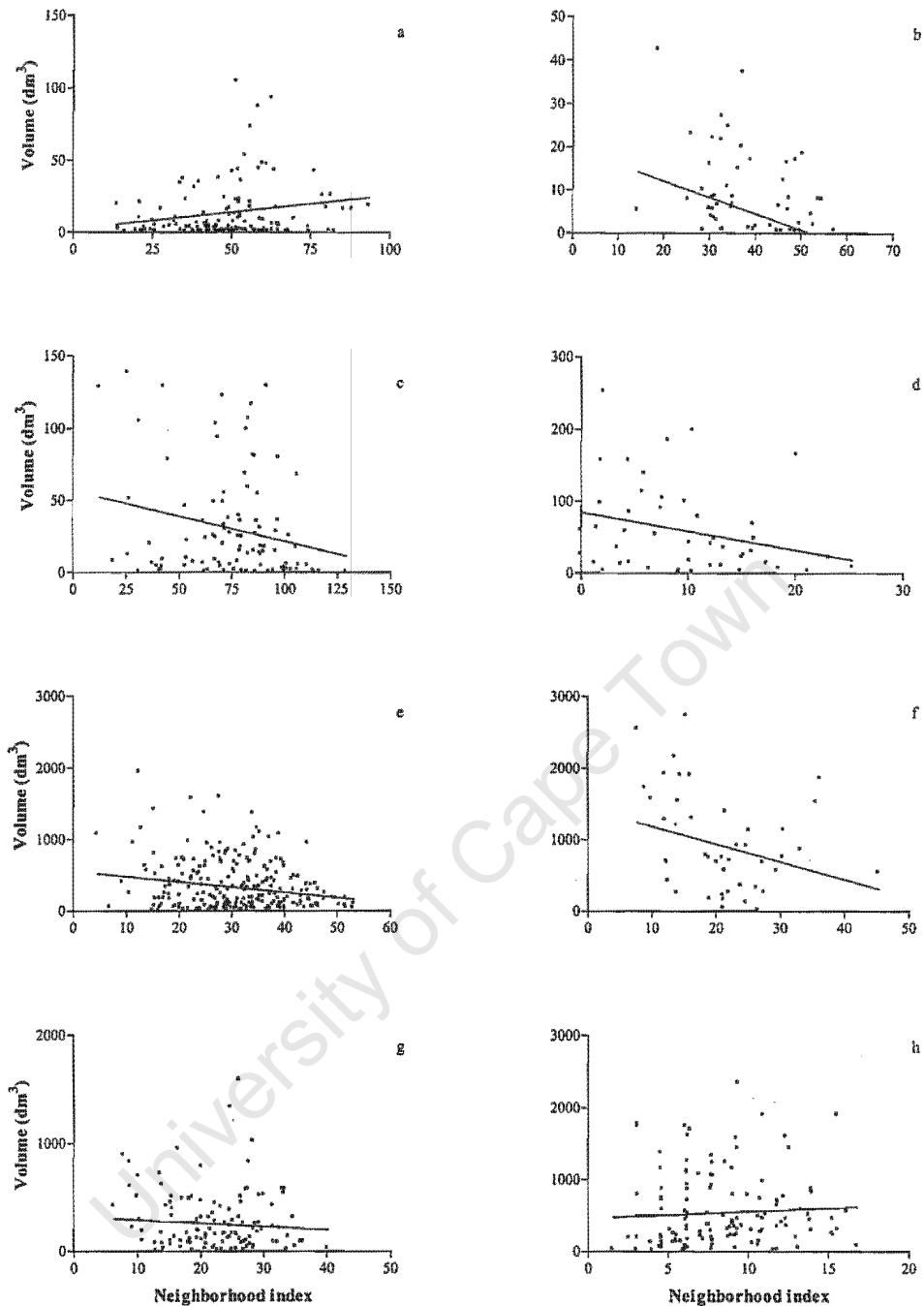


Figure 1. Scatter plots of the most significant relationships between individual plant volumes and their neighborhood indices together with the appropriate fitted lines. (a. *Cephalophyllum spongiosum* at 1.75m, b. *Osteospermum oppositifolium* at 1.5m, c. *Ruschia fugitans* at 2.25m, d. *Galenia crystallina* at 0.75m, e. *Pteronia onobromoides* at 3m, f. *Eriocephalus africanus* at 2.5m, g. *Osteospermum oppositifolium* at 2.5m, h. *Tetragonia fruticosa* at 1.5m. a to d are from the Short Strandveld while e to h are from the Medium Strandveld.)

structures. There was no evidence (at either the 5 or 10% level) that mortality was related to neighborhood index in any of the 11 species for which I conducted logistic regression. Rates of recruitment were generally lower than mortality (Table 3), ranging from 16% in the case of *Zygophyllum spinosum* to 0% in *Galenia crystallina*. The vast majority of recruitment that did occur took place under vegetation clumps (Table 4). The occurrence of individuals in 1998 that could not be matched to individuals mapped in 1997 was generally relatively low (around 5%) and this probably reflects the actual mapping error rate.

Table 1. Summary of the regression *F*-probabilities for the relationships between the neighborhood indices and individual volumes in the Short Strandveld plot. The values in bold indicate instances where the null hypothesis of independence can be rejected at the 5% (<0.05) level. The sign in parenthesis below significant values indicates the sign of the slope of the fitted curves. The species codes are: Cs – *Cephalophyllum spongiosum*; Po – *Pteronia onobromoides*; Dc – *Didelta carnosa* var. *tomentosa*; Oo – *Osteospermum oppositifolium*; Ht – *Helichrysum trichostatum*; Rf – *Ruschia fugitans*; Oc – *Othonna cylindrica*; Eb – *Euphorbia burmannii*; Gc – *Galenia crystallina*; Zs – *Zygophyllum spinosum*; Am – *Arctotis merxmuelleri*; Vs – *Vanzijlia annulata*.

Radius (m)	Species											
	Cs	Po	Dc	Oo	Ht	Rf	Oc	Eb	Gc	Zs	Am	Vs
0.5	0.172	0.146	0.438	0.086	0.378	0.031 (-)	0.872	0.962	0.050 (-)	0.640	0.570	0.305
0.75	0.471	0.567	0.642	0.137	0.724	0.054	0.877	0.947	0.022 (-)	0.417	0.743	0.121
1	0.293	0.420	0.674	0.331	0.971	0.099	0.811	0.928	0.031 (-)	0.672	0.333	0.195
1.25	0.216	0.412	0.812	0.230	0.719	0.077	0.460	0.462	0.064	0.489	0.306	0.362
1.5	0.041 (+)	0.759	0.629	0.026 (-)	0.806	0.036 (-)	0.727	0.738	0.049 (-)	0.865	0.311	0.154
1.75	0.015 (+)	0.646	0.658	0.030 (-)	0.921	0.032 (-)	0.696	0.996	0.224	0.809	0.359	0.168
2	0.017 (+)	0.558	0.657	0.027 (-)	0.627	0.030 (-)	0.680	0.871	0.299	0.719	0.337	0.161
2.25	0.024 (+)	0.585	0.610	0.062	0.511	0.021 (-)	0.401	0.922	0.473	0.703	0.201	0.119

In the Medium Strandveld plot, ten species (with >40 individuals), accounting for about 82% of the total number of individuals were investigated. Again, neighborhoods within eight radii (Table 5) were considered. Out of the 80 relationships considered, 12 were significant at the 5% level (Table 5). These were again restricted to four species: *Pteronia onobromoides*, *Eriocephalus africanus* and *Osteospermum oppositifolium* (all asteraceous shrubs); and *Tetragonia fruticosa* (a scrambling, deciduous species in the Aizoaceae). The slopes of lines fitted to the significant relationships in *Tetragonia fruticosa* were positive while for the other three species they were negative (Table 5, Figure 1). Once again, the amount of variance accounted for by the fitted

models was generally less than 10% (Table 6). The only exception was *Eriocephalus africanus* at a radius of 2.5m where the fitted model accounted for 10.9%. The reason for the relatively strong relationships in the case of *Eriocephalus* was also very clear from the scatter plots of the relationships (Figure 1). This is the only species where a visual assessment suggests an overall trend towards a negatively sloping line. Such a trend would indicate the possibility of negative interactions (competition, exploitation or amensalism) between individuals of this species and their neighborhood plants. In all the other scatter plots the forms tend towards the cone shape that is expected with random sampling from a size class distribution with a negative exponential shape and a normal shaped neighborhood index frequency distribution (Figure 1).

Table 2. Summary of percentage variance in the relationships between focal plant volumes and neighborhood indices accounted for by the regression models in the Short Strandveld. The "*"s indicate instances where the residual variance exceeds the variance the y-variate (volume). Species codes are as in Table 1.

Radius (m)	Species											
	Cs	Po	Dc	Oo	Ht	Rf	Oc	Eb	Gc	Zs	Am	Vs
0.5	0.6	0.8	*	3.6	*	3.7	*	*	5.0	*	*	0.1
0.75	*	*	*	2.3	*	2.8	*	*	9.3	*	*	0.2
1	1.6	*	*	*	*	1.8	*	*	8.1	*	*	0.2
1.25	1.3	*	*	3.8	*	2.2	*	*	5.5	*	*	0.1
1.5	2.2	*	*	7.2	*	3.5	*	*	6.3	*	*	0.1
1.75	3.4	*	*	6.8	*	3.6	*	*	1.1	*	*	0.1
2	3.2	*	*	7.0	*	3.7	*	*	0.2	*	*	0.1
2.25	2.8	*	*	4.6	*	4.3	*	*	*	*	0.5	0.1

Mortality in the Medium Strandveld plot was on average higher than in the Short Strandveld plot (28% vs. 18%) (Table 7). This unexpected difference can to some extent be explained by exceptionally high mortality in two species: *Arctotis merxmeuleri* (95%) and *Pharnaceum lanatum* (55%), neither of which contributes a great deal to the total plant biomass in the community. In addition to the skewing effect of these two species, the percentages of individuals mapped in 1997 but absent in 1998 (first "Unexplained" column in Table 7) were generally lower in the Medium Strandveld than in the Short Strandveld. They were also generally more in line with the corresponding unexplained percentages present in 1998 but absent in 1997. This suggests that the mortality rates in the Medium Strandveld are the actual mortality rates rather than just part of the rates as is probably the case in the Short Strandveld. The exception to this is *Tetragonia fruticosa* where 31% of the individuals mapped in 1997 could not be accounted for in 1998. This almost certainly represents mapping error as dead individuals of *Tetragonia* are very difficult to distinguish from the plant canopies in which they usually grow. It should also be noted

that the apparent mortality in the case of *Arctotis* might be inflated in both the Short and Medium Strandveld plots as this species is a hemicryptophyte. Recorded mortality may simply represent die back of above-ground structures and subsequent failure to emerge from buds owing to the dry season. As was the case in the Short Strandveld, there was no evidence (at either the 5 or 10% level) that mortality was related to neighborhood index in any of the eight species for which I was able to conduct logistic regression.

Table 3. Demographic data for the 12 most abundant species in the Short Strandveld community. "Mortality" refers to the number of individuals that were alive in 1997 but were dead in 1998. The first "Unexplained" column refers to individuals that were alive in 1997, but which were absent without trace in 1998. "Recruitment" refers to individuals in the smallest size classes that were present in 1998 but which were not mapped in 1997. Finally, the second "Unexplained" column refers to individuals not in the smallest size classes that were present in 1998 but which were not mapped in 1997. The species codes are as for Table 1.

Species	Total 97	Total 98	Mortality	Unexplained	Recruitment	Unexplained
Cs	145	135	22	11	12	11
Po	141	129	13	10	2	9
Dc	216	66	71	86	5	2
Oo	63	52	7	10	3	3
Ht	44	35	7	6	1	3
Rf	103	97	9	5	2	6
Oc	46	41	8	5	5	3
Eb	43	41	8	1	5	2
Gc	48	44	5	2	0	3
Zs	50	46	11	4	8	3
Am	205	86	41	88	6	4
Va	61	50	12	4	1	4

"Recruitment" rates in the Medium Strandveld were generally less than 20% with the exception of *Stoeberia utilis* and *Pharnaceum lanatum* which both had recruitment in the order of 37%. The high recruitment (and indeed the high mortality) in *Pharnaceum* is fairly easy to explain. *Pharnaceum* is the only species in the Medium Strandveld that has a very definite preference for living in open gaps between vegetation clumps (Chapter 2) and as a result it is likely to be exposed to very high levels of disturbance from both wind and animals. The fact that it has a preference for gaps also explains the fact that only 22% of the observed recruitment occurred under clumps making this species very much the exception (Table 4). It is also a relatively short-lived species. The recruitment in *Stoeberia* is far more difficult to explain other than to guess that recruitment in this species may be episodic and that this may represent a cohort of recruits.

Table 4. Summary of recruitment positions for species with adequate numbers of recruits in the Short and Medium Strandveld communities. Species codes are as in Tables 1 and 4.

Short Strandveld	
Species	Percentage of recruitment under vegetation
Cs	83%
Dc	80%
Oc	60%
Eb	100%
Zs	83%
Am	83%
Expected by chance:	50%
Medium Strandveld	
Zm	80%
Po	88%
Oo	75%
Oc	66%
Su	83%
*Pl	22%
Expected by chance:	54%

Table 5. Summary of the regression *F*-probabilities for the relationships between the neighborhood indices and individual volumes in the Medium Strandveld plot. Again the values in bold indicate instances where the null hypothesis of independence can be rejected at the 5% (<0.05) level. The sign in parenthesis below significant values indicates the sign of the slope of the fitted curves. The species codes are: Zm – *Zygophyllum morganiana*, Po – *Pteronia onobromoides*; Ea – *Eriocephalus africanus*; Oo – *Osteospermum oppositifolium*; Oc – *Othonna cylindrica*; Am – *Arctotis merxmülleri*; Su – *Stoeberia utilis*; Ht – *Helichrysum tricostatum*; Pl – *Pharnaceum lanatum*; Tf – *Tetragonia fruticosa*.

Radius (m)	Species									
	Zm	Po	Ea	Oo	Oc	Am	Su	Ht	Pl	Tf
1	0.769	0.914	0.351	0.141	0.772	0.962	0.799	0.766	0.101	0.036 (+)
1.5	0.401	0.307	0.360	0.076	0.766	0.582	0.979	0.199	0.153	0.025 (+)
2	0.183	0.352	0.197	0.150	0.419	0.171	0.937	0.424	0.730	0.670
2.5	0.138	0.068	0.017 (-)	0.046 (-)	0.257	0.203	0.950	0.693	0.611	0.591
3	0.187	0.001 (-)	0.025 (-)	0.334	0.273	0.300	0.675	0.692	0.886	0.656
3.5	0.532	0.025 (-)	0.038 (-)	0.311	0.410	0.279	0.705	0.953	0.836	0.702
4	0.690	0.027 (-)	0.028 (-)	0.297	0.319	0.228	0.837	0.964	0.230	0.724
4.5	0.996	0.046 (-)	0.025 (-)	0.562	0.805	0.280	0.991	0.995	0.397	0.716

Table 6. Summary of percentage variance in the relationships between focal plant volumes and neighborhood indices accounted for by the regression models in the Medium Strandveld. The "*"s indicate instances where the residual variance exceeds the variance the y-variate (volume). Species codes are as in Table 5.

Radius (m)	Species									
	Zm	Po	Ea	Oo	Oc	Am	Su	Ht	Pl	Tf
1	*	*	*	0.9	*	*	*	*	1.4	2.6
1.5	*	1.6	*	1.7	*	*	*	1.5	0.8	1.5
2	*	1.5	1.6	0.8	*	2.2	*	*	*	*
2.5	1.1	1.2	10.9	4.0	0.5	1.6	*	*	*	*
3	0.7	3.7	8.9	*	0.3	0.3	*	*	*	*
3.5	*	3.7	7.4	*	*	0.5	*	*	*	*
4	*	4.8	8.4	0.1	*	1.2	*	*	0.4	*
4.5	*	5.4	8.9	*	*	0.5	*	*	*	*

Table 7. Demographic data for the 10 most abundant species in the Medium Strandveld community. "Mortality" refers to the number of individuals that were alive in 1997 but were dead in 1998. The first "Unexplained" column refers to individuals that were alive in 1997, but which were absent without trace in 1998. "Recruitment" refers to individuals in the smallest size classes that were present in 1998 but which were not mapped in 1997. Finally, the second "Unexplained" column refers to individuals not in the smallest size classes that were present in 1998 but which were not mapped in 1997. The species codes are as for Table 4.

Species	Total 97	Total 98	Mortality	Unexplained	Recruitment	Unexplained
Zm	121	112	11	13	5	10
Po	270	247	26	26	17	12
Ea	49	45	4	5	2	3
Oo	133	117	22	15	12	9
Oc	60	62	9	2	9	4
Am	44	0	42	2	0	0
Su	149	198	7	7	56	7
Ht	53	44	5	7	1	2
Pl	97	81	53	6	36	7
Tf	194	124	28	61	2	17

Discussion

There are three important general results that emerge from this Chapter. The first is that, while subtle relationships between individual sizes and neighborhood indices in some species do appear to exist, strong directional interactions are non-existent. This finding is reinforced by the second general result that there is no evidence that mortality is related to neighborhood index in any of the species studied. The third important result is that the species turnover in these two communities is remarkably high when compared with most other desert systems (Martin & Turner

1977, Jordan & Noble 1982, Goldberg & Turner 1986, Bower *et al.* 1995). The first two of these results reinforce the suggestion made in Chapter 3 that populations in these communities have signs of stochastic domination. In such systems, stochastic “events” disrupt trajectories away from demographic equilibria between species where competitive (or other interaction) hierarchies could otherwise manifest themselves (DeAngelis & Waterhouse 1987). Sources of both temporal and spatial heterogeneity are crucial to the functioning of these systems (Menge & Sutherland 1987, Heino 1998, Palmqvist & Lundberg 1998, Ranta *et al.* 1998).

An interesting possibility in these two communities is that both temporal and spatial heterogeneity appear to emerge as a result of intrinsic characteristics of the vegetation itself. Such autogenic heterogeneity has also been reported in the context of shrub invasion of arid grasslands in North America (Reynolds *et al.* 1999). While the observed high levels of plant mortality may be interpreted as an effect of some underlying disturbance, an alternative perspective is that this in itself may represent a substantial source of uncertainty for the individuals that remain. My argument follows much the same lines as that presented by Hubbell & Foster (1986) for their diverse tropical forest system. For any given individual, the selective environment that determines its reproductive success is the interaction between its abiotic neighborhood and its immediate biotic neighborhood. High turnover of neighbors will result in unpredictable and complex plant neighborhoods over the life span of individuals in most species let alone integrated over entire populations.

Even as underlying causes of turnover, abiotic features of this system do not seem to hold much explanatory promise (at least not in ecological time). Given the arid nature of this system, the most likely abiotic source of heterogeneity that could lead to mortality would be variable precipitation. However, in comparison with other deserts that have similar mean annual rainfall, the rainfall in the Namaqualand Strandveld is remarkably reliable (Desmet & Cowling 1999, Esler *et al.* 1999) making this an unusually benign desert system. In addition the spatial extent of such drought related heterogeneity (i.e. large-scale indiscriminate disturbance that totally resets the system) would not be compatible with the nature of mortality that is observed. While the mortality rates in my mapped plots were high, they were (with the exception of one or two species) far from catastrophic despite the fact that this mapping period was during a dryer than usual period. This level of turnover is far more compatible with biotic sources of disturbance.

Animals (both domestic and wild) are certainly one source of such disturbance. It is also possible to build further on this speculation that intrinsic plant processes produce a great deal of the heterogeneity in these communities. Perhaps the most important cause for the high turnover rates, is the fact that species in these two communities appear to have inherently short life spans. The evolution of longevity characteristics is a subject that has received relatively little attention

although the notion of trade-offs seems to be central (Loehle 1987). In a desert community very similar to these Strandveld communities, Jürgens *et al.* (1999) have suggested that the observed short life spans of many perennial species may reflect a necessary trade-off between reproductive allocation and the ability to persist. They argue that a relatively benign climate shifts the balance in favor of allocation to reproduction. The prevalence of sympodial branching habit in Strandveld species (14 out of the 17 in this study) is compatible with this. Sympodial branching favors high reproductive output but may place severe structural constraints on the plant growth and ultimately on the longevity of individuals.

In terms of spatial heterogeneity, I demonstrated in Chapter 2 that the majority of individuals in both of these communities occur in multi-species clumps, which confers a very patchy structure on these communities. I speculated that these clumps are likely to be the manifestation of gregarious seed dispersal phenomena (as is the case in several other desert systems (Guo *et al.* 1998)), and loose facultative mutualisms. To some extent, this latter suggestion may be interpreted as contrary to the data that I present in this chapter. Only a two species (*Cephalophyllum spongiosum* in the Short Strandveld and *Tetragonia fruticosa* in the Medium Strandveld) showed any evidence that positive interactions have any population-level impact on growth of individuals. However, positive interactions are very likely to operate during the recruitment phase in an “all-or-nothing” type of way. Seeds that germinate in the open are unlikely to establish, partly as a result of herbivore effects (trampling and browsing), and partly as a result of harsh physical conditions (Breshears *et al.* 1998). In this way positive interactions may be a crucial force maintaining patch structure. An analogous “all-or-nothing” competition on the other hand would not be compatible with the clumped patterns demonstrated in Chapter 2 (or for that matter with an “all-or-nothing” facilitation).

In conclusion, my search for evidence of demographic equilibria has led me full-circle, back to early speculation that these two Strandveld communities may in fact be largely governed by stochastic phenomena (Cowling *et al.* 1994). Not only do both communities have certain demographic characteristics of non-equilibrium systems, but they also have the necessary “raw materials” in the form of temporal heterogeneity (disturbance) as well as spatial heterogeneity (or patch structure) for non-equilibrium conditions to persist. Interestingly, intrinsic properties of the vegetation itself appear to play a central role in generating both of these sources of heterogeneity. Whatever the source of the heterogeneity though, the explanatory implications of non-equilibrium dynamics are great. Given this non-equilibrium model, it can be argued that the “species in these systems coexist not in spite of, but because of being functionally equivalent generalists” (Hubbell & Foster 1986).

References

- Bower, J.E., Webb, R.H. & Rondeau, R.J. 1995. Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA. *Journal of Vegetation Science* 6:551-564.
- Breshears, D.D., Nyhan, J.W., Heil, C.E. & Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Science* 159(6):1010-1017.
- Cowling, R.M., Esler, K.J., Midgely, G. & Honig, M. 1994. Plant functional diversity, species diversity and climate in arid and semi arid southern Africa. *Journal of Arid Environments* 27:141-158.
- DeAngelis, D.L. & Waterhouse, J.C. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57(1):1-21.
- Desmet, P.G. & Cowling, R.M. 1999. 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. & Cowling, R.M. 1999. The succulent karoo in a global context: plant structural and functional comparisons with North American winter rainfall deserts. - In: Dean, W.R.J. and Milton, S.J. (eds), *The Karoo: ecological patterns and processes*. Cambridge University press, Cambridge.
- Goldberg, D.E. & Turner, R.M. 1986. Vegetation change and plant demography in permanent plots in the Sonoran desert. *Ecology* 67(3):695-712.
- Guo, Q., Rundel, P.W. & Goodall, D.W. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes and implications. *Journal of Arid Environments* 38:465-478.
- Heino, M. 1998. Noise colour, synchrony and extinctions in spatially structured populations. *Oikos* 83:368-375.
- Hubbell, S.P. & Foster, R.B. 1986. Biology, chance and history and the structure of tropical rain forest tree communities. In: Diamond, J. & Case, T.J.(eds), *Community Ecology*. Harper & Row, New York.
- Jordan, P.W. & Noble, P.S. 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment, and growth. *Botanical Gazette* 143(4):511-517.
- Jürgens, N., Gotzmann, I.H. & Cowling, R.M. 1999. Remarkable medium-term dynamics of leaf succulent Mesembryanthemaceae shrubs in the winter-rainfall desert of northwestern Namaqualand, South Africa. *Plant Ecology* 142(1-2):87-96.
- Loehle, C. 1987. Tree life history strategies: the role of defenses. *Canadian Journal of Forestry*

Research 18:209-222.

- Martin, S.C. & Turner, R.M. 1977. Vegetation change in the Sonoran Desert region, Arizona and Sonora. *Arizona Academy of Science Journal* 12(2):59-69
- Menge, B.A. & Sutherland, J.P. 1987. Community regulation: variation in disturbance competition and predation in relation to environmental stress and recruitment. *The American Naturalist* 130(5):730-757.
- Palmqvist, E. & Lundberg, P. 1998. Population extinction in correlated environments. *Oikos* 83:359-367.
- Randall, J.M. & Rejmánek, M. 1993. Interference of bull thistle (*Cirsium vulgare*) with growth of ponderosa pine (*Pinus ponderosa*) seedlings in a forest plantation. *Canadian Journal of Forestry Research* 23:1507-1513.
- Ranta, E., Kaitala, V. & Lundberg, P. 1998. Population variability in space and time: the dynamics of synchronous population fluctuations. *Oikos* 83:376-382.
- Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., van Hulst, R., Johansson, M.E., Nilsson, C., Gurevitch, J., Grigulis, K. & B.E. Beisner, B.E. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* 75(6):1753-1760.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G. & Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* 69(1):69-106.
- Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos* 52:3-18.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239-250.

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Chapter 5:

THE RELATIVE PERFORMANCE OF CLUMPED VS. EXPERIMENTALLY ISOLATED PLANTS IN THE MEDIUM STRANDVELD.

Abstract

In order to test the hypothesis that perennial Medium Strandveld species with a preference for occurring in multi-species clumps should derive benefit from their association into clumps, I conducted a factorial removal experiment. Contrary to this hypothesis, there was evidence of competition for water in the clumped non-succulent species studied in the form of depressed water potentials. No effect of isolation on leaf water contents was detected though, suggesting that clumped plants are able to compensate physiologically in response to competitive stress. Isolating individuals also had no effect (positive or negative) on branch growth. Finally, the data suggested that isolating individuals exposed them to a far greater risk of damage by wind or animals. In light of these results I conclude that the spatial arrangement of plants in this community reflects a situation where the benefits associated with occurring in clumps exceed any competitive costs.

Keywords

branch growth, positive interactions, leaf water contents, risk, water potentials

Introduction

In Chapter 2 I speculated that the clumped vegetation patterns in Strandveld communities were a result of a positive feedback between physical benefits associated with microhabitat modification and mutual protection and the dominant seed dispersal strategies. This is not the only possible interpretation. As discussed in Chapter 2, the most popular interpretation of these patterns has been the “maturation thinning” model which is nested in competition theory (Phillips & MacMahon 1981, Prentice & Werger 1985, Miriti et al. 1998). This model involves a combination of seed dispersal processes that produce aggregated patterns in juveniles, and competition that will convert these into random, and ultimately into regular ones (Phillips & MacMahon 1981).

There are, however, two weaknesses with this competition-based model. The first is that empirical support for the model is often not convincing. The possibility that maturation thinning is occurring has usually been explored by dividing populations into size classes and characterizing the

spatial patterns of these size classes separately (Phillips & MacMahon 1981, Prentice & Werger 1985, Wright & Howe 1987, Haase *et al.* 1997). In these studies, complete sequences of patterns (i.e. clumped to random to regular) are seldom resolved. The most common trend is clumped to random. It is possible to argue that if individuals are clumped to start with, and if some mortality is inevitable (as it must be even in the absence of competition) then a tendency towards randomness may also be inevitable. In addition to this, the failure to identify individuals growing close together may often bias the interpretation of patterns (Ebert & McMaster 1981, Cox 1987). Prentice & Werger (1985) for instance made this error explicitly by exploring the spatial arrangement of clumps rather than the spatial arrangement of individuals. The second weakness with the model is that it neglects the likely possibility that seed dispersal is subject to selection (Diekmann *et al.* 1999). Evolutionary theory suggests that if there is a net disadvantage associated with living in clumps (e.g. reduced fecundity due to competition) then dispersal strategies that ensure that juveniles do not aggregate should evolve.

So, while few would deny that some competition between plants is axiomatic, several authors have begun to question whether competition on its own is a suitable framework within which to interpret clumped patterns (e.g. Wright & Howe 1987, Schlesinger *et al.* 1990, Couteron & Kokou 1997, Evans & Belnap 1999, Reynolds *et al.* 1999). Another alternative interpretation of clumped vegetation patterns is the notion of "pseudointeraction" (Garret & Dixon 1997). These authors argue that abiotic environmental heterogeneity may produce spatial characteristics that suggest interactions even in the absence of actual interactions. This idea is complicated by the fact that most biotic interactions are mediated by changes in the environment (Schlesinger *et al.* 1990, Jones *et al.* 1997, Reynolds *et al.* 1999).

Thus I return to positive interactions, or rather, the balance between positive and negative interactions (Callaway & Walker 1997, Holmgren *et al.* 1997, Feldman *et al.* 1999, Herre *et al.* 1999, Chapter 2). According to this notion, plants will have a preference for clumping if there is some net benefit associated with occurring in clumps (i.e. if the benefits accruing through association with neighbors are greater than the inevitable competitive costs). Armed with this basic prediction that plants with a preference for clumping should derive a net benefit through association into clumps, and with the observed strong tendency towards clumping in Strandveld communities, I set out to establish whether there were any apparent advantages associated with living in clumps. I focused on mature individuals rather than seedlings and recent recruits. My experimental approach was to isolate individuals from their clumps and to compare the performance of these individuals against matched controls over a year. In addition to assessing growth (of tagged branches), I monitored plant water relations and any physical damage to the plants by herbivores and wind.

Materials and Methods

In order to test the hypothesis that mature individuals (as opposed to seedlings and recent recruits) benefit by living in multi-species vegetation clumps, I conducted a factorial removal experiment. Pairs of individuals matched as closely as possible in terms of size and clump characteristics (Figure 1) were selected from eight species. Besides being among the most abundant species in this community, these species exhibited a wide range of physiological traits (Table 1). One of the paired individuals was then experimentally isolated from their clump while the other was left with its clump intact. The isolation was achieved by cutting neighboring plants off at their base and carefully removing their aerial parts so as to minimize damage to the focal plants. Any re-growth from the cut stems was removed periodically. These 16 treatments (8 species x 2 removal treatments) were replicated in three complete blocks (Rep1: 30°52'00''S, 17°35'21''E; Rep2: 30°52'03''S, 17°35'34''E; Rep3: 30°52'06''S, 17°35'34''E). The treatments were imposed in late winter (August 1998). The trial was assessed in October and November 1998 and January, April and late July 1999. At each assessment date pre-dawn and mid-day water potentials were measured using a digital pressure chamber (PMS Instruments, Corvallis, Oregon, USA, model 1003) and leaf water contents were determined [(wet weight – dry weight)/wet weight]. For the wet weights, leaves were weighed on site or wrapped in plastic film, kept cool and in the dark, and weighed within 2 hours of collection. They were then frozen at -16 °C to hasten drying, dried at 70 °C for 48 hours and then re-weighed for the dry weight. A paired t-test revealed that overall pre-dawn and mid-day leaf water contents did not differ and I therefore only present the pre-dawn results. In addition to these indirect measures of plant performance, I also measured the growth (as a more ultimate integrator of plant response) of five randomly selected marked branches per plant between April 1999 and July 1999. Finally, any damage to the tagged branches resulting from wither animal activity or wind was also noted.

Table 1. List of the eight species used in this study along with their families, photosynthetic mode and an index of their succulence (turgid mass/leaf area ratio).

Species	Family	Photosynthetic pathway	Turgid/area ratio
<i>Salvia lanceolata</i>	Lamiaceae	C3	0.5484
<i>Eriocephalus africanus</i>	Asteraceae	C3	0.9715
<i>Pteronia onobromoides</i>	Asteraceae	C3	0.9961
<i>Zygophyllum morskana</i>	Zygophyllaceae	C3	1.0111
<i>Othonna cylindrica</i>	Asteraceae	C3	2.6286
<i>Senecio sarcooides</i>	Asteraceae	C3	4.1825
<i>Stoeberia utilis</i>	Mesembryanthemaceae	CAM	4.2853
<i>Ruschia fugitans</i>	Mesembryanthemaceae	CAM	5.5009

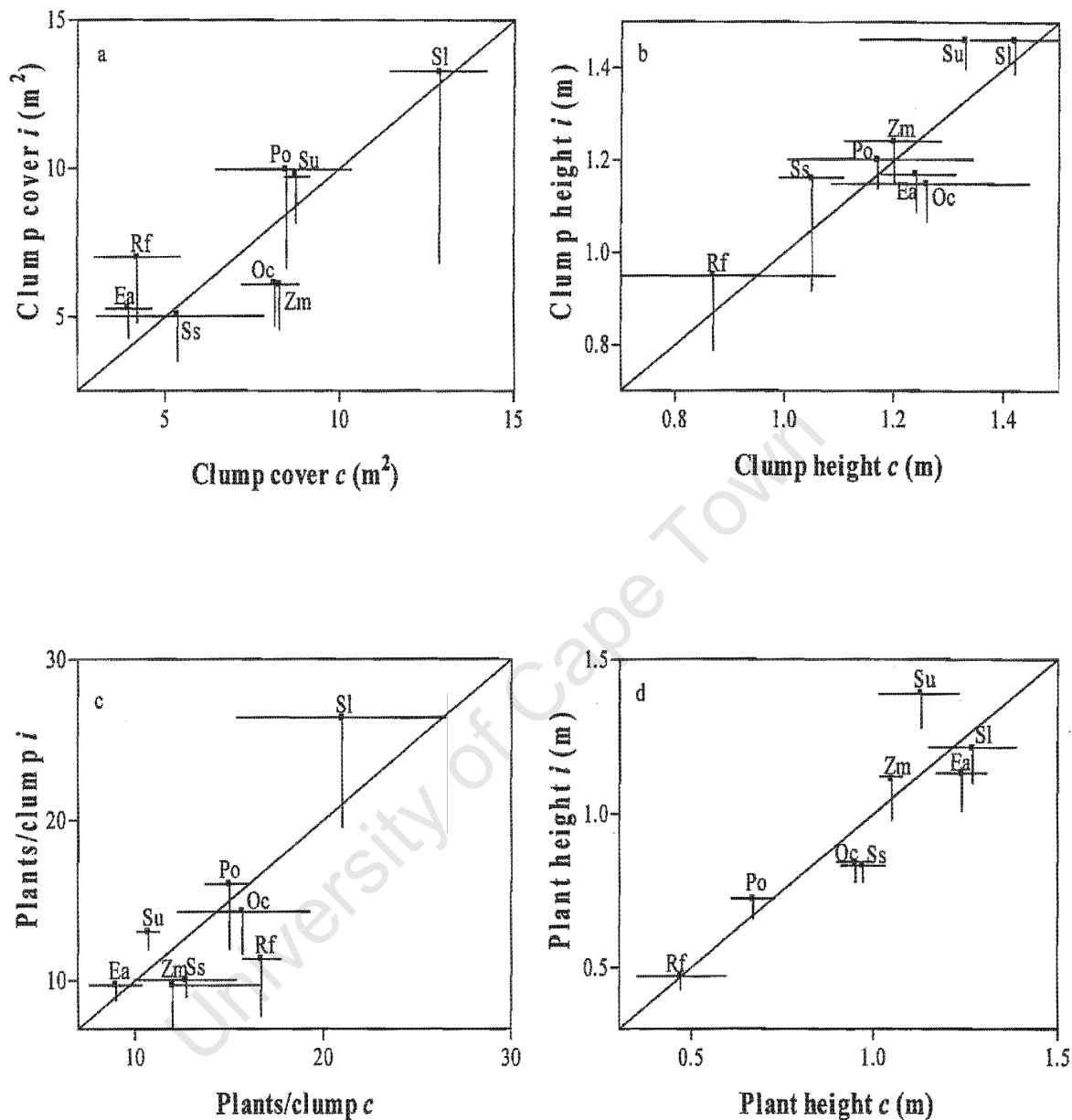


Figure 1. Attributes of clumps and individuals that were isolated (i) plotted against their paired controls (c). Points falling on the diagonal line would correspond exactly. Bars represent standard errors. Po = Pteronia, Sl = Salvia, Ea = Erioccephalus, Su = Stoeberia, Rf = Ruschia, Zm = Zygophyllum, Oc = Othonna, Ss = Senecio.

I analyzed the water relations variables using the repeated measures analysis of variance procedure in the Genstat procedure library (Genstat Committee, 1993). This procedure uses maximum likelihood to estimate an adjustment factor for degrees of freedom in order to account for non-sphericity of data in the "subject.time" stratum of the ANOVA (Greenhouse & Geisser 1959, Everitt 1995). Following on from this analysis, I used normal order plots (Perry 1986, Cousens 1987) to explore groupings of treatments at the "species.treatment" level, where appropriate, based on the results of the ANOVA. I opted for this approach because I could find no evidence to support the basic hypothesis that plants should benefit from living in clumps, and as such, this exploration was unplanned. I analyzed the branch growth data by conventional ANOVA, treating each plant as the experimental unit and using average branch growth per plant as the variate. In this way, the data met the assumptions of normality and homogeneity of variance necessary for a valid ANOVA. I did not analyze the incidental damage data in any statistical way.

Table 2. Repeated measures ANOVA table for the pre-dawn and mid-day water potentials and pre-dawn leaf water contents. Values presented are the variance ratios. When assessing the significance of these, the degrees of freedom in the (site.subject).time stratum should be multiplied by the Greenhouse-Geisser (G-G) epsilon value.

Source of variation	d.f.	Pre dawn water pot.	Mid-day water pot.	Pre-dawn leaf water content
G-G epsilon		0.7814	0.6396	0.7594
Site stratum	2	0.27	5	0.34
Site.Subject stratum				
Species	7	186.59	189.89	170.77
Treat	1	16.91	19.29	0.4 <i>ns</i>
Species.treat	7	5.64	4.93	0.7 <i>ns</i>
Residual	30	1.31	1.88	2.33
Site.Subject.Time stratum				
Time	4	218.49	148.34	411.72
Time.species	28	23.1	13.63	57.65
Time.treat	4	1.91 <i>ns</i>	4.87	0.76 <i>ns</i>
Time.species.treat	28	1.04 <i>ns</i>	1.39 <i>ns</i>	0.82 <i>ns</i>
Residual	128			
Total	239			

Results

Plant water relations – In terms of water relations the experiment failed to confirm the hypothesis that plants should benefit by living in clumps. In the case of leaf water contents there was no evidence that the isolation of individuals had any significant effect (negative or positive) (Table 2). Different species certainly showed clear differences over time (significant species.time interaction) (Table 2, Figure 2). As expected, the water contents in the more succulent species (*Senecio*, *Othonna*, *Stoeberia* and *Ruschia*) were generally higher and generally changed less over the season than the non-succulent species (*Pteronia*, *Eriosephalus* and *Salvia*). Although *Zygophyllum* is summer deciduous, prior to losing its leaves its performance was much the same as the succulent group. The pre-dawn and mid-day water potentials were slightly more difficult to interpret. Once again there was a significant species.time interaction (Table 2). *Zygophyllum* was unusual in that it behaved more like the non-succulents than the succulents which is in contrast to the leaf water contents.

In addition to these species.time interactions, the species.treatment interactions were also significant in both pre-dawn and mid-day water potentials, and there was a significant treatment.time interaction in the case of the mid-day water potentials (Table 2). The treatment.time interaction reflects the fact that the treatment effect was more pronounced in mid-summer than in winter. In the case of the species.treatment interactions, once again, the general distinction between the succulent species and the non-succulent species was apparent. Clumped and isolated individuals of the succulent species showed no evidence of performing differently while the non-succulent species did exhibit a treatment effect (Figure 3). *Salvia* was an anomaly since its lack of response resembled the behavior of succulents while *Zygophyllum* behaved in the same way as the non-succulents. Where treatment effects were evident, they indicated that isolated individuals were less stressed (higher water potentials) than their counterparts in clumps. Finally, it would appear that within the succulent group (*Senecio*, *Othonna*, *Stoeberia* and *Ruschia*), the CAM Mesembryanthemaceae species (*Stoeberia* and *Ruschia*) generally had higher water potentials than the C₃ Asteraceae (*Senecio* and *Othonna*).

Plant growth and damage – While there was a significant species effect ($P < 0.001$) on branch growth, there was no significant treatment main effect or species.treatment interaction (at the 5 or 10% levels). The two Mesembryanthemaceae species (*Stoeberia* and *Ruschia*) responded most to the light rains that fell during this growth period (Figure 4). At the other end of the spectrum, *Pteronia* hardly showed any response to the rains. In terms of plant damage, it is clear that in the case of the experimental plants, clumping affords a high degree of protection (Table 3). *Senecio* individuals in particular were highly susceptible to browsing damage when isolated from their clumps. The damage in *Eriosephalus*,

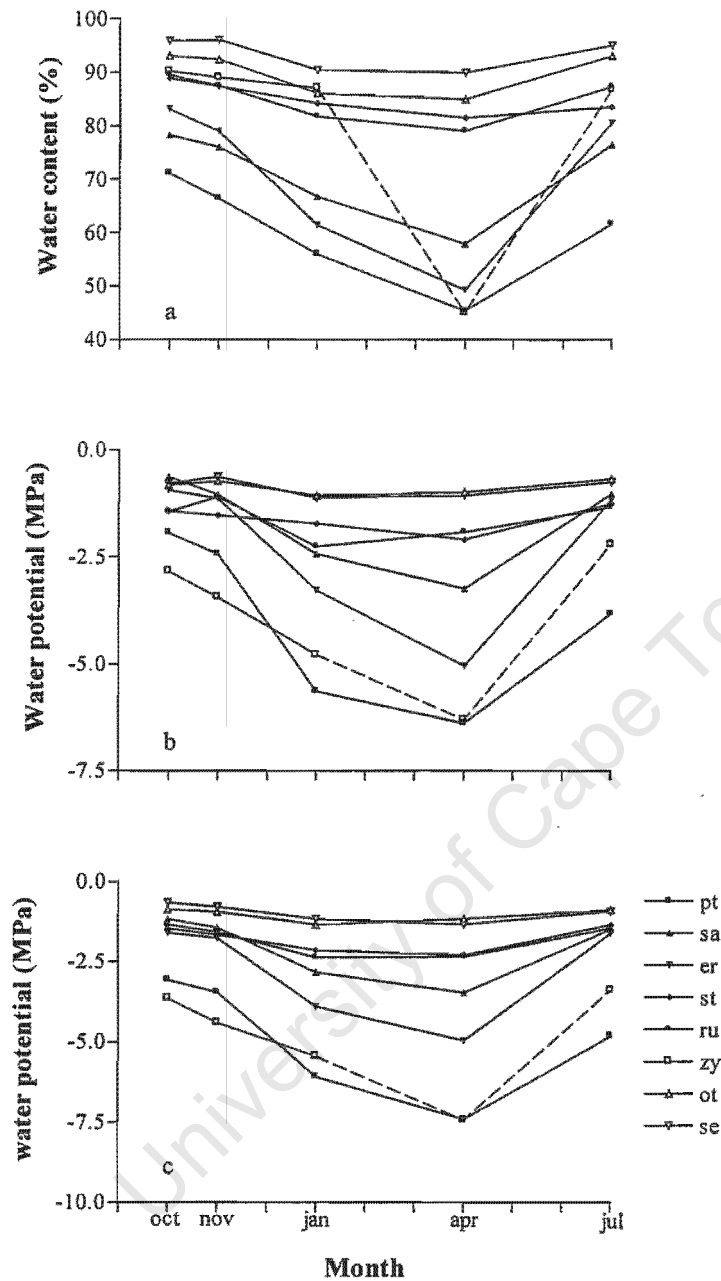


Figure 2. Time series showing the development of the significant species.time interactions for a) pre-dawn leaf water contents and b) pre-dawn and c) mid-day water potentials. The species codes are as in Figure 1. The dotted line in the case of *Zygotrichum* indicates the fact that this species was summer deciduous and there was therefore no data recorded in April. We simply set the April value to the lowest observed value for the purposes of this graph.

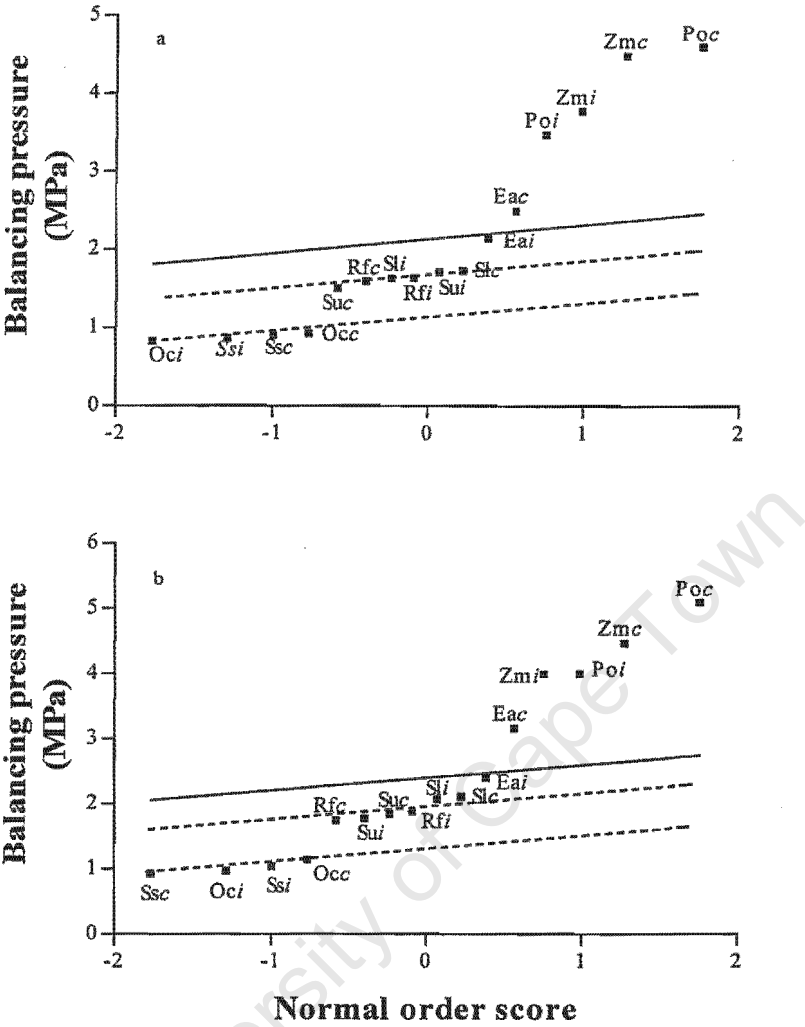


Figure 3. Normal order plots illustrating the significant species.treatment interactions evident in a) pre-dawn and b) mid-day balancing pressures (water potentials $\times -1$). The values are means for all 5 sampling times. The solid line has a slope equivalent to the standard error of the mean and intersects the y-axis at the overall mean. The dotted lines are simply parallel lines (i.e. same slope). Points falling along any one of these lines form natural groups that behave similarly. The points are coded with the species codes as in Figure 1 together with an i or a c indicating the treatment (isolated or clumped).

and *Salvia* isolated plants appeared to have been caused by either sheep walking through the plants or wind damage, while the damage in *Stoeberia* and *Zygophyllum* resulted from sheep using the plants as scratching posts. The damage in isolated *Pteronia* and *Othonna* plants appeared to be the result of animals brushing past or wind.

Table 3. Percentage of tagged branches (out of a total of 15) that were damaged between April and late July (14 weeks).

Species	Isolated	Clumped
<i>Pteronia</i>	13.3	0.0
<i>Salvia</i>	26.7	0.0
<i>Eriocephalus</i>	26.7	0.0
<i>Stoeberia</i>	33.3	0.0
<i>Ruschia</i>	0.0	6.6
<i>Zygophyllum</i>	13.3	0.0
<i>Othonna</i>	13.3	0.0
<i>Senecio</i>	66.7	26.7

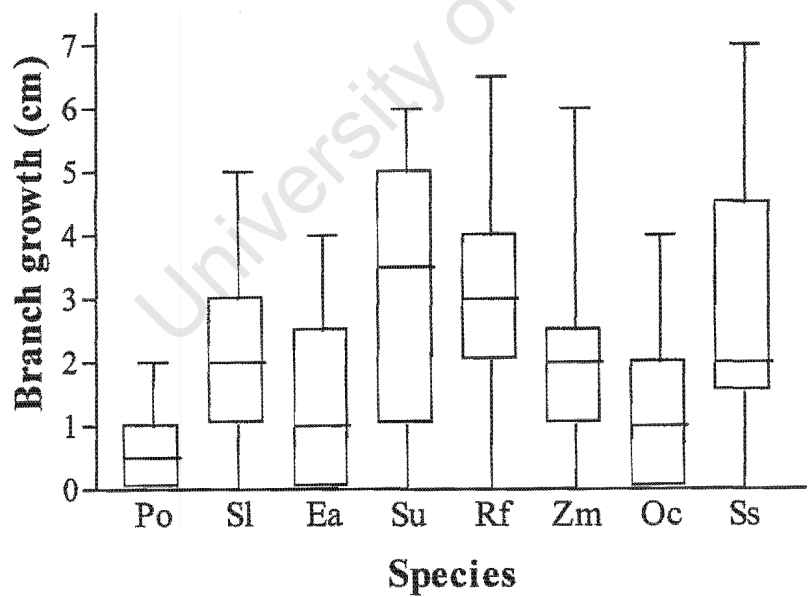


Figure 4. Box & whisker plot of branch growth for the eight species considered in this experiment. Once again species codes are as in Figure 1.

Discussion

The working premise was that clumped vegetation patterns in the Medium Strandveld, most likely represents the situation where the benefits accrued by plants through their association with neighbors are greater than the inevitable competitive costs. In line with this notion of net effect, the variates that I measured did indeed reflect the full spectrum of interactions (negative in the case of water potentials in some species; neutral in the case of leaf water contents and growth; and positive in the case of physical damage). In support of the findings of Briones *et al.* (1998) in a Chihuahuan system, occurring in clumps had little or no effect on plant water relations in the more succulent species studied (*Senecio*, *Othonna*, *Stoeberia* and *Ruschia*). In contrast, the less succulent species (*Pteronia*, *Eriosephalus*, and *Zygophyllum* but not *Salvia*), showed some evidence of competition for water in the form of lower (more negative) water potentials in clumped individuals. There were, however, no differences in leaf water contents between clumped and isolated individuals in any species. If we assume that leaf water content is a better indicator of plant water status than water potentials (Turner 1981, Lamont 1999), it would appear that the non-succulent species may be able to minimize the effects of negative interactions by means of some form of osmotic adjustment. Compensatory responses to stress at similar time scales (an entire season) have recently been reported in other desert systems (Reynolds *et al.* 1999). In addition, while one would assume that such compensatory responses are associated with metabolic costs, these are not manifest in any significant growth response. This suggests that the costs are either insignificant, or that some other growth related benefit balances them out. Both of these suggestions (osmotic compensation and insignificant metabolic costs) are speculative and remain to be proven.

This still leaves the question of why occur in clumps and it would appear that the risk of damage might hold the key. Of the 24 isolated plants in the experiment, no less than 13 (or 54 %) were damaged to some extent by the end of the experiment. This is in contrast to about 4 (or 16 %) in the clumped plants. The degree and type of damage ranged from broken branches and isolated browsing to wind throw of whole plants and severe browsing. It can be argued that by isolating mature individuals that had benefited from associational defenses for most of their lives, the experimental design may have exaggerated this effect. These plants would have had no need to invest in structural growth or defense prior to treatment and reallocation of resources following treatment would obviously have been impossible over the time frame of a single season. However, this does not weaken my main contention that these plants are faced with making trade-offs between the costs and benefits of living in clumps as opposed to living in the open. On the costs side, competition for water appears to be a

problem for non-succulent species, although it seems that these plants are able to compensate physiologically for this. On the benefits side is the fact that plants are exposed to much lower risks of damage and are free to allocate resources (that might otherwise have gone to structural or defense functions) into other activities. In addition, while the experiment described in this chapter only addressed the impacts on adult plants, it is likely that seedlings and juveniles would be even more vulnerable to trampling, consumption and wind damage.

Whether or not this simple 'balance sheet' is enough to conclude that plants experience a net benefit through association with other plants is still open to debate. It is possible that the net interaction in adults is neutral and that stronger positive interactions during other life stages (e.g. seedlings) have, over evolutionary time, resulted in the observed preference to clump. Several authors have presented data to suggest that establishment in many desert species is facilitated by the presence of existing vegetation (Yeaton & Manzanares 1986, Yeaton & Esler 1990, Valiente-Banuet & Ezcurra 1991). However, very often these facilitative relationships become competitive during adult stages and a cyclical succession phenomenon emerges. While there is little doubt that facilitation during establishment is a feature of the Strandveld (around 80% of recruitment occurs under clumps [Chapter 4: Table 3]), it does not appear that cyclical succession occurs.

To conclude, the results provide evidence that adult plants in the Medium Strandveld at least, experience both positive and negative interactions with other plants. While this evidence does not constitute proof that plants experience a net overall benefit (although it points in that direction), I am confident that at worst the interactions between adults are neutral. In addition, I feel justified in advancing the circular argument that if, over the entire life span of individuals, the net interactions were not usually positive, then plants would not occur in clumps because there would have been strong selection against this.

References

- Briones, O., Montaña, C. & Ezcurra, E. 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. *Oecologia*. 116:365-372.
- Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*. 78(7):1958-1965.
- Cousens, R. 1988. Misinterpretations of results in weed research through inappropriate use of statistics. *Weed Research* 28:281-289.
- Couteron, P. & Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology*. 132:211-227.

- Cox, G.W. 1987. Nearest-neighbor relationships of overlapping circles and the dispersion pattern of desert shrubs. *Journal of Ecology*. 75:193-199.
- Dieckmann, U., O'Hara, B. & Weisser, W. 1999. The evolutionary ecology of dispersal. *Trends in Ecology and Evolution*. 14(3):88-91.
- Ebert, T.A. & McMaster, G.S. 1981. Regular pattern of desert shrubs: A sampling artifact? *Journal of Ecology*. 69:559-564.
- Evans, R.D. & Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology*. 80(1):150-160.
- Everitt, B.S. 1995. The analysis of repeated measures: a practical review with examples. *The Statistician* 44(1):113-135.
- Feldman, R., Tomback, D.F. & Koehler, J. 1999. Cost of mutualism: Competition, tree morphology, and pollen production in limber pine clusters. *Ecology*. 80(1):324-329.
- Genstat 5 Committee. 1993. *Genstat 5 Release 3 Reference Manual*. Oxford Scientific Publications, Oxford.
- Garrett, K.A. & Dixon, P.M. 1997. Environmental pseudointeraction: The effects of ignoring the scale of environmental heterogeneity in competition studies. *Theoretical Population Biology*. 51(1):37-47.
- Greenhouse, S.W. & Geisser, S. 1959. On methods in the analysis of profile data. *Psychometrika*. 24:95-112.
- Haase, P., Pugnaire, F.I., Clark, S.C. Incoll, C.D. 1997. Spatial pattern in *Anthyllis cystoides* shrubland on abandoned land in southeastern Spain. *Journal of Vegetation Science*. 8:627-634.
- Herre, E.A., Knowlton, N., Mueller, U.G. & Rehner, S.A. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends in Ecology and Evolution*. 14(2):49-53
- Holmgren, M., Scheffer, M. & Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. *Ecology*. 78(7):1966-1975.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*. 78(7):1946-1957.
- Lamont, B. 1999. Pressure volume curves. *Plants in Action* (eds B.J. Atwell, P.E. Kriedemann & C.G.N. Turnbull), pp 465-467. MacMillan Australia, South Yarra, Vic.
- Miriti, M.N., Howe, H.F. & Wright, S.J. 1998. Spatial patterns of mortality in a Colorado desert plant community. *Plant Ecology*. 136:41-51.
- Perry, J.N. 1986. Multiple-comparisons procedures: a dissenting view. *Journal of Economic Entomology*. 79(4):1149-1155.

- Phillips, D.L. & MacMahon, J.A. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology*. 69:97-115.
- Prentice, I.C. & Werger, M.J.A. 1985. Clump spacing in a dwarf desert shrub community. *Vegetatio*. 63:133-139.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G. & Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*. 69(1):69-106.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science*. 247:1043-1048.
- Turner, N.C. 1981. Techniques and experimental approaches for the assessment of plant water status. *Plant and Soil*. 58:339-366.
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán valley, Mexico. *Journal of Ecology*. 79:961-971.
- Wright, S.J. & Howe, H.F. 1987. Pattern and mortality in Colorado Desert plants. *Oecologia*. 73:543-552.
- Yeaton, R.I. & Esler, K.J. 1990. The dynamics of a succulent karoo vegetation. A study of species association and recruitment. *Vegetatio*. 88:103-113.
- Yeaton, R.I. & Manzanares, A.R. 1986. Organization of vegetation mosaics in the *Acacia schaffneri* – *Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology*. 74:211-217.

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Chapter 6:

THE HORIZONTAL DISTRIBUTION OF ROOT BIOMASS IN STRANDVELD COMMUNITIES.

Abstract

In this chapter I set out to address the question of whether the spatial distribution of root biomass mirrored the highly clumped distribution of shoot biomass the Short and Medium Strandveld communities. The results indicate that this is generally not the case. In both communities, there was no significant difference between the fine root (< 2 mm diameter) biomass under clumps compared with gaps between clumps. In the Short Strandveld, this was also the case for structural root mass. The only exception to this general trend was in the case of structural roots in the Medium Strandveld where there was more biomass under vegetation clumps. I argue that these patterns point to the fact that Strandveld plants are shaped by the trade off between advantages due to associational defense and the inevitable competition for water that this association brings. They do not support the suggestion that fertile islands are a feature of these communities.

Key words

Fine roots, structural roots, soil cores, vegetation clumps and gaps

Introduction

Throughout this thesis, the starting point for most of the discussion has been the observation that the majority of individuals from most of the perennial plant species (which in turn constitute the bulk of shoot biomass) are concentrated into multi-species vegetation clumps (Chapter 1). The findings in Chapter 5 suggest that this arrangement provides individuals with substantial protection against damage by wind or animals and that this offsets any competitive disadvantage that they may experience. An inevitable question that emerges is what about the roots? This is particularly relevant in desert systems such as the Strandveld where resources that are likely to be most limiting (water and as a result nutrients) are below-ground resources (Fowler 1986, Casper & Jackson 1997). For this reason one might expect the spatial arrangement of roots to differ fundamentally from the shoots. It is also for this reason that root studies have a long history in desert systems (e.g. Scott & van Breda 1937, Phillips & MacMahon 1981, Briones *et al.* 1996, Heitschmidt *et al.* 1998).

In terms of vertical root distributions, a variety of patterns have been reported in arid systems. Theoretically much attention has been paid to the possibility that different species may partition the soil profile in such a way as to minimize competition (e.g. Cody 1986, Briones *et al.* 1996). This is supported to some extent by evidence from broad scale surveys that certain species do occasionally specialize in resource acquisition across a range of depths (Sun *et al.* 1997). However, most empirical studies seem to indicate that the bulk of root biomass in arid systems is confined to the top 30cm of soil (Heitschmidt *et al.* 1988, Schultze *et al.* 1996, Briones *et al.* 1996, Nobel & Linton, 1997, Sun *et al.* 1997) and it is difficult to see how such limited vertical space might be partitioned. The predominance of shallow rooting certainly appears to be the case in the Namaqualand communities (Esler & Rundel 1999). In the Strandveld, the available rooting depth is constrained by impenetrable subsoils between 0.6 and 2m. Despite this potentially available soil profile, my observations from several soil pits indicate that in the Short Strandveld more than 90% of the root biomass is found in the top 30 cm. In the Medium Strandveld on the other hand at least 60% of root material is found in the top 30 cm. In the context of Namaqualand, this vertical distribution of roots makes sense. As described in Chapter 1, the rainfall events are small but fairly regular and dew and fog may contribute significantly to total precipitation (Desmet & Cowling 1999). The result of this precipitation regime is that deep wetting of soil profiles is an infrequent occurrence. A similar argument is echoed by Breshears *et al.* (1998) in another arid system.

Perhaps a more interesting aspect of root patterns in Strandveld communities then is whether or not the below-ground distribution of biomass mirrors the highly clumped above-ground pattern horizontally. The balance of evidence in the literature suggests that in arid systems lateral roots may extend a great deal beyond the crowns of individuals which in turn suggests that roots should fill the gaps (Phillips & MacMahon 1981, Heitschmidt *et al.* 1988, Beukman 1991, Brisson & Reynolds 1994). In contrast, Hook *et al.* (1994) have reported some evidence suggesting that root biomass declines in gaps in arid grasslands and they argue that these horizontal root gaps may be very important for establishment. In the case of the Namaqualand Strandveld, circumstantial evidence certainly does not support this gap recruitment hypothesis as the bulk of recruitment occurs under vegetation clumps rather than in gaps (Chapter 4: Table 3). From a theoretical perspective Schlesinger *et al.* (1990) have emphasized the importance of nutrients in certain arid systems and have suggested that vegetation clumps may play a central role in concentrating these nutrients. If this model holds true then one might expect to find that below-ground, root patterns do in fact mirror above-ground clumping patterns.

Given the profound implications that either of these two situations have in terms of our understanding of plant resource acquisition strategies, and in terms of resource heterogeneity I set to

explore this in representative examples of the Short and Medium Strandveld communities. My focus was on root biomass in general, rather than on species-specific patterns. There are two reasons for this. Firstly, the large element of chance in species associations in clumps does not suggest that rigid clump assembly rules are common (Chapter 3), and without evidence for these it is difficult to visualize how species-specific niche differentiation could be at work. Secondly, the fact that there is fairly limited vertical distribution of roots once again suggests little scope for niche differentiation.

Materials and Methods

In both communities I sampled 20 soil cores (7.5cm diameter x 30cm deep) each from under clump canopies and in the center of gaps. To avoid biases in locating these cores I sampled consecutive clumps and gaps along randomly positioned transects. I did however restrict my gap-coring to gaps with a diameter of at least 1m in the Short Strandveld and at least 2m in the Medium Strandveld. These gaps represent the upper 50% gap size category. Before taking the cores, the first cm or so of soil of soil was scraped away until the shallowest roots were exposed. The cores therefore represent the 1-31 cm rooting zone that contains the bulk of root biomass in both communities. Root biomass was separated from the soil using a combination of sieving and manual methods. Roots with a diameter greater than 2mm (considered structural) were separated from the finer material. All root material was oven dried at 60°C for 48 hours and then weighed. Since I were specifically interested in the within-community distribution of root biomass rather than in between community comparisons, I analyzed the data from the two communities (clump vs open) separately by means of t-tests.

Results

In the Medium Strandveld, there was no significant difference between the fine root biomass under clumps and in the open ($p=0.372$). In contrast, the coarse (or structural) root biomass was significantly greater under clumps than in the open ($p=0.028$, Figure 1). In the Short Strandveld the probability that the fine root biomass at the two positions was not significantly different fell just outside the 5% threshold ($p=0.053$) with the mean fine root biomass in the open being slightly greater than under clumps (Figure 1). There was however no evidence to suggest that the coarse root mass differed with position ($p=0.419$).

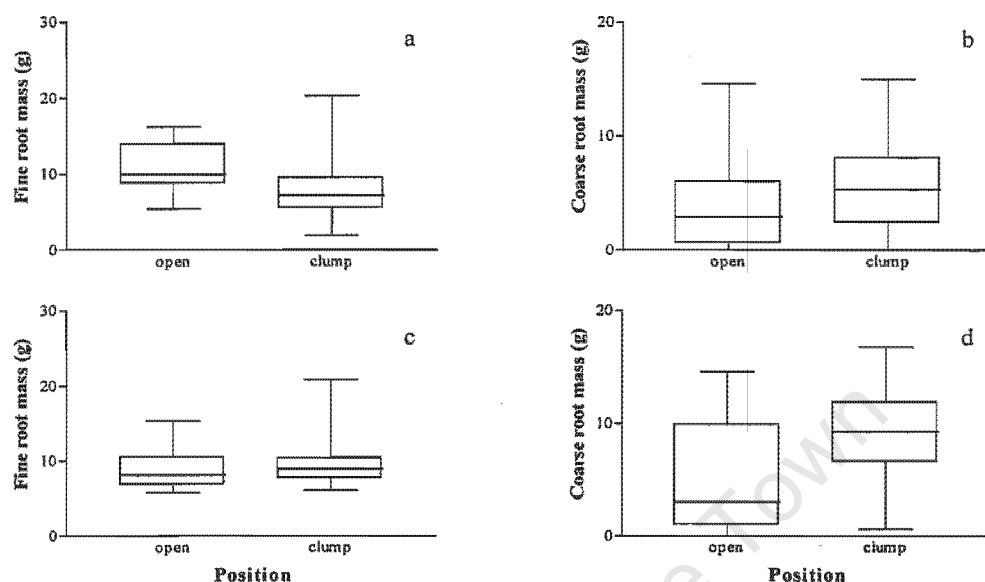


Figure 1. Box and whisker plots of biomass under clumps and in the open. Figures a. and b. are the fine and coarse biomass components respectively in Short Strandveld community while c. and d. are the fine and coarse biomass components respectively in Medium Strandveld community.

Discussion

The results indicate that below-ground biomass in these communities is far more regularly distributed than above-ground biomass. The only exception to this is in the case of structural roots in the Medium Strandveld community, and even here, we do not see the clear two-phase mosaic that has been described above-ground (Chapter 1). Interpreted in the most traditional sense, regular spatial patterns have usually been used to infer the existence of competition (Ludwig & Reynolds 1988), and I believe this to be a likely explanation in the Strandveld communities. This competition based interpretation is supported, in the case of the Medium Strandveld at least, by the results in Chapter 5 where plants of several important species that were isolated from their clumps exhibit higher (more positive) water potentials than equivalent individuals in clumps. From Chapter 5 it would also appear that these species are able to osmotically adjust to mitigate this competitive effect, and I believe that the regular spatial arrangement of roots reflects yet another strategy to minimize the effects of

competition for water. From this perspective the plants in these communities appear to exhibit at least partial "compensatory root growth" (Brisson & Reynolds 1994). The evidence once again points to the fact that plants in these communities are shaped by the trade off between associational defense advantages associated with existing in clumps and the inevitable competition for water that this association brings.

In addition, the apparently regular distribution of root biomass compliments the findings of Stock *et al.* (1999) which suggest that fertile islands associated with vegetation clumps are of little consequence in these communities. While it is possible to argue that Stock *et al.*'s (1999) conclusions are based on an anthropocentric interpretation which is conditional on our ability to detect conditions to which plants respond, the findings in this chapter suggest that even if there is nutritional enrichment under clumps, plants do not appear to respond to this. In fact in the case of the Short Strandveld it would appear that plants might even favor having their roots in the open. From this perspective, these communities seem to differ fundamentally from several other arid systems (Schlesinger *et al.*, 1990). One possible explanation for this difference is that the rapid turnover of plants that has been reported both in this thesis and elsewhere (Jürgens *et al.* 1999) in these Namaqualand communities precludes the development of foci of enrichment.

What my results do not illuminate is whether there is any evidence for niche differentiation below-ground. As I have already argued, circumstantial evidence in terms of the species make-up of clumps and rooting depths suggests that this may not be the case. However, this argument remains to be convincingly supported by detailed below-ground excavations.

To conclude this short chapter, the fact that the spatial distribution of roots in these two Strandveld communities appears to be far more regular than the highly clumped shoot distribution suggests that the below-ground growth behavior is shaped by competition rather than facilitation. This result together with our previous findings based on above-ground patterns clearly points to the importance of the trade-off between positive and negative interactions in shaping these desert plant communities.

References

- Beukman, R.P. 1991. *The role of nurse plants in the vegetation dynamics of the succulent Karoo*. MSc thesis, University of Cape Town, South Africa.
- Breshears, D.D., Nyhan, J.W., Heil, C.E. & Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Science* 159(6):1010-1017.

- Briones, O., Montaña, C. & Ezcurra, E. 1996. Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution. *Journal of Vegetation Science* 7:453-460.
- Brisson, J., & Reynolds, J.F. 1994. The effects of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. *Ecology* 75(6):1693-1702.
- Casper, B.B. & Jackson, R.B. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28:545-570.
- Cody, M.L. 1986. Structural niches in plant communities. In: Diamond, J. & Case, T.J. (eds), *Community Ecology*. Harper & Row Publications, New York. pp. 381-405.
- Desmet, P.G. and Cowling, R.M. 1999. 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. pp.
- Esler, K.J. & Rundel, P.W. Comparative patterns of phenology and growth from diversity in two winter rainfall deserts: the Succulent Karoo and the Mojave Desert ecosystems. *Plant Ecology*. 142(1-2):97-104.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid systems. *Annual Review of Ecology and Systematics* 17:89-110.
- Heitschmidt, R.K., Ansley, R.J., Bowhower, S.L., Jacoby, P.W., & Price, D.L. 1988. Some observations from the excavation of honey mesquite root systems. *Journal of Range Management* 41(3):227-231.
- Hook, P.B., Lauenroth, W.K. & Burke, I.C. 1994. Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration in gaps. *Journal of Ecology* 82:485-494.
- Jürgens, N., Gotzmann, I.H. & Cowling, R.M. 1999. Remarkable medium-term dynamics of leaf succulent Mesembryanthemaceae shrubs in the winter-rainfall desert of northwestern Namaqualand, South Africa. *Plant Ecology*. 142(1-2):87-96.
- Ludwig, J.A. & Reynolds, J.F. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley and Sons, New York.
- Nobel, P.S. & Linton, M.J. 1997. Frequencies, microclimate and root properties for three codominant perennials in the northwestern Sonoran Desert on north- vs. South-facing slopes. *Annals of Botany* 80:731-739.
- Phillips, D.L. & MacMahon, J.A.. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69:97-115.

- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247:1043-1048.
- Schulze, E.-D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J.R. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108:503-511.
- Scott, J.T. & van Breda, N.G. 1937. Preliminary studies on the root system of *Galenia africana* on the Worcester veld reserve. *South African Journal of Science* 34:268-274.
- Stock, W.D., Dlamini, T. & Cowling, R.M. 1999. Plant-induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecology* 142(1-2):161-167.
- Sun, G., Coffin, D.P. & Lauenroth, W.K. 1997. Comparison of root distributions of species in North - American grasslands using GIS. *Journal of Vegetation Science* 8:587-596.

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Chapter 7:

GENERAL CONCLUSIONS

In Chapter 1 I introduced a conceptual model proposed by Cowling *et al.* (1999) to explain the unique species richness of Namaqualand communities. I now return to this model armed with the major findings that have emerged from my work in the Short and Medium Strandveld communities (Figure 1). Very early on in the thesis (Chapter 2) it became evident that the overwhelming above-ground structural feature of these particular Namaqualand communities (as is the case in many other arid systems [Aguir & Sala 1999]) was that the bulk of the perennial species occur in multi-species vegetation clumps. My initial explanation for this clumping was that it reflects a positive feedback between physical benefits associated with microhabitat modification (“ecosystem engineering”) and mutual protection, and the dominant seed dispersal strategies.

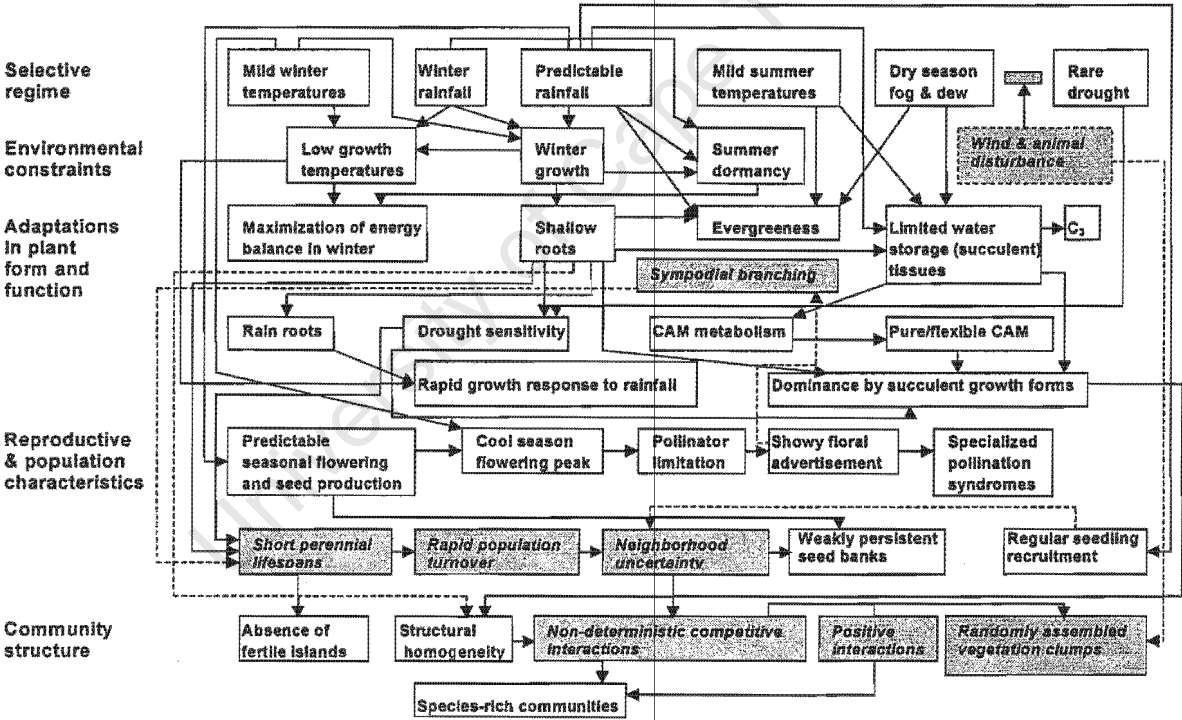


Figure 1. The Cowling *et al.* (1999) model modified in light of the major findings of this thesis. Boxes that have been added or updated are shaded while updated linkages are dotted.

Later on in the thesis, however, it became clear that this interpretation was perhaps somewhat simplistic. For instance, in contrast with the situation above-ground, it would appear that the spatial distribution of below-ground biomass in these communities is fairly even (Chapter 6). This

observation suggests that the above- and below-ground selective regimes to which individuals are exposed differ substantially. With hindsight and with reference to the literature (Cody 1986) this makes sense. Above-ground we might expect the harsh physical environment to exert an overriding effect, driving plants into vegetation clumps where they derive some mutual protection (as initially speculated). Below-ground on the other hand, competition between individuals for water may be the major force structuring communities.

This notion of net interactions (competition on the one hand and facilitation on the other) is borne out (in the case of the Medium Strandveld at least), in the results of the removal experiment described in Chapter 5. Here, the effects on the measured variates of isolating adult individuals of certain species reflected the full spectrum of interactions: negative in the case of water potentials in some species; neutral in the case of leaf water contents and growth; and positive in the case of physical damage. The finding that the major benefit that adult plants experience as a result of clumping appears to be physical protection against wind damage and browsing was one not anticipated by the Cowling *et al.* (1999) model. Another very interesting observation that emerged from this experimental work (Chapter 5) was that, in those species where the plant water potentials suggested competition, leaf water contents did not indicate the same effect. The implication of this is that these species are in some way able to osmotically compensate for competition. Interpreted in this light, the regular distribution of roots represents yet another form of compensation.

Thus, in as much as the Strandveld communities represent the behavior of Namaqualand communities as a whole, we can see Cowling *et al.* (1999) were correct in suggesting that these communities are characterized by "weak competition" and "positive interactions". At this stage though, it is important to draw the distinction between the interactions of individuals and the interactions of species. While evidence for the former is common in the Strandveld communities, there is very little to suggest that interactions between particular species result in any deterministic outcome. This is clearly indicated by the large element of chance involved in species composition of vegetation clumps (Chapter 3). It is further reinforced by the apparent weakness of relationships between the size of individuals and the collective size of their neighbors, and between the probability of individuals dying and the size of their neighbors (Chapter 4). Taken together with the fact that these communities have all the necessary "raw materials" (in the form of temporal and spatial heterogeneity) for non-equilibrium conditions to persist, there is strong evidence that the outcome of an interaction between individuals of two species may be largely governed by stochastic phenomena. This has profound implications, not least of which is the argument that "species in these systems coexist not in spite of, but because of being functionally equivalent generalists" (Hubbell & Foster 1986). The reference cited here (Hubbell & Foster 1986) is particularly pertinent. The theoretical work conducted by these

authors has largely been based on their empirical findings in diverse tropical forests. Stochastic theories have also been invoked to explain the coexistence of species in a shared niche in the diverse Cape Fynbos (Laurie *et al.* 1997). It is tantalizing to speculate that stochasticity may be central to the coexistence of species in all three of these unusually diverse systems. Returning to the Namaqualand model (Figure 1), whether the selective regime offered adequately explains the evolution of this non-equilibrium characteristic is open to debate. If however, these other diverse systems do in fact share this characteristic, it may prove very insightful to search for common features of the selective regimes in these systems. But that is another thesis.

Summing up then the two major findings of this thesis, we see that while the spatial distribution of biomass in Namaqualand Strandveld communities appears to be shaped by a combination of facilitation and competition between individuals, these interactions seem to have little bearing on whether or not any two species can co-exist. In addition to these findings, several unanswered questions emerge. For a start, while our results indicate that most recruitment in Strandveld communities occurs under vegetation clumps, nothing is known about the mechanics of this. My suggestion that this is facilitated by seed dispersal strategies remains speculation. Nothing is known about the spatial or temporal structure of the seed banks or about the physical conditions to which seedlings are exposed. In terms of established plants, while I argue on the grounds of the shallow rooting depths, that there is limited scope for below-ground niche differentiation between species, there is as yet no real empirical evidence to support this.

In addition to these obvious emergent questions, both this thesis and the Cowling model can be accused of ignoring the biggest contemporary source of disturbance and arguably the single most important suite of selective forces that the Namaqualand Strandveld is likely to be exposed to in the future - humankind. In many areas, mining has already transformed the landscape. Many of these mines are today reaching the end of their lives and rehabilitation is becoming an important issue (see Appendix 2). Also, what to do with this land in the socio-economic vacuum left behind by the end of mining is a pressing question. At a global scale, what are the impacts of climate change and elevated ultraviolet radiation likely to be on this system? This emphasis in closing on the human dimension of the system represents a combination of an evolution in my personal interests, and a growing recognition among ecologists that ecology in the absence of the human component is only part of the picture. Thus, while I believe that this thesis provides many valuable insights into the biological fundamentals of the system, and even introduces a number of new questions along a similar vein, I feel that integrating the human component is the logical next step. This is certainly the key to the future.

References

- Aguiar, M.R. & Sala, O.E. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14(7):273-277.
- Cody, M.L. 1986. Structural niches in plant communities. In: Diamond, J. & Case, T.J. (eds), *Community Ecology*. Harper & Row Publications, New York. pp. 381-405
- Cowling, R.M., Esler, K.J. & Rundel, P.W. 1999. Namaqualand, South Africa - an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology* 142(1-2):3-21.
- Hubbell, S.P. & Foster R.B. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond, J. & Case, T.J. (eds), *Community Ecology*. Harper & Row Publications, New York. pp. 381-405.
- Laurie, H., Mustart, P.J. & Cowling, R.M. 1997. A shared niche? The case of the species pair *Protea obtusifolia* - *Leucadendron meridianum*. *Oikos* 79:127-136.

Appendix 1:

DERIVATION OF THE C-FUNCTION

The C -function is calculated as the coefficient of variation (CV) between the densities of individuals (corrected for edge effects) from one population within a certain radius (t) of individuals in another population. From Steele & Torrie (1980) the CV is computed as (E1):

$$CV = \frac{100 \cdot s}{\bar{Y}}$$

where s is the sample standard deviation and $\bar{Y}$ is the sample mean. The sample mean in this case is the average number of individuals from one population ($P2$) within a defined area of individuals from another population ($P1$) and can be estimated as (E2):

$$\bar{Y} = \frac{n_2}{A}$$

where n_2 is the total number of individuals in population $P2$ in the mapped plot and A is the ratio of the area of the mapped plot to the area of the circle defined by the radius t .

The numbers of individuals from population $P2$ within the radius t of individuals of population $P1$ [$D_{12}(t)$] can be calculated as follows (E3):

$$D_{12}(t) = \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij})$$

where u_{ij} is the distance between the i th plant in population $P1$ and the j th plant in population $P2$; $I_t(u)$ is defined to be 1 if $t \geq u$ or 0 otherwise (i.e. a counter variable); and w_{ij} is the weighting factor described by Diggle (1983) to correct for edge effects (the proportion of the circumference of the circle with radius u_{ij} and centered on the point i and passing through j that lies within the plot boundaries).

The standard deviation of these counts can then be calculated as (E4):

$$s = \sqrt{\left(\sum_{i=1}^{n_1} (D_{12}(t))^2 - \left(\sum_{i=1}^{n_1} D_{12}(t) \right)^2 / n_1 \right) / (n_1 - 1)}$$

where n_1 is the total number of individuals in population $P1$.

Thus by substituting equation E3 into equation E4, and then substituting this, together with equation E2 into equation E1 we get the following equation for the C -function:

$$C_{12}(t) = \frac{100 \cdot A \cdot \sqrt{\left(\sum_{i=1}^{n_1} \left(\sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 - \left(\sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) \right)^2 / n_1 \right) / (n_1 - 1)}}{n_2}$$

Referenes

- Diggle, P.J. 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London.
- Steele, R.G.D. & Torrie, J.H. 1980. *Principles and Procedures of Statistics. A Biometrical Approach*. (2nd Ed.) McGraw-Hill International Editions, Singapore.

