

A Study on an Altitudinal Gradient Investigating the  
Potential Effects of Climate Change on Fynbos and the  
Fynbos-Succulent Karoo Boundary

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## Declaration

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I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature .....

Date .....

## SUMMARY

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Global circulation models predict that the Cape Floristic Region (CFR), a biodiversity hotspot, in the near future will be subjected to rising temperatures and widespread droughts as a result of rising atmospheric CO<sub>2</sub> causing global climate change. It is predicted that climate change will lead to a southward shift of the Succulent Karoo, a neighbouring more drought tolerant biome, and a possible invasion of Fynbos, the main vegetation type of the CFR, by succulent species. In this research project, the effects of climate change on Fynbos, and the likelihood of Succulent Karoo invading Fynbos are assessed by means of various monitoring and experimental studies on an altitudinal gradient spanning a natural transition between fynbos and succulent karoo vegetation. An analysis of plant species diversity and turnover on the gradient revealed high species turnover between succulent karoo and the rest of the gradient, associated with a boundary between two soil types: shale (associated with succulent karoo) and sandstone (associated with fynbos). Phenological monitoring of fynbos species across the gradient showed how growth of fynbos species is affected negatively by high temperatures, and that low but regular rainfall is required to sustain growth during the dry Mediterranean summer. Retrospective growth analysis of Proteaceae species pairs with contrasting range sizes revealed that small geographic ranges do not signify low tolerance of climate variation, but rather that faster growing species are more sensitive to interannual climate variation than slow growing species. Exposing fynbos species to experimental drought confirmed that faster growing species will be more severely affected by climate change than slow growing species with conservative water use strategies. This experiment also confirmed the importance of rainfall reliability for growth in fynbos species when a naturally occurring prolonged dry period affected some species more severely than the drought treatment of an average reduction in rainfall. A reciprocal transplant experiment exposed fynbos seedlings to both warmer and drier conditions when they were planted outside of their natural ranges in the succulent karoo. Soil type as a barrier to invasion of fynbos by succulent karoo was also tested. Soil type was found to be not limiting to succulent karoo species and competition and disturbance was revealed to be more important in determining the fynbos-succulent karoo boundary than climate. It was concluded that productivity in fynbos will be adversely affected by rising temperatures and that differing responses to climate change between slow and fast growing species will lead to shifts in dominance among species, and consequently altered community structures and vegetation dynamics. Fires are likely to facilitate invasions of marginal habitats by succulent karoo because of sensitivity of fynbos regeneration stages to high temperatures and drought.

## OPSOMMING

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Klimaatsmodelle dui aan dat, as gevolg van stygende vlakke van koolstofdiksied in die atmosfeer, die klimaat van die Wes Kaapse Fynbos Blommeryk in die toekoms drasties sal verander. Daar word verwag dat stygende temperature en dalende reënval klimaatstoestande tot gevolg sal bring wat vergelykbaar is met die klimaat wat tans met die sukkulente karoo, 'n droë streek noord van die Fynbos Blommeryk, geassosieer word. Dit laat die vraag ontstaan of die unieke diverse plantegroei van groot gedeeltes van die Fynbos Blommeryk moontlik sal verdwyn, en dat dié areas moontlik deur sukkulente karoo ingeneem sal word. In hierdie studie is moontlike verskuiwings in die verspreiding van fynbos en sukkulente karoo as gevolg van klimaatsveranderinge deur middel van eksperimentele studies ondersoek. Die eksperimente is onder veldtoestande op 'n noordelike berghang in die Riviersonderend Berge gedoen, waar natuurlike variasie in temperatuur en reënval geassosieer met variasie in hoogte bo seevlak ideale geleenthede bied vir 'n ondersoek na die klimaats- en ander faktore wat plantegroei verspreidings beheer. Die studie area is ook so geleë dat dit 'n natuurlike oorgang tussen fynbos en sukkulente karoo verteenwoordig. Eerstens is patrone in plant spesies diversiteit en verspreiding oor die klimaatsgradiënt geanaliseer. Daar is gevind dat daar groot verskille in spesiesamestelling tussen die fynbos en sukkulente plantegroei tipes, wat ook met verskillende grondtipes geassosieer is, bestaan. Verder is die groei en blomfases van fynbos spesies wat wydverspreid oor die gradient voorkom vir twee jaar gemonitor, en die data is in verband gebring met klimaatstoestande wat terselfdertyd by die studie area gemeet is. Daar is gevind dat fynbos spesies, wat gedurende die droë somermaande groei, sensitief is vir hoë temperature, en dat gereelde lae reënval gedurende die somermaande vereis word om groei aan die gang te hou. Groeipatrone in volwasse Proteaceae struik is ook retrospektief geanaliseer vir moontlike verbande tussen jaarlikse variasie in groei en klimaatstoestande. Daar is gevind dat spesies met kleiner verspreidingsareas nie noodwendig meer sensitief vir klimaatsveranderinge is nie, en dat die gemiddelde groeitempos van spesies moontlik 'n goeie aanduiding van klimaat sensitiwiteit is. In nog 'n eksperiment, waar reënval deur middel van reënskuilings beheer is, is ook gevind dat spesies met hoër groeitempos en minder konserwatiewe water verbruik strategieë erger deur droogtes geraak word. 'n Natuurlike droogte wat gedurende die eksperiment plaasgevind het, het daartoe gelei dat die verdere afleiding ook gemaak kon word dat die betroubaarheid van reënval dalk selfs meer belangrik is as die hoeveelheid reën wat val

in die negatiewe impak wat droogtes op plante kan hê. Die potensiële beperking wat grondtipe op die verskuiwing van plantegroei tipes kan plaas is ook eksperimenteel ondersoek. Saailinge van fynbos en sukkulente karoo spesies is regoor die klimaatsgradiënt in verskillende grondtipes uitgeplant, sodat saailinge aan klimaat- sowel as grondtoestande van buite hulle natuurlike verspreidings blootgestel is. Daar is gevind dat sukkulente spesies nie deur grond of klimaat beperk word nie, maar fynbos spesies wel, wat die moontlikheid dat sukkulente karoo fynbos wel as gevolg van klimaatsveranderinge sal kan oorneem bevestig. Daar word egter vermoed dat die brande wat gereeld in fynbos voorkom tans 'n groot rol speel om die grens tussen fynbos en sukkulente karoo in stand te hou, aangesien sukkulente nie vir gereelde brande aangepas is nie. Maar brande kan moontlik ook 'n sleutelrol speel in die verskuiwing van plantegroei tipes in die toekoms: indien fynbos produktiwiteit in terme van groei en saadproduksie negatief deur klimaatsveranderinge beïnvloed word, kan droogtes wat op brande volg moontlik daartoe lei dat die natuurlike fynbos plantegroei nie weer herstel nie. Sulke areas kan dan moontlik deur meer droogtebestande spesies, soos sukkulente, gekoloniseer word.

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## INTRODUCTION

*“The most serious threat to the diversity of the Cape Flora [under climate change] is its complete replacement by adjoining biomes.”*  
(Bond 1997a)

The largest part of the overwhelming diversity and exceptionally high levels of endemism of the Cape Floristic Region is contained in the evergreen shrublands of the Fynbos Biome. At least 7000 of the 8700 vascular plant species found in the Cape Floristic Region belong to the Fynbos Biome (Rebelo 1998). An estimated 68% of species are endemic to the region, and 80% of the endemics are fynbos species (Rebelo 1998). All of this unique diversity is confined to an area of roughly 90 000 km<sup>2</sup>, which makes the Cape Floristic Region, situated at the extreme southwestern tip of South Africa, the smallest floral kingdom in the world (Bond 1997a).

The Fynbos Biome, which includes two main vegetation types, fynbos and renosterveld, has long been threatened by agriculture, forestry, alien invasive species and urban expansion (Hilton-Taylor and Le Roux 1989). Nevertheless, much has been done to conserve and protect the Fynbos Biome. It is one of only three southern African biomes with more than 10% of its area conserved, and 10 of its 19 centres of endemism have more than half of their total area formally conserved (Rebelo 1997).

There is, however, one threat to diversity worldwide against which not even conservation areas are immune (Hannah et al. 2005): Global Climate Change could lead to immense losses of diversity in the Fynbos Biome. In a worst-case scenario, Bond (1997a) predicts that the tiny, island-like Cape Flora could possibly be completely replaced by adjoining biomes.

Within the Cape Floristic Region, the Fynbos Biome is bordered by five other biomes. On the dry lowlands of the north and northwest, and in the dry interior valleys between the Riviersonderend-Langeberg-Outeniqua and the Hexrivier-Witteberg-Swartberg mountain ranges, Fynbos is bordered by an arid shrubland, the Succulent Karoo. In the east, where rainfall patterns shift towards a larger proportion of summer rain, Grassland and subtropical Thicket communities adjoin fynbos, while towards the northeastern interior, the fynbos boundary is with another arid shrubland, the great Nama Karoo. On the south coast, and in many moist mountain ravines

protected from fire, Forest replaces the open shrubland of the Fynbos Biome (Biome names according to Low & Rebelo 1998).

Schulze and Perks (2000) used the HadCM2 global circulation model to simulate potential climate conditions over South Africa for 2050, should current trends in increases in atmospheric CO<sub>2</sub> not be halted. Modelling results indicated that much of the Cape Floristic Region will be subjected to widespread droughts, with up to 25% reduction in mean annual precipitation, while a slight increase of 0.5-1°C in mean annual temperature is expected. Further modelling results also showed that extensive areas of the northern ranges of the Fynbos Biome will in future experience warmer and drier climate conditions similar to that which is currently associated with the Succulent Karoo Biome (Midgley et al. 2003). This raises two important questions:

1. How will warmer and drier conditions affect fynbos?
2. Will fynbos disappear from areas predicted to experience succulent karoo associated climate, and will these areas be subsequently invaded by succulent karoo vegetation?

In order to assess the seriousness of the potential threat of invasion of fynbos by succulent karoo, it is essential that the determinants of biome boundaries are well understood. This is not an easy task, as many and diverse abiotic and biotic factors could be involved in shaping the geographical distributions of individual species, vegetation types and biomes (Brown et al. 1996). The Fynbos Biome has strong climatic limitations associated with its distribution (Rutherford 1997): fynbos does not occur where annual rainfall is below 200 mm (Rebelo 1998), and is only found in areas where more than 40% of annual rainfall occurs during the winter months (Cowling et al. 1997). Disturbance such as fire is considered as one of the main sculptors of vegetation patterns in southern Africa (Bond 1997b). Fire is the main driving force of ecological processes in fynbos, and appears to be an important factor in preventing other biomes from intruding into fynbos (Masson and Moll 1987, Cowling and Pierce 1988, Manders et al. 1992, Bond 1997a).

Fynbos is also strongly associated with highly leached, extreme nutrient poor soils derived from quartzites and sandstone of the Cape Supergroup, and transitions to other vegetation types often occur with borders between sandy, nutrient poor soils and less sandy and more fertile soils, such as those derived from shales (Cowling and Holmes 1992). Two studies have thus far attempted to assess the relative importance of climate and soil type as the determinants of the

boundary between fynbos and succulent karoo. Euston-Brown (1995) investigated edaphic factors and climate as determinants of the boundary between fynbos and non-fynbos vegetation types in a reciprocal transplant experiment in the Eastern Cape. He concluded that rainfall is the most important factor controlling vegetation distribution, with soil type as a secondary determinant, because transplanted fynbos seedlings survived on finer textured shale derived soils at high rainfall sites, but not in more arid sites. Lechmere-Oertel and Cowling (2001) found similar results in a greenhouse-based study. They also concluded that succulent karoo is not limited by soil type or moisture regime, but possibly by competition and/or fire.

It seems therefore, that fynbos habitats could be invaded by succulent karoo, but only if fynbos as a vegetation type is so affected by climate change that ecosystem processes such as fire regimes and competitive interactions are severely altered. As early as the 1990's Bond and Richardson (1990) urged that the use of global circulation models for predicting vegetation change should be supported by population level studies on the effects of climate change on productivity of various growth forms and on reproductive biology. In recent studies Dunne et al. (2003, 2004) have showed the importance of field-based research combining experimental and natural environmental gradient monitoring in understanding complex ecosystem responses to global warming. A number of other studies have shown how climatic variation associated with changing altitude along elevational gradients can be used to simulate climate change scenarios for performing field based experiments, and monitoring plant responses (Chapin et al. 1995, Levesque et al. 1997, Bruelheide 2003, Link et al. 2003, Penuelas et al. 2004).

The Cape Floristic Region is characterised by many steep environmental gradients, with high species turnover over short geographical distances (Oliver et al. 1983, Campbell and Cowling 1985, Cowling and Holmes 1992). On low rainfall, north-facing mountain slopes of the southwestern interior, soil type and rainfall gradients lead to the intersection of fynbos, generally found at higher altitudes on sandy soils, with succulent karoo, which is associated with shale derived soils generally confined to the dry lower foothills and valleys (Campbell and Cowling 1985, Campbell 1986). These gradients provide the ideal setting to test the potential effects of climate change on fynbos, as well as the fynbos-succulent karoo boundary. Not only does it allow the investigation of soil types and climate as determinants of species and biome boundaries, but research into historical vegetation shifts due to past changes in climate has shown that transitional habitats such as these are the areas where changes are likely to be observed first (Cole 1985, Jackson and Overpeck 2000, Allen 2003). Due to biological inertia,

vegetation in most favourable habitats is likely to show lagged responses to climate change (Camill and Clark 2000, Von Holle et al. 2003), while marginal habitats, such as vegetation boundaries, are considered the most likely areas where climatic change could lead to dramatic shifts in vegetation and the development of novel ecosystems (Chapin and Starfield 1997, Allen and Breshears 1998, Camill and Clark 2000). Kupfer and Cairns (1996), and Allen and Breshears (1998) have indicated through studies on ecotones how important such sites are as early indicators of climate change responses.

## RESEARCH OBJECTIVES AND THESIS STRUCTURE

The objectives of this study are therefore, to address the two questions mentioned earlier, namely how will fynbos be affected by climate change, and what will the effects of climate change be on the fynbos-succulent karoo boundary, through experimental and monitoring field studies on an environmental gradient.

The study site, an elevational gradient on the north-facing slope of Jonaskop in the Riviersonderend Mountain range, Western Cape, is described in CHAPTER ONE. The study site, which consists of a natural transition between fynbos and succulent karoo, is characterised in terms of plant diversity and turnover, soil chemistry and climate variation across the gradient.

The effects of natural variation in temperature and rainfall on the gradient on growth and flowering phenology of selected common fynbos species of different growth forms are described in CHAPTER TWO. Information on the timing and duration of phenophases gathered during the two year monitoring period is used as baseline information to interpret results of further chapters.

The effects of interannual variation in temperature and rainfall on growth and flowering in selected Proteaceae species are investigated in CHAPTER THREE. Retrospective growth analyses were performed on two species pairs of *Leucadendron* and *Protea*, with contrasting natural range sizes.

The effects of a 30% reduction in mean annual rainfall on the growth of eight selected fynbos species is reported in CHAPTER FOUR. Three year old, newly established plants were subjected to experimental drought conditions under specifically designed rainout shelters. Growth responses in drought treated plants were compared with growth of control plants outside

the shelters. The selected species were analysed and characterised according to functional traits, in order to assess the potential of functional traits as indicators of drought sensitivity in fynbos species.

The relative importance of climate and soil type as determinants of the fynbos-succulent karoo boundary are assessed through a reciprocal transplant experiment in CHAPTER FIVE. Seedlings of selected fynbos and karoo species were planted into containers of either shale or sandstone derived soils at selected points across the gradient. Through assessing the responses of fynbos seedlings planted into the karoo environment, the potential effects of a succulent karoo associated climate on the growth and survival of fynbos seedlings could be determined.

The results of the previous chapters and their relevance in addressing the research objectives are synthesized in the concluding CHAPTER SIX.

#### Notes to the text:

1. Chapters 1 to 5 are written as separate research papers ready for submission for publication in peer reviewed journals. Therefore some degree of repetition in the text is unavoidable. Chapters are written in the format prescribed by the journal *Ecology*.
2. Restionaceae, an important component of fynbos vegetation, has not been included in the studies reported in Chapters 2-5. This is because the restioid growth form does not lend itself well to the growth monitoring technique used in this study. An attempt was made to include a restio species in the reciprocal transplant experiment (Chapter 5), but germination was unsuccessful.
3. Taxonomy follows Germishuizen and Meyer (2003), except for Proteaceae, which is according to Rebelo (2001). A plant species checklist for Jonaskop is included as an appendix (Appendix II).

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# DIVERSITY AND SPECIES TURNOVER ON A CLIMATIC GRADIENT IN THE RIVIERSONDEREND MOUNTAINS, WESTERN CAPE

*Abstract.* A temperature and moisture gradient on the north-facing slope of Jonaskop in the Rivieronderend Mountains, Western Cape has been selected as an important site for monitoring the effects of climate change on fynbos and the fynbos-succulent karoo boundary. This study reports the results of three years of climate monitoring at selected points along the gradient, as well as a description of plant diversity patterns, growth form composition and species turnover across the gradient. The aim of this study is to provide data for a focused monitoring strategy for the early detection of climate change related shifts in species' ranges, as well as gaining a better understanding of the role of climate in shaping species' distributions and other ecosystem processes.

## INTRODUCTION

The vegetation of mountain ranges of the southwestern Cape is characterized by gradients of high species turnover. These gradients are associated with increasing precipitation and lower temperatures with increasing elevation, as well as edaphic diversity (Goldblatt 1997). The vegetation of Cape mountain ranges is dominated by fynbos, the main vegetation type of the Cape Floristic Region. However, on north facing slopes towards the Western Cape interior, fynbos is replaced by succulent karoo, an arid shrubland, at lower elevations (Cowling and Holmes 1992).

Ecotones, or areas of transition between distinct biomes or vegetation types, have been pointed out as important areas for monitoring the effects of global climate change (Kupfer and Cairns 1996). Modelling of future climate scenarios for the western Cape indicate that large areas of fynbos will be subjected to warmer and drier climate conditions similar to what is currently associated with succulent karoo, and that vegetation shifts might take place resulting in a loss of distribution area of fynbos due to a southward shift of succulent karoo (Rutherford et al. 1999). Therefore vegetation gradients incorporating transitions between fynbos and succulent karoo are important areas to monitor for the early detection of climate change induced biome shifts.

The elevational gradient on the north facing slope of Jonaskop, one of the highest peaks in the Riviersonderend Mountains, Western Cape, has been identified as a key site for monitoring the effects of climate change on fynbos and the fynbos-succulent karoo boundary. On the northern foothills of Jonaskop, fynbos vegetation type FFs13, North Sonderend Sandstone Fynbos intersect with succulent karoo vegetation type SKv7, Robertson Karoo (Mucina et al. 2006). The Jonaskop gradient has been described in terms of vegetation biomass turnover (Rutherford 1978), but no formal description of species diversity on the gradient has been done to date. Other studies conducted at the site include investigations into *Protea* species and rodent pollinator interactions (Fleming and Nicolson 2002a, Fleming and Nicolson 2002b), leaf functional classification of a number of species in a Mediterranean context (Vile et al. 2005), and a comparative study between nectar qualities of Cape and Australian Proteaceae (Nicolson and van Wyk 1998). These studies mark Jonaskop as an important site for ecological research that would benefit greatly from a formal description of the biotic and abiotic environment.

The aim of this paper, therefore, is to describe the Jonaskop gradient in terms of species turnover, soil chemistry and climate and to serve as a source of reference for future monitoring.

## STUDY AREA

### *Location*

The Riviersonderend Mountains are situated on the western end of a chain of east-west trending mountain ranges at the southern edge of the Cape Fold Belt. Jonaskop (33°58'00 S 19°30'00 E, altitude 1646 m) is located within the Riviersonderend Mountain Catchment – a protected area which is managed by CapeNature as an important water supply to the Sonderend River below the southern slopes and the Breede River towards the north. The protected area is bordered by privately owned agricultural land. A service road leading up to a Sentech radio mast on the mountain summit provides access to the north facing slope of Jonaskop.

### *Topography, geology and soils*

The Jonaskop gradient spans roughly a change of 1200 m in elevation between foothills in the Breede River Valley and the Jonaskop peak. While the south facing slope of Jonaskop is extremely steep, the north facing slope rise somewhat less rapidly and reach a wide plateau in the middle of the gradient, at around 900 m a.s.l. Several drainage lines leading down from the

northern slope converge in the Sand River, which at around 400 m a.s.l. is the lowest point of the gradient. This small stream joins the Doorn River, a tributary of the Breede River, further down the valley. Beyond the stream bed the landscape rises again in a series of low hills.

Soils on the mountain are shallow and very rocky. The coarse grey sandy soils of the mountain slope are derived from quartzitic sandstone of the Table Mountain Series. At the foot of the mountain (below 600 m a.s.l.) soils are finer grained and less rocky. Here the geology is alternating bands of arenaceous shale and argillaceous sandstone from the Bokkeveld Series (Besaans 1966).

### *Vegetation*

Vegetation changes from succulent karoo at the very lowest elevations (around 500-600 m) through an ecotonal area with succulent as well as fynbos elements (roughly around 600-800 m), to fynbos from 800 m upwards. The boundary between the succulent karoo and ecotone coincides with the transition from shale derived to sandstone derived soils. Ecotonal and fynbos vegetation on either side of the road leading to the top of the mountain differs in fire history: one side burned fairly recently (2000), while on the other side mature vegetation has established after the last fire in 1992.

## METHODS

### *Climate monitoring*

Climate change monitoring and experimental studies have thus far been focused at six points along the length of the gradient (Figure 1). Weather stations (Watchdog Model 600 Weather Station 3325WD), recording air temperature, relative humidity, rainfall, soil moisture and wind speed and direction are placed at the top (1303 m), middle (953 m) and lowest (545 m) end of the gradient, while data loggers (Watchdog 450 Relative Humidity/Temperature Data Logger) record relative humidity, air temperature and soil moisture at the intermediate sites (1196 m, 1044 m, 744 m). Weather stations have been recording climate continuously since February 2002. Readings are taken automatically every 30 minutes. Climate data were analyzed to show patterns in temperature, rainfall and wind conditions across the gradient.

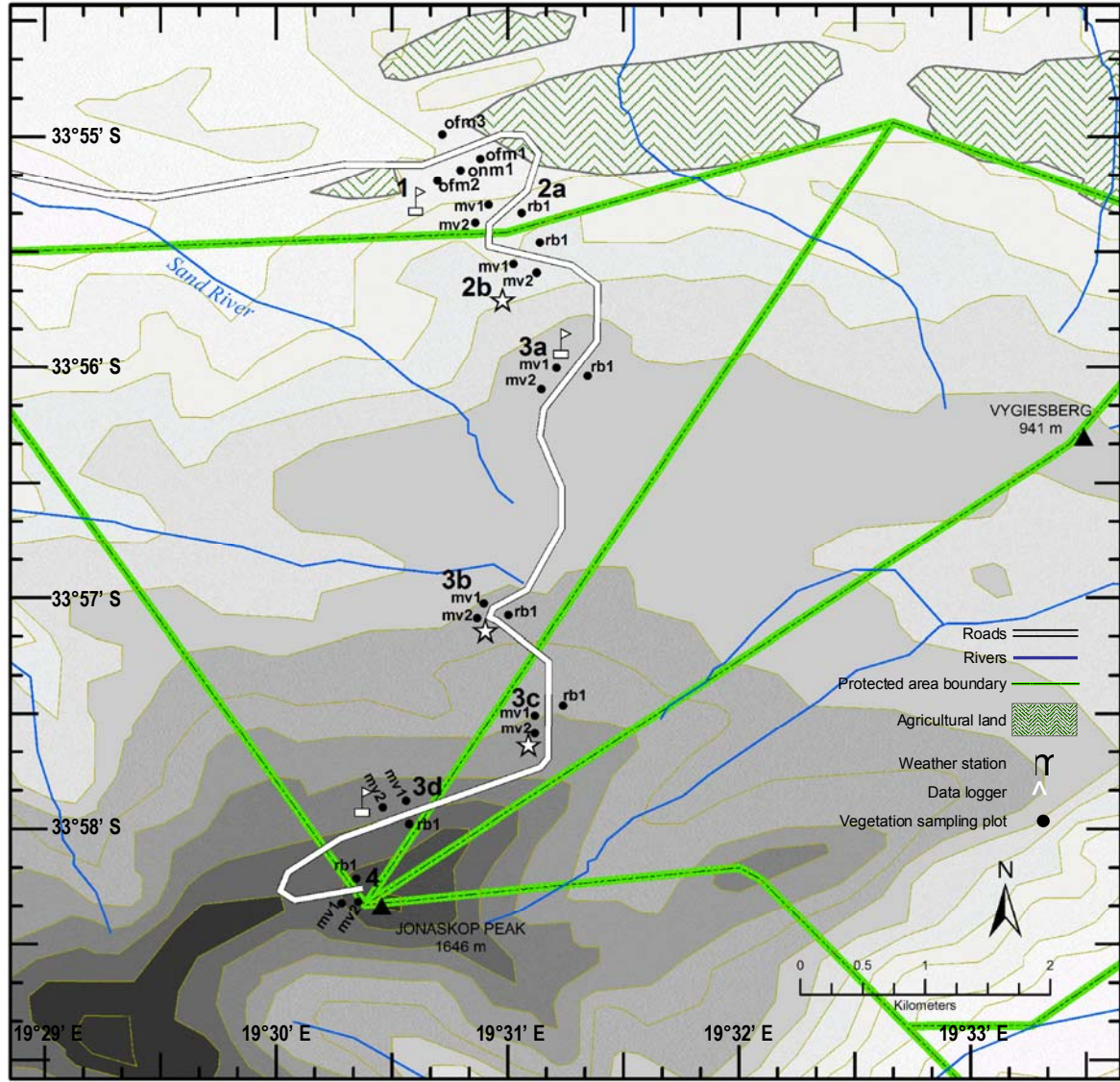


FIGURE 1. Topographical map of the study site indicating the location of weather stations, data loggers and vegetation sampling plots. Contours represent 100 m intervals. 1. Karoo site; 545 m. 2. Ecotone sites – 2a 690 m, 2b 744 m; 3. Fynbos sites – 3a 953 m, 3b 1044 m, 3c 1196 m, 3d 1303 m; 4. Summit site, 1576 m. Vegetation plot codes: onm – plot on mima-like mound, ofm – plot in karoo matrix vegetation, rb – plots in recently burnt fynbos/ecotone vegetation, mv – plots in mature fynbos/ecotone vegetation. GIS data provided by CapeNature, Department of Land Affairs: Surveys and Mapping and the Department of Agriculture.

### *Soil analysis*

Soil samples were taken at each of the monitoring sites along the gradient and analysed for P, Ca, Mg, K, Na, N and pH according to standard methods: To analyze for P, a 5g sample was added to 50 ml 1% citric acid solution. To an aliquot of the clear and colourless extract was added an acidified ammonium molybdate solution. The phosphomolybdate complex is then reduced with stannous chloride and the absorbance of the resulting blue colour is measured with

a spectrophotometer and compared with the absorbances obtained from standard phosphorus. To analyze for N, a known mass of soil is digested with sulphuric acid using selenium as a catalyst. The resultant ammonia are distilled into a saturated boric acid solution and titrated with standard acid. Macro elements (Ca, Mg, Na, K) were determined by measuring a 1 mol dm<sup>-3</sup> ammonium acetate extraction by atomic absorption against known standards.

#### *Field sampling methods*

For the vegetation analysis, two more sites were added to the existing climate monitoring sites: one in the ecotonal zone (690 m), and another one near the mountain summit (1576 m). Vegetation sampling was done in October and November 2003. Relevés of 10 x 10 m were used, with 2 relevés located in mature vegetation and one in recovering vegetation at each site. Species cover values were scored according to the Braun-Blanquet system (Braun-Blanquet 1928). At the succulent karoo site, at the lowest end of the gradient (545 m), a fourth relevé was added to include sampling of unique vegetation on nutrient enriched 'heuweltjies' or mima-like mounds (Esler and Cowling 1995).

Physical characteristics noted at each relevé include slope, aspect, percentage rock cover, soil type and soil depth. Soil depth was determined up to 0.5 m deep at 10 points at regular intervals across one diagonal of each relevé. Soil depth for each relevé was then expressed as a range from shallow to deepest, with depths of more than 0.5 m indicated by 0.5 m+.

#### *Data analysis*

Species data were assembled into a phytosociological table and sorted according to constancy and affinity to determine plant communities and their characteristic species. Braun-Blanquet scores were then converted to percentage cover values for the calculation of species diversity (See Table 1 for conversion values). The diversity of each relevé was calculated according to the Shannon-Wiener Index (Kent and Coker 1994) with the formula:

$$\text{Diversity } H' = -\sum_{i=1}^s p_i \ln p_i \quad (1)$$

where  $s$  is the number of species, and  $p_i$  is the proportion of the  $i$ -th species to the total vegetation cover. Diversity values of the relevés of each site were then averaged to arrive at a diversity estimate for each site. Within site comparisons of diversity between recently burned



and mature vegetation were also done for all sites except the karoo site (545 m), which did not burn.

TABLE 1. Conversion of Braun-Blanquet scores to percentage cover values.

Braun-Blanquet score	Converted % cover
R	1
+	1
1	3
2M	4
2A	8.5
2B	19
3	39
4	63
5	88

All sampled species were classified according to growth form. Growth forms were assigned according to a scheme adapted from Cowling et al. (1994), (Table 2). The contribution of each growth form to total vegetation cover in each relevé was calculated by summing converted percentage cover values of all species belonging to each growth form, and expressing it as a proportion of total vegetation cover. Site specific growth form composition was then calculated by averaging cover values of each site's relevés. Comparisons of growth form composition between recently burned and mature vegetation were done for all sites except the karoo site (545 m). Relevés of mature vegetation of all sites were lumped, and the average growth form composition was compared with the average composition of all recently burned relevés across the gradient.

Similarity of species composition of different sites were compared using Jaccard's coefficient (Kent and Coker 1994). The formula is:

$$S_j = \frac{a}{a+b+c} \quad (2)$$

where  $S_j$  is the Jaccard similarity coefficient,  $a$  is the number of species common to both sites compared,  $b$  is the remaining number of species present at the first site, and  $c$  is the remaining number of species present at the second site.  $S_j$  was multiplied by 100 to arrive at a percentage similarity. The average turnover rate across the gradient was determined according to the

methods of Itow (1991). Log percentage similarity between every pair of sites (on y-axis) was plotted against their difference in altitude (on x-axis). The slope of the regression line fitted is taken as the average turnover rate of species per 1 m altitudinal difference.

TABLE 2. Categorization of growth forms, adapted from Cowling et al. (1994).

Main groups	Code	Subgroups
Herbs	AH	Annual herb
	PH	Perennial herb
	HV	Herbaceous vine
Dwarf shrubs (< 0.25 m)	PHP	Perennial herb, parasite
	DES	Dwarf evergreen shrub
	DSP	Dwarf shrub, parasite
Low shrubs (0.25-1 m)	LES	Low evergreen shrub
	LSP	Low shrub, parasite
Mid-high shrubs (1-2 m)	MES	Mid-high evergreen shrub
Succulents	DSS	Dwarf succulent shrub, < 0.25 m
	LSS	Low succulent shrub, 0.25-1 m
	PHS	Perennial herb with succulent leaves
	SP	Succulent parasite
Geophytes	GEO	
Graminoids	GRA	Includes all grasses, sedges and restios

## RESULTS AND DISCUSSION

### *Temperature*

Temperatures are known to decrease with increasing altitude (Barry 1992), however, the rate at which temperatures decrease can vary spatially as well as seasonally (Rolland 2003). On Jonaskop, there is an average difference of 4.4°C between the highest (1303 m) and lowest site (545 m) on the gradient (Table 3). Temperatures generally decrease by 0.58°C with every 100 m altitude gained, as indicated by the slope of a regression line fitted to mean annual temperatures recorded at each of the monitoring sites (not shown). However, diurnal and seasonal temperature lapse rates on the mountain slope vary between -0.40°C.100 m<sup>-1</sup> for winter (April to September) minimum temperatures and -0.77°C.100 m<sup>-1</sup> for summer (October to March) maximum temperatures (Figure 2). This is consistent with patterns found in mountainous regions elsewhere (Rolland 2003 and references therein). Complex factors contribute to seasonal and diurnal variation in lapse rates. These include wind regime, cloud cover, amount of incoming

solar radiation and the moisture content of the air (Barry 1992) and it is therefore difficult to explain the variations observed on Jonaskop.

TABLE 3. Summary of mean annual temperatures (MAT), mean minimum temperatures of the coldest month (Tmin), mean maximum temperatures of the warmest month (Tmax) and mean annual precipitation recorded at different altitudes on the Jonaskop elevational gradient. % Winter indicates the proportion of the total MAP recorded during winter (April-September). nr = not recorded.

Altitude (m)	MAT (°C)	Tmin (°C)	Tmax (°C)	MAP (mm)	% Winter
545	16.5	6.9	30.2	315.4	62
744	15.7	6.7	29.3	nr	nr
953	13.6	3.6	27.4	411.3	66
1044	14.0	4.7	27.0	nr	nr
1196	12.9	4.1	25.2	nr	nr
1303	12.1	3.3	24.6	719.6	57

It should be noted that the middle site (953 m) is somewhat colder than the site directly above it (1044 m) (Table 3). This effect is particularly strong at night during winter (Figure 2), when mean minimum temperatures recorded at the site are on average 1.6°C colder than the expected trend. Such local temperature inversions are generally the result of cold air drainage, and are often observed in valley bottoms (O'Hare et al. 2005). The fact that the middle site is located on a plateau probably results in cold air flowing downwards from the steeper slopes above collecting at this site during the long winter nights.

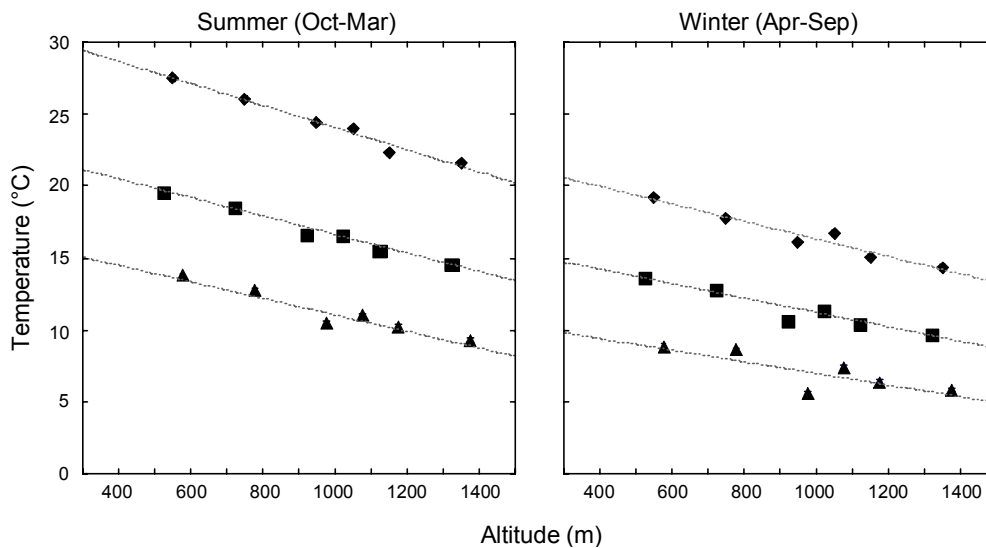


FIGURE 2. Plot of mean daily temperatures (■), mean daily maximum temperatures (◆) and mean daily minimum temperatures (▲) against altitude, showing seasonal variation in temperature decreases with increasing altitude.

Monthly mean temperature summaries indicate that August is the coldest month at the site (Figure 3), with mean minimum temperatures ranging from 3.3-6.9°C between the highest and lowest monitoring points. Highest temperatures were recorded during February, when daily maximum temperatures are on average around 30°C at the karoo site (545 m) at the lowest end of the gradient.

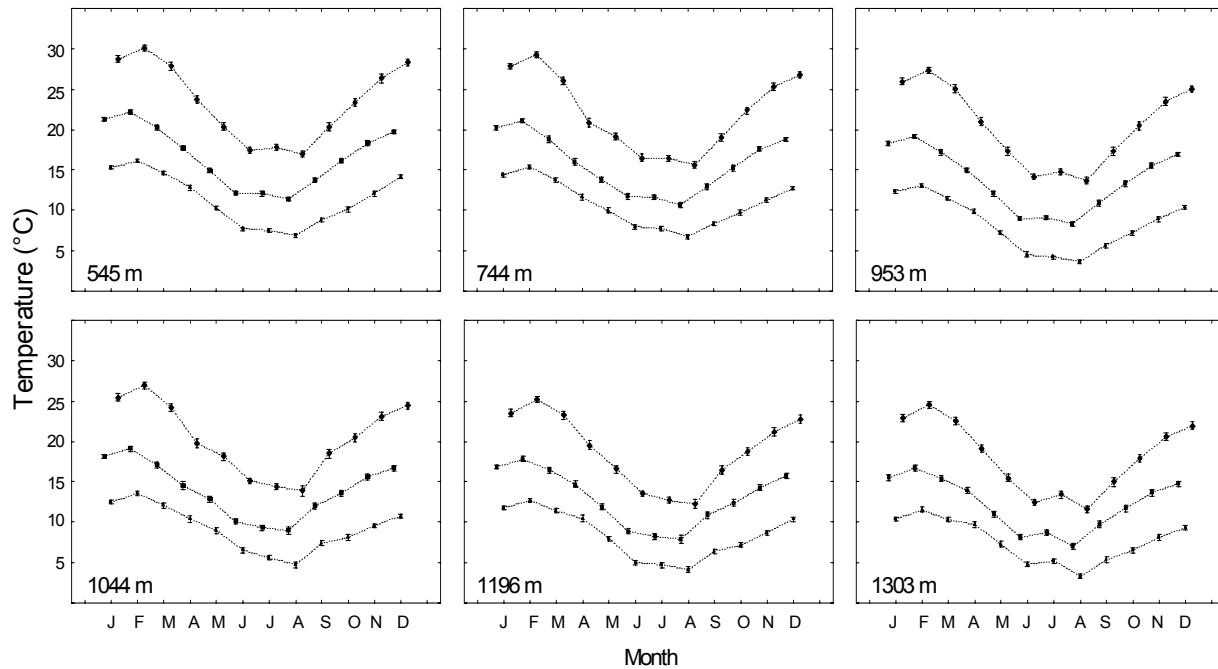


FIGURE 3. Monthly mean daily (■), mean daily maximum (◆) and mean daily minimum (▲) temperatures recorded at 6 sites across the gradient. Numbers in lower left corner of graphs indicate altitude at which temperatures were recorded.

### Rainfall

During three years of climate recording (2002-2004), the highest site (1303 m) received an average of 719.6 mm annual precipitation, the middle site (953 m) 411.3 mm and the karoo site (545 m) 315.4 mm. The highest site receives on average a slightly lower proportion of its annual rainfall during winter (Table 3, Figure 4). Higher summer rainfall at the highest site is possibly due to orographic effects, with southerly and south-westerly winds pushing clouds over the mountaintop and bringing rain to the highest site but not to lower sites. According to Aschmann (1973), Mediterranean climates are defined by winter rainfall constituting at least 65% of the annual rainfall. The proportions of winter rainfall recorded across the Jonaskop gradient, which range from 57-66%, therefore indicates that the study site does not fall within the strictly winter rainfall zone of the Cape Floristic Region. Long term rainfall data for the Riviersonderend Mountains confirm that many large rainfall events, associated with post-frontal cut-off lows occur

during summer, resulting in the area not being subjected to as severe summer droughts as elsewhere in the Cape Floristic Region (R.M. Cowling, pers.comm.)

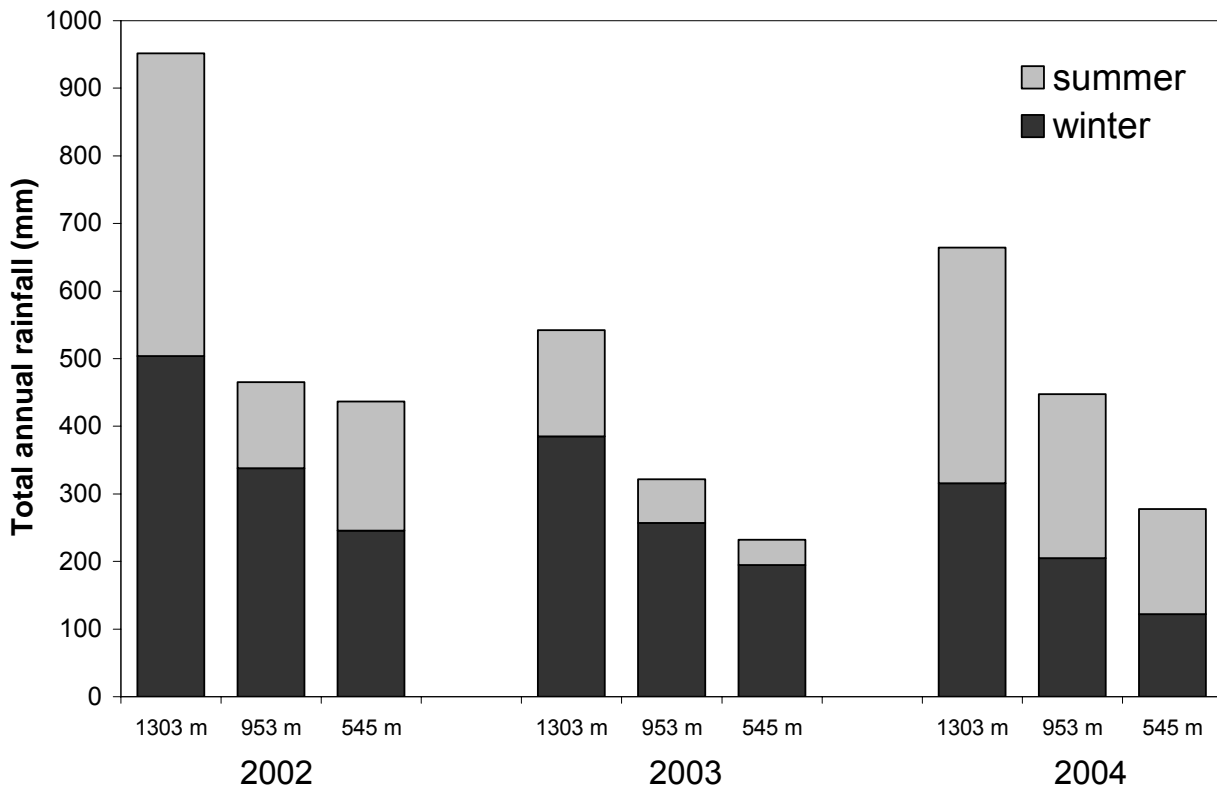


FIGURE 4. Total annual (April to March) rainfall recorded at the top (1303 m), middle (953 m) and lower (545 m) monitoring points on the Jonaskop gradient. Total annual rainfall is split into winter rain season (April to September) and summer growth season (October to March) rainfall.

Monthly rainfall patterns recorded during 3 years of this study were very variable (Figure 5). The year 2002 had good winter rains and a relatively dry summer. The high monthly total precipitation of March 2003 was due to a single extreme rainfall event on 24 March when 174.5 mm was recorded at the highest site (1303 m) and 103.9 mm at the lowest site (545 m). The year 2003 was an extremely dry year throughout the whole Western Cape, and the low rainfall, especially during the winter months, is reflected in the data from Jonaskop. Although 2004 had in total a much higher annual precipitation, it also had a very dry winter, with most of the annual precipitation recorded during October.

Cowling et al. (2005) highlighted the importance of rainfall reliability in terms of interannual variation in rainfall, as well as the size and structure of rainfall events, as a driver of plant traits in Mediterranean ecosystems. Rainfall data recorded at Jonaskop were therefore further analyzed to explore seasonal patterns in the size, duration and frequency of rainfall events. Whenever

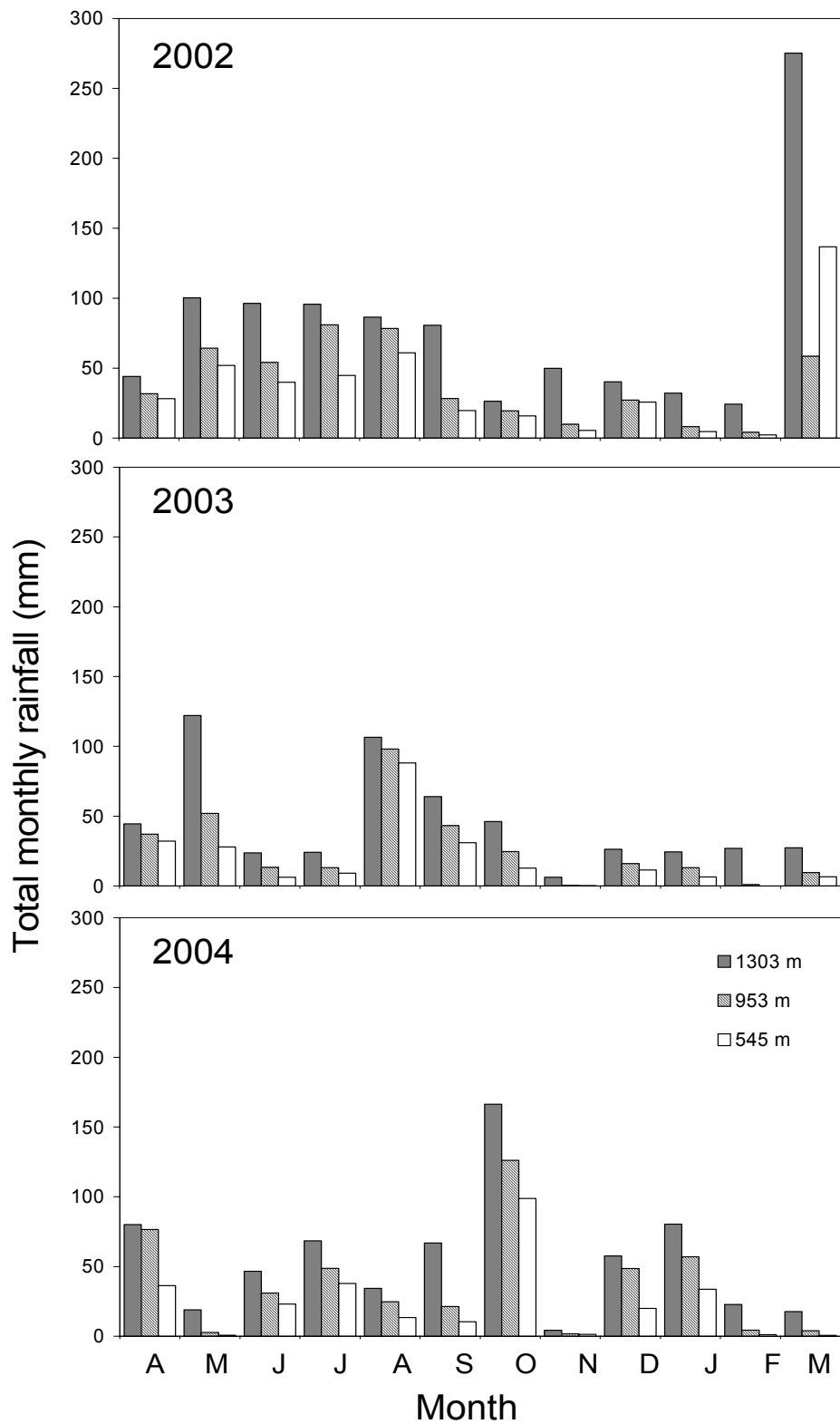


FIGURE 5. Monthly rainfall recorded from April 2002 to March 2005 at the top (1303 m), middle (953 m) and lower (545 m) monitoring points on the Jonaskop gradient.

rain was recorded on a number of consecutive days, rainfall recorded over the period was added together as a single rainfall event. Cowling et al. (2005) also mentioned the importance of the regularity of rainfall events in Mediterranean climates, especially with regards to the germination of seedlings. Mustart and Cowling (1993) showed that the duration of dry periods between rainfall events is an important factor determining the successful germination of Proteaceae seeds. Therefore a frequency analysis of the number of days between rainfall events was also done.

At all sites, rainfall events occur most often as small (<5 mm) events lasting only one day (Figure 6). This trend was observed during winter and summer. However, larger rainfall events (>10 mm), and events lasting longer than two days occur much more frequently in winter than summer at all sites. In terms of the duration of dry periods between rainfall events, patterns are more divergent among sites and seasons. At the highest site (1303 m), rainfall events were most often separated by less than four days during winter and summer. At the middle site (953 m), winter rainfall events are far more frequently within four days apart than in summer. Summer rainfall events show a larger frequency distribution towards longer dry intervals. At the lowest site (545 m), the winter trend towards shorter dry intervals is far less marked than at the higher sites, indicating that even during winter, rainfall at this site can be very sporadic. Also, at this site dry intervals of longer than 14 days are more often recorded during winter and summer than at the higher sites.

### *Wind*

An analysis of wind patterns at the top (1303 m), middle (953 m) and lowest (545 m) sites (Figure 7) shows altitudinal as well as seasonal differences. All sites experience predominantly southerly winds during summer months (October to March), although south-westerly winds at the highest site (1303 m) and south-easterly winds at the middle (953 m) and lowest (545 m) are also important during summer. During winter (April-September) wind patterns shift to predominantly north-westerly at the top site and westerly at the middle site, while winter wind patterns at the lowest site are essentially the same as summer conditions, with a slight shift towards more north and north-westerly winds and less easterly winds.

Wind speeds tend to increase with increasing altitude (Barry 1992), and can have an impact on plant growth. High wind speeds in combination with very low temperatures on exposed mountain

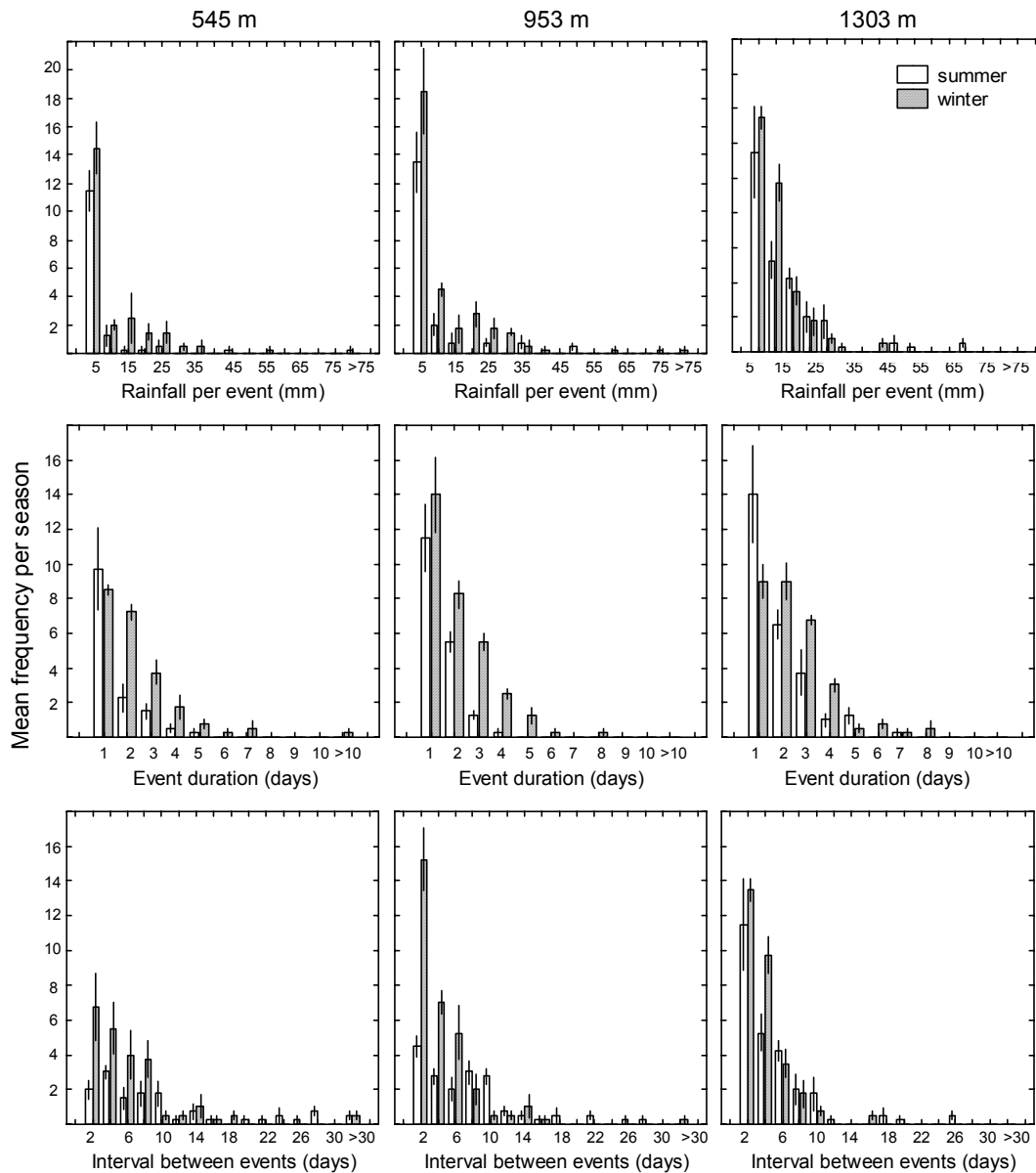


FIGURE 6. Amount of rainfall per rainfall event, the duration of rainfall events, and the duration of dry intervals between rainfall events summarized as mean frequencies per season. The altitude in meter above sea level where rainfall was recorded on the gradient is indicated above each column. Error bars indicate 1 standard error.

peaks can cause stunted growth in plants, such as the prostrate cushion forms of pine trees found in the Krummholz zone of alpine regions.

However, mean seasonal wind speeds on Jonaskop do not indicate an increase of wind speed with increasing altitude (Figure 8). When wind speeds are compared across the gradient, lowest mean wind speeds are recorded during both winter and summer the middle site (953 m). The southerly and southeasterly winds of summer reach highest speeds (mean 11.8 km/h) at the



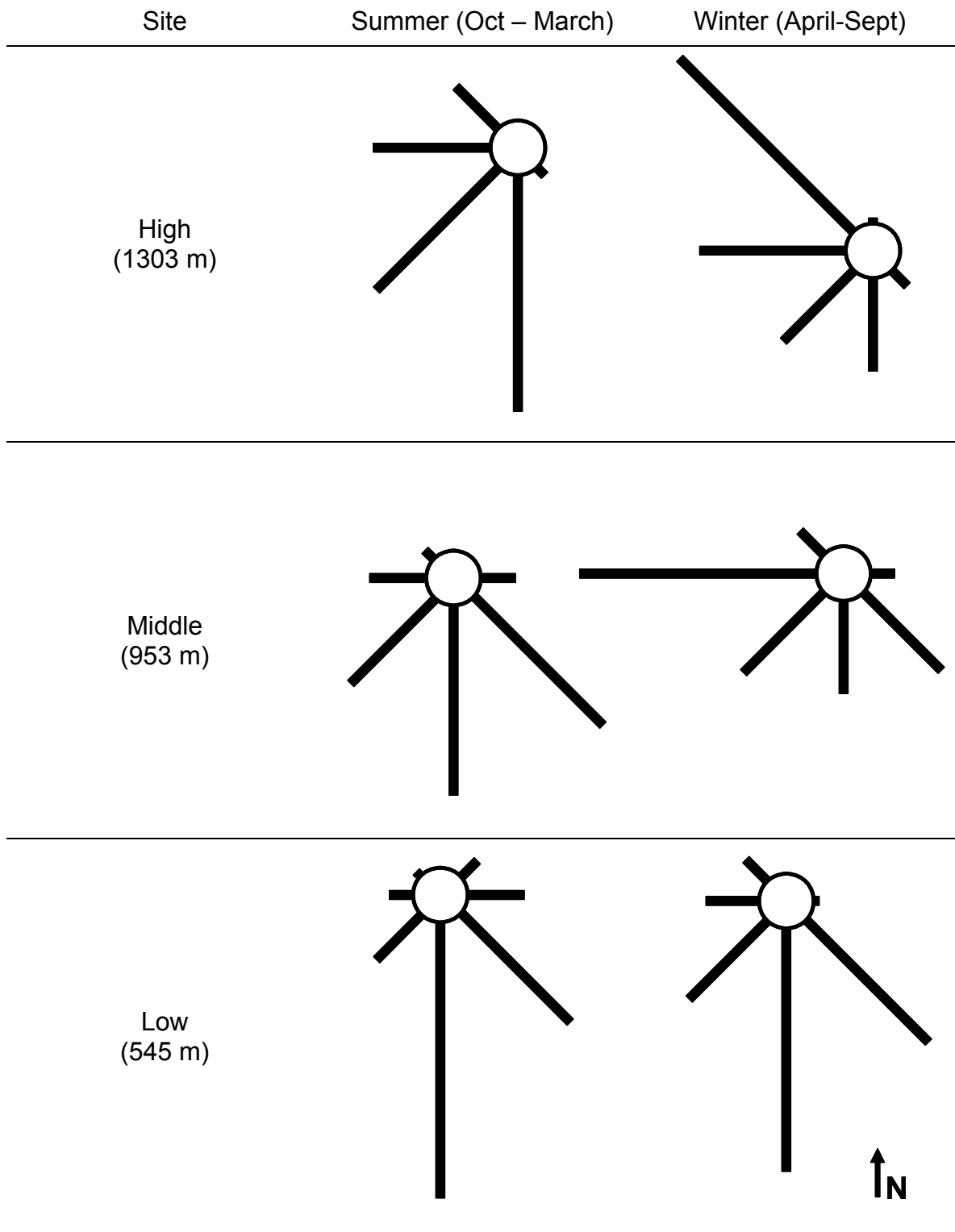


FIGURE 7. Seasonal wind patterns recorded at the top, middle and lower monitoring points on the Jonaskop gradient. Lengths of bars indicate number of days.

lowest site. At the middle and lowest sites winds are stronger during summer than winter, but the predominantly north-easterly winds associated with advancing rain bearing cold fronts are much stronger during winter at the highest site. It is difficult to place wind speed data recorded on Jonaskop into context, as windspeed data for mountain slopes elsewhere in the Cape Floristic Region are not readily available. According to Barry (1992), mean wind speeds of around 25 km/h is 'typical' for mountain peaks in the mid-latitudes of the northern hemisphere, which is much higher than wind speeds recorded on Jonaskop. Whether wind on Jonaskop is likely to affect the vegetation is also not certain. Controlled experimental studies have indicated that wind speeds higher than 10 km/h negatively affects the growth of herbaceous annuals and grasses (Whitehead 1962, Woodward 1993). On Jonaskop mean wind speeds during the growth season (summer) are higher than 10 km/h only at the lowest site, but it is unlikely to affect growth in the sturdy perennial shrubs of the site, except when associated with high temperatures and low relative humidity, as under berg wind conditions.

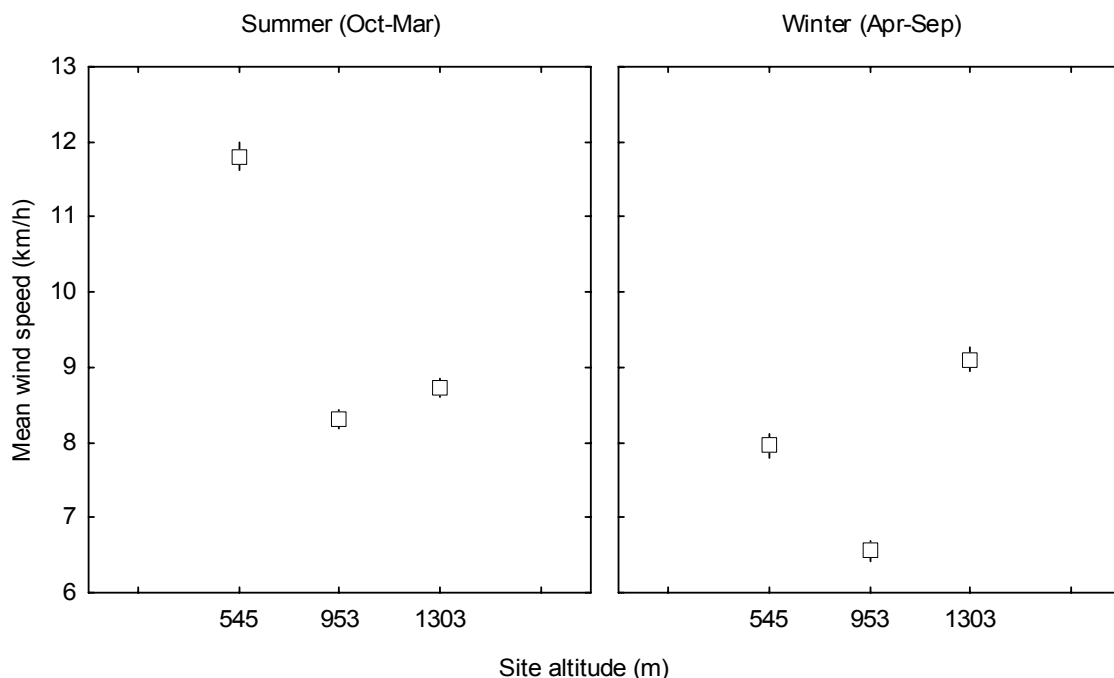


FIGURE 8. Mean seasonal wind speeds recorded at the top (1303 m), middle (953 m) and lowest (545 m) end of the Jonaskop gradient. Error bars indicate 1 standard error.

#### *Soil characteristics*

Soils on the gradient are generally very shallow and rocky, with rockiness increasing with increasing altitude (Table 4). The main differences in soil chemistry between shale derived soils at the karoo site (545 m) and the sandstone derived soils of the rest of the mountain are in

TABLE 4. Soil characteristics of selected sites along the Jonaskop gradient.

Monitoring site	Geology	Mean rock cover (%)	Soil depth (range, cm)	Ph
545 m on mound	shale	0	14-31	6.3
545 m off mound	shale	0	5-32	4.2
744 m	sandstone	15	0-38	4.9
953 m	sandstone	13	0-50+	4.3
1044 m	sandstone	22	0-50+	4.1
1196 m	sandstone	19	4-50+	3.6
1303 m	sandstone	43	0-34	4.0

terms of P, Ca and Mg, which were much higher in shale derived soils. Soil on 'heuweltjies' are very different from sandstone derived soils as well as shale derived soils off 'heuweltjies'. 'Heuweltjie' soils have much higher Ca, K and N content than either sandstone or off-mound shale. Off-mound shale has roughly double the Na content of either 'heuweltjie' or sandstone derived soils.

#### *Vegetation communities*

A total of 286 species were recorded on the gradient. The highest number of species recorded in a single 10x10 m relevé was 50 species at the middle site (953 m). A total of 105 species were recorded in a single relevé only. Species accumulation curves, calculated for each site, revealed that vegetation sampling did not approach complete sampling of communities (Data not shown).

#### 1. Karoo site (545 m)

Out of a total of 56 species recorded at this site, 45 occurred nowhere else on the gradient. A number of species were found on 'heuweltjies' alone (Group I, Appendix I), while all other species found on 'heuweltjies' were found at low abundances elsewhere in the karoo site, but nowhere else on the gradient (Group II, Appendix I). Species typical of 'heuweltjies' are *Galenia africana*, *Schismus barbatus* and *Galium tomentosum*. Off-mound communities are defined by *Dicerotheramnus rhinocerotis*, *Oedera squarrosa* and *Pteronia paniculata* (Group III, Appendix 1). Other species typical of the karoo site in general are *Ruschia lineolata*, *Euphorbia burmanii*, *Pteronia incana* and *Tylecodon paniculatus*. These species are found in high abundance on 'heuweltjies', and to a lesser extent elsewhere at the site (Group II, Appendix 1). Three species found frequently at the karoo site are able to successfully cross the soil barrier between the

TABLE 4. Extended.

P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	N (mg/kg)
45.7	3206.3	854.0	165.0	22.0	3446.9
36.3	651.7	620.7	87.7	53.3	1390.5
2.3	394.3	87.3	74.7	19.7	1245.2
3.3	417.3	85.3	56.0	15.7	1120.7
2.0	148.3	71.0	79.0	18.0	694.3
3.7	133.3	55.7	41.7	12.0	888.6
2.0	190.7	65.7	52.7	24.7	632.3

karoo and ecotonal site are *Anthospermum aethiopicum*, *Drosanthemum speciosum* and *Montinea caryophyllacea* (Group IV, Appendix I). Eight other species were found on both sandstone and shale derived soils, but these were rare and had low cover values.

*Dicerotheramnus rhinocerotis* (renostervos) and *Oedera genistifolia* which have quite high cover in relevé 6D (Appendix II), are associated with renosterveld (Mustart et al. 1997, Goldblatt and Manning 2000), a vegetation type of the Fynbos Biome which is found on more nutrient rich soils (Rebello 1998). According to Mucina et al. (2006), the vegetation on the lower eastern slope of Jonaskop, which is quite close to the karoo site, is classified as Breede Shale Renosterveld (FRs8). Holmes (2002), in an environmental impact study on the vegetation of the Breede River Valley north east of Jonaskop, found that in this area succulent karoo is found on the foothills of north facing slopes, while renosterveld is found on south facing slopes. The karoo site is located between the foot of the north facing slope of Jonaskop and the south facing slope of a low hill, with relevé 6D (plot OFM3 in Figure 1) located on the south facing hillslope. The species composition of this site, considered in combination with the topography, therefore points to either to transitional vegetation, or a mosaic of succulent karoo and renosterveld, which resulted in an inevitable mix of species from both vegetation types found in the sampling plots.

The site also has a relatively high incidence of unpalatable asteraceous shrubs such as *Pteronia* spp., *Galenia africana* (kraalbos) and *Chrysocoma ciliata* (bitterbos), which indicates that the vegetation at this site is also somewhat degraded by overgrazing.

## 2. Ecotone (690-744 m)

Within the two sites located in the ecotone, a total of 105 species were found. Fifty five species were found nowhere else on the gradient. Species typical of the ecotone are *Protea humiflora*,

*Ficinia oligantha* and *Cannomois scirpoides* Group VII, Appendix I). The lower ecotonal site (690 m) has a number of highly abundant species occurring only at this site, which could define this site as a subcommunity within the ecotonal zone (Group V, Appendix I). They are *Lachnospermum fasciculatum*, *Polygala fruticosa*, *Ischyrolepis sieberi* and *Cliffortia crenata*. A number of species were also found uniquely to the higher ecotonal site (744 m), but they were not of sufficient abundance or constancy to justify classification as a separate community (Group VI, Appendix I).

The vegetation of the ecotone is very similar in species composition and physical aspects to the *Cannomois parviflora* – *Passerina obtusifolia* shrublands described by McDonald (1993), which occurs on the lower northern slopes of the nearby Langeberg. These arid shrublands are also found near a transition between Table Mountain Sandstone and Bokkeveld Shales, which support Little Karoo vegetation.

### 3. Fynbos (953-1303 m)

Although there were a number of species characteristic of different sites within fynbos (Groups IX, X and XI, Appendix I), as a whole these sites seem to represent variations within a specific community, characterised by *Phaenocoma prolifera*, *Edmondia sesamoides*, *Protea amplexicaulis*, *Protea magnifica*, *Leucadendron laureolum* and *Hypodiscus aristatus* (Group VIII, Appendix I). The middle site on the gradient, and the lowest site within the fynbos section (953 m), has by far the highest species number on the gradient, with 85 species recorded at this site alone. This site has a high number of rare species which were recorded in low abundances in one or two relevés only. Some of the more frequently recorded species unique to this site, such as *Wahlenbergia neorigida* and *Tetaria flexuosa* are grouped under Group XI in Appendix I, but because of their low cover values, cannot be used to characterise this site. The site above the middle site (1044 m) has 11 unique species, but all were recorded once only and also cannot be used as characteristic species. The sites at 1196 m and 1303 m, however, do have characteristic species, but interestingly, in both cases these species were not found in the recently burned vegetation. Species characteristic of 1196 m are *Elegia filacea* and *Nebelia laevis* (Group X, Appendix I), while *Erica longifolia*, *Elegia racemosa* and *Adenandra villosa* are characteristic of 1303 m (Group XI, Appendix I).

#### 4. Mountain summit (1576 m)

Structurally, vegetation at the mountain summit is very low compared to the rest of the gradient. Some species found at this site which also occur elsewhere on the gradient, such as *Helichrysum zwartbergense*, are found near the summit as dwarfed growth forms, compared to taller individuals lower down. Soils are extremely shallow and very rocky, with an average of 75% rock cover. Species number at this site is very low, with only 26 species found. Vegetation at this site is dominated by grasses, sedges and restios. Species characteristic of summit vegetation are *Ehrharta ramosa*, *Restio triticeus* and a *Metalsia* species (Group XII, Appendix 1).

#### *Diversity*

Shannon diversity indices indicated highest diversity at the lowest fynbos (953 m) and ecotonal sites (690 and 744 m, Figure 9a). When diversity was compared within sites between recently burned and mature vegetation, burned relevés had higher diversity in all fynbos sites (953, 1044, 1196 and 1303 m) as well as at the summit (1576 m, Figure 9b). Ecotone sites (690 and 744 m) have lower diversity in recently burned relevés. Other studies in fynbos have also found that richness is highest in the first few years after fires, due to the presence of ephemeral species (Bond and van Wilgen 1996, Holmes and Cowling 1997).

#### *Growth form composition*

A comparison of the relative contribution of various growth forms to vegetation cover shows clear shifts in dominant growth forms across the gradient (Figure 10a). From the karoo site (545 m) up to the lowest fynbos site (953 m) vegetation is dominated by low shrubs. At the karoo site, succulents are also a significant contributor to vegetation cover, but not at any of the other sites. Above 953 m the dominant growth form shifts to graminoids, which includes grasses, sedges and restios. The low vegetation at the summit site (1576 m) is reflected in a high proportion of vegetation cover represented by dwarf shrubs, with heights lower than 0.25 m. At this site, herbs also represent a larger proportion of the vegetation cover than at other sites.

When growth form composition between recently burned and mature vegetation is compared, ecotone sites show very similar composition (Figure 10b). In fynbos sites, however, recently burned vegetation has higher cover in herbs, succulents and graminoids, while mature vegetation consists of largely of long-lived low and mid-high shrubs, as well as graminoids.

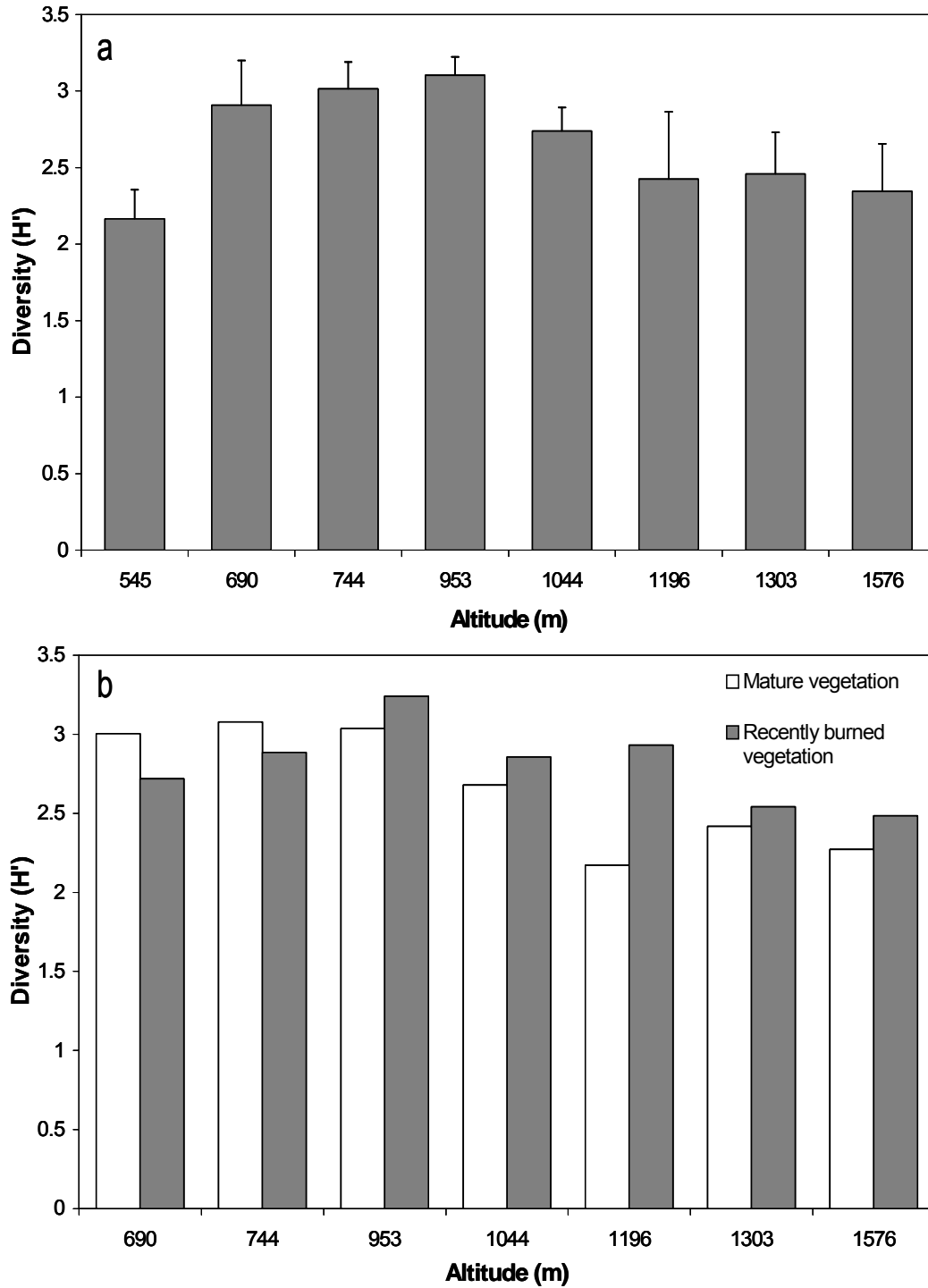


FIGURE 9. (a) Shannon-Wiener diversity indices ( $H'$ ) recorded across the gradient.  $H'$  values for each altitude is the mean of three 10x10 m relevés and (b) comparative diversity indices ( $H'$ ) between recently burned and mature vegetation at selected altitudes along the Jonaskop gradient. Diversity values for mature vegetation is the mean of two 10x10 m relevés, while only one relevé was sampled in recently burned vegetation at each altitude. Error bars indicate 1 standard error.

Taking a closer look at the relative contribution of the families Cyperaceae, Poaceae and Restionaceae to graminoid cover across the gradient, some more interesting patterns are revealed (Figure 11a). Grasses dominate at the karoo site (545 m), and are found only in very low proportions elsewhere on the gradient, except again for the summit (1576 m), where grasses, sedges and restios make roughly equal contributions to total graminoid cover. Restionaceae show increasing dominance from the ecotone upwards to 953 m, after which sedges become slightly more important. Grasses decrease, except for 1044 m showing a high proportion of grass cover. Comparing graminoid cover between recently burned and mature vegetation reveals that in fynbos Cyperaceae dominate recently burned vegetation, while Restionaceae are dominant in mature vegetation (Figure 11b). In the ecotone, grasses are slightly more abundant in recently burned than mature vegetation.

#### *Similarity and turnover rates*

Similarity between all sites is relatively low, suggesting high species turnover even between sites with similar vegetation. Similarity between the karoo site and the rest of the gradient, as well as between the summit and the rest of the gradient is the lowest (Table 5), suggesting that strong climatic and/or soil factors are limiting species distributions between these and other areas on the gradient. Highest similarities were found among the ecotone sites (25.6%) and among fynbos sites (15.7 – 25.5%). Similarities of 11.3%, 17.1% and 16.2% between the ecotone and lower fynbos sites (953 and 1044 m) suggests that the ecotone vegetation is more closely related to fynbos than karoo, as similarities between ecotone sites and the karoo site are only 7.5% (690 m) and 2.7% (744 m). Mean turnover rate for the gradient was determined as -0.0014, with the equation fitted to the plot of difference in altitude against similarity being  $\text{Log \% similarity} = -0.0014 \times \text{difference in altitude} + 1.41$ ,  $r^2 = 0.52$  (Figure 12). Similarity values between the karoo site and other sites were generally much lower than predicted by the regression line for similar changes in altitude elsewhere along the gradient, again suggesting that the area between 545 and 690 m is governed by strong environmental factors affecting species distributions.

## CONCLUSION

Climate change studies report increasing evidence that species' ranges shift upwards on mountain slopes as a result of climate warming, and that high altitude species are therefore particularly vulnerable to extinction as they reach the limits of mountain summits (Grabherr et al.



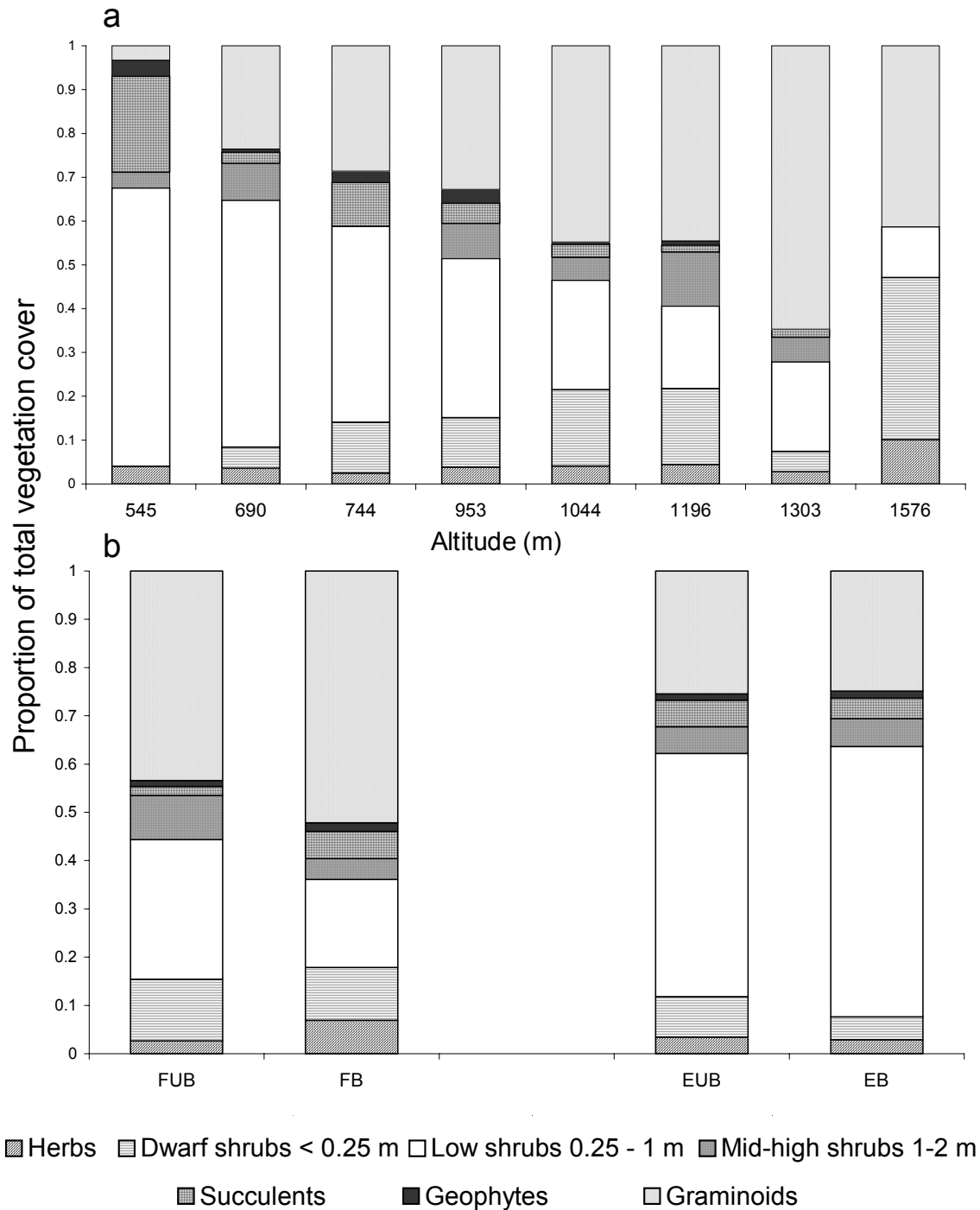


FIGURE 10. (a) Comparative contributions of various growth forms to total vegetation cover at selected altitudes along the gradient. (b) Comparative growth form composition between recently burned and mature vegetation in fynbos and ecotone sites. FUB – fynbos mature vegetation, FB – recently burned fynbos, EUB – ecotone mature vegetation, EB – recently burned ecotone vegetation.

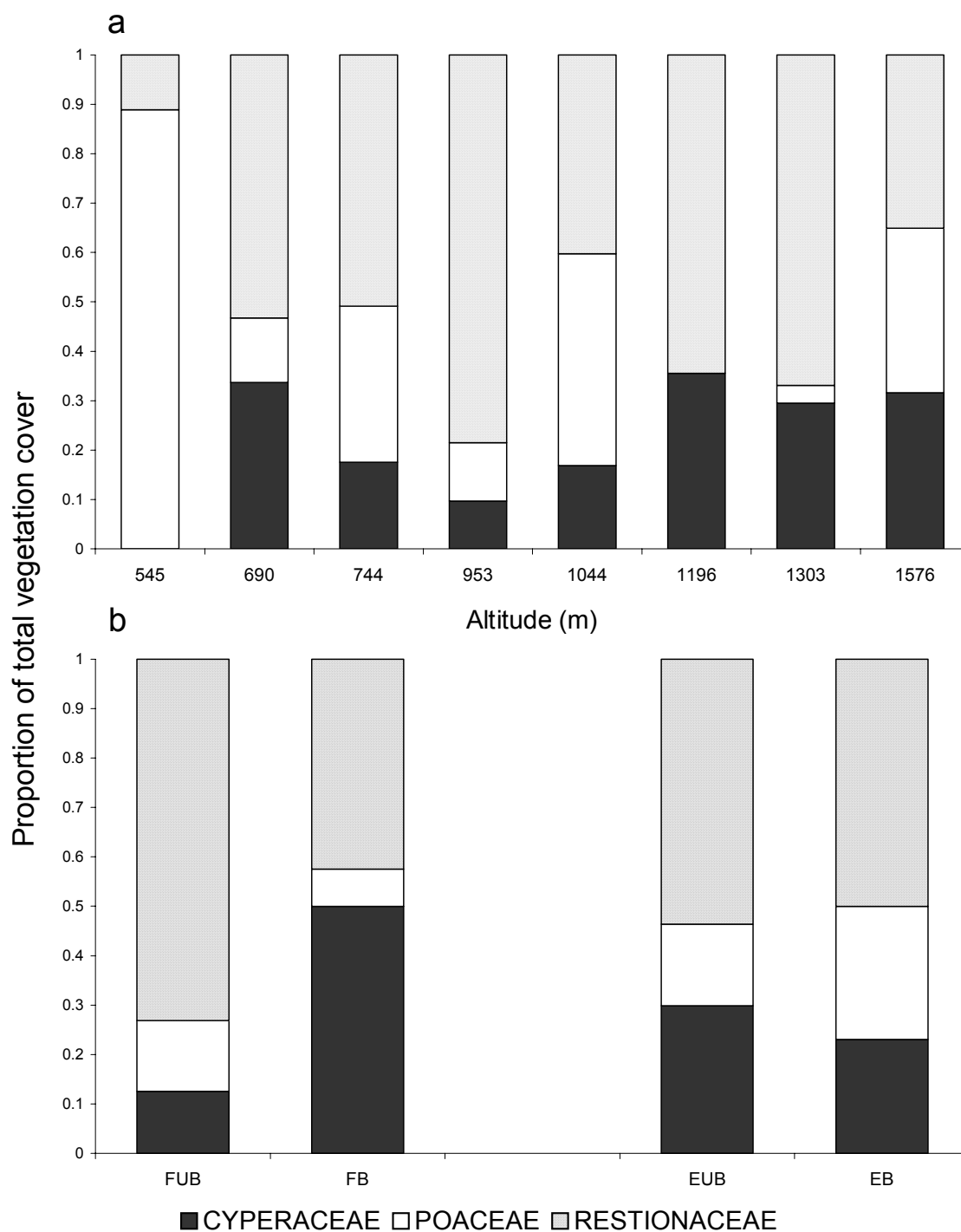


FIGURE 11. (a) Relative contribution of sedges (Cyperaceae), grasses (Poaceae) and restios (Restionaceae) to total graminoid cover at selected altitudes across the Jonaskop gradient. (b) Comparative contribution of sedges (Cyperaceae), grasses (Poaceae) and restios (Restionaceae) to total graminoid cover between recently burned and mature vegetation. FUB – fynbos mature vegetation, FB – recently burned fynbos, EUB – ecotone mature vegetation, EB – recently burned ecotone vegetation.

TABLE 5. Total number of species and number of unique species recorded at selected sites along the Jonaskop gradient, including percentage similarity values for all sites compared. The shaded diagonal represents similarity values between adjacent sites.

		Karoo	Ecotone		Fynbos				Summit
	<b>Altitude</b>	<b>545</b>	<b>690</b>	<b>744</b>	<b>953</b>	<b>1044</b>	<b>1196</b>	<b>1303</b>	<b>1576</b>
	No of spp recorded at site	56	73	59	85	56	62	53	26
	No of spp unique to site	45	25	11	30	11	26	14	11
Karoo	<b>545</b>								
Eco- tone	<b>690</b>	7.5							
	<b>744</b>	2.7	25.7						
Fynbos	<b>953</b>	1.4	11.3	17.1					
	<b>1044</b>	0.9	7.5	16.2	24.8				
	<b>1196</b>	0	3.8	7.1	15.7	25.5			
	<b>1303</b>	0	5.9	5.7	18.0	23.9	22.3		
Summit	<b>1576</b>	0	2.1	1.2	5.7	3.8	8.6	12.9	

1994, Parmesan and Yohe 2003). Therefore the summit community on the Jonaskop gradient, with its very restricted range, is possibly quite vulnerable to the warmer and drier conditions predicted for the Western Cape.

However, monitoring species for extinctions and shifts in ranges across the entire gradient will provide valuable insights into the responses of fynbos and succulent karoo vegetation dynamics to climate change. The area around the lower ecotonal site (550-700 m) is the most important area to monitor for the first signs of shifts in species and growth form composition as indication of an upward shift of succulent karoo into fynbos territory. Since karoo vegetation was revealed by analysis of species similarity, diversity and growth form composition to be very different from the rest of the gradient, changes should be detected relatively easily.

Monitoring efforts should not only focus on upward shifts in species ranges, but also on contraction of ranges at the lower elevational limits of species (Hampe et al. 2005). Data collected in this study revealed clearly defined upper and lower altitudinal limits on the gradient for many species sampled, and focusing monitoring on changes in abundance of these species at their upper and lower limits, along with continued climate data recording could reveal much about the climatic controls of species' ranges.

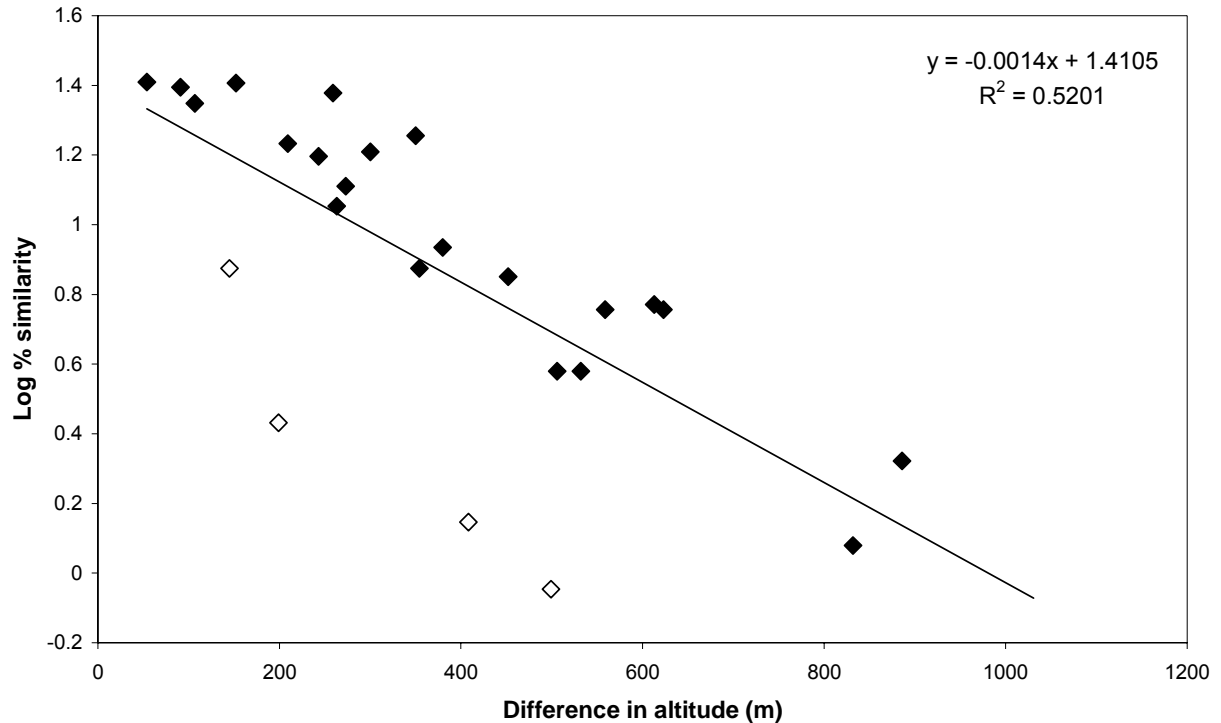


FIGURE 12. Plot of difference in altitude against log percentage similarity between pairs of all sites sampled (closed symbols). Slope of fitted regression line represents the mean turnover rate across the gradient. Open symbols represent karoo sites, closed symbols indicate sites elsewhere on the gradient.

It is of course necessary to investigate the importance of the change in soil type between 545 m and 690 m as a potential barrier to climate change induced shifts in species' ranges, and this is possibly best achieved through experimental studies. As Dunne et al. (2004) have indicated, a combination of gradient monitoring and experimental investigation strategies provide the best insights into complex ecosystem responses to climate change, and it is anticipated that this study should provide useful baseline data for a focused and directed monitoring effort leading to a better understanding of the potential effects of climate change on fynbos and the fynbos-succulent karoo boundary.

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# GROWTH AND FLOWERING RESPONSES OF SELECTED FYNBOS SPECIES TO VARIATION IN TEMPERATURE AND RAINFALL ON AN ALTITUDINAL GRADIENT

*Abstract.* Phenological stages in flowering plants are sensitive indicators of the effects of climate warming on plants. Climatic controls of phenology in nine fynbos species were investigated with the aim of predicting how these species might respond to climate change. The species represent putative shrub functional types, including common tall, broad leaved proteoid, short, needle leaved ericoid shrubs and a rare succulent leaved form. The study site, an altitudinal gradient, is situated in a Mediterranean climate, which presents interesting climatic constraints on phenology. Hypotheses regarding the effects of temperature and rainfall on timing and duration of phenophases, growth rates and biomass accumulation across the gradient were tested. Indications of temperature and/or moisture control of growth across the gradient were evaluated through linear and non-linear regression analysis of growth responses to climate recorded at monitoring points during the experiment. Among broad leaved proteoids, only *Protea amplexicaulis* (Proteaceae), showed no response to climate variation in terms of timing and duration of phenophases, growth rates or biomass accumulation across the gradient. Growth patterns of the leaf succulent *Erepsia gracilis* showed strong indications of temperature control. The other seven species showed variable growth control by combined optimum temperature and moisture conditions that shift across the gradient temporally as well as altitudinally. Further analysis of growth responses in relation to climate revealed that growth trends across altitudes are a poor indicator of climatic controls of growth phenology, especially where growth responses are to complex interactive effects of climate. Highest growth recorded at mid altitudes was revealed not to be the result of moisture stress at drier low altitudes, but sensitivity to high temperatures. Highly variable responses in growth at mean daily temperatures above 15°C and below 1 mm mean daily rainfall were found to be the result of fynbos species' dependence on regular low rainfall during summer. Climate change, which is predicted to involve rising temperatures and lower and more unpredictable rainfall, will therefore severely affect growth in the monitored species, and most likely also other fynbos species with similar growth phenologies. Potential climate change impacts on flowering remain unresolved, but reduced growth may lead to reduced reproductive output in Proteaceae with sympodial architecture.



## INTRODUCTION

Long-term observations in phenology, the study of the seasonal timing of life cycle events of plants and animals (Rathcke and Lacey 1985), have recently reported changes in the timing of phenological events. These changes have been linked to temperature increases as a result of global climate change (McCarty 2001, Penuelas and Filella 2001, Walther et al. 2002, Root et al. 2003). Extended growth seasons, associated with earlier spring budburst as well as later autumn leaf fall (Menzel and Fabian 1999, Chmielewski and Rotzer 2001, Penuelas et al. 2002, Badeck et al. 2004), and earlier flowering and fruiting (Thórhallsdóttir 1998, Penuelas et al. 2002, Dunne et al. 2003, Aerts et al. 2004) have been reported. The effects of climate warming on shifts in timing of autumn phenology are however more variable and show less clear direction than spring trends (Menzel et al. 2001). Comparatively few studies have attempted to assess the effects of changes in precipitation on phenological stages, and results appear to be complex (Penuelas et al. 2004, Llorens and Penuelas 2005).

Changes in plant phenology as a result of climate change could have far reaching and diverse impacts on ecosystems. Studies suggest extended growth seasons will impact ecosystem productivity (James and Grace 1994, Keyser et al. 2000, Renzhong and Qiong 2003) which may lead to alterations in global carbon cycling (Keeling et al. 1996, Keyser et al. 2000). Differential growth responses across different species might lead to alterations in competitive interactions and consequently shifts in community composition and structure (Starr et al. 2000, Penuelas et al. 2002, Llorens et al. 2004). Changes in flowering phenology may cause decoupling of species interactions between plants and their pollinators, affecting reproductive output of plant species (Thórhallsdóttir 1998, Dunne et al. 2003, Root et al. 2003, Llorens and Penuelas 2005), but little evidence has been reported to date.

In order to monitor and predict species and ecosystem responses to ongoing climate change, it is important to firstly understand the potential impacts of climate change on plant growth and phenology, which underpins relative species performance and ecosystem productivity and dynamics. Phenological stages are easily observable and have proven to be very sensitive indicators of ecosystem responses to climatic changes, especially in the northern hemisphere (Penuelas and Filella 2001). However, for many areas elsewhere in the world long-term phenological records do not exist. In the absence of long term records of phenological change, alternative strategies for investigating the effects of climate changes on phenological patterns

include simulating climate change scenarios through experimental manipulations of field conditions (Suzuki and Kudo 1997, Starr et al. 2000, Aerts et al. 2004, Llorens et al. 2004, Ogaya and Penuelas 2004, Llorens and Penuelas 2005) or monitoring of phenology across an altitudinal gradient (James and Grace 1994, Levesque et al. 1997), substituting temporal variation in climate with spatial variation.

According to bioclimatic modelling studies the Cape Floristic Region, a plant biodiversity hotspot, is facing severe threats to biodiversity as the result of climate change (Midgley et al. 2002, Midgley et al. 2003, Bomhard et al. 2005, Hannah et al. 2005). However, no studies have attempted to assess the effects of climate change on the ecosystem dynamics of fynbos, the main vegetation type of the Cape Floristic Region, as a result of changes in productivity and reproductive output due to shifting phenological phases. Phenology of many fynbos species has been described (Bond 1980, Kruger 1981, Sommerville 1983, Le Roux et al. 1984, Pierce and Cowling 1984a, b), but no long-term monitoring data exist. Situated within a Mediterranean climate, fynbos plants are faced with unique constraints to growth: during the winter rain season, when moisture is plentiful, growth is prevented by low temperatures (Oliveira and Penuelas 2002). Growth seasons commence as soon as spring temperatures increase, but Mediterranean summers are dry and hot, and moisture and heat stress is generally constraining to growth (Chaves et al. 2002). How summer drought affects the timing and duration of phenological stages is not well understood (Spano et al. 1999), since in spite of potential moisture stress, some Mediterranean species are able to maintain high growth rates all through summer. Indications are that Mediterranean plant species have various strategies to deal with dry summer conditions (Chaves et al. 2002). In fynbos, generally deep rooted members of the Proteaceae grow throughout the summer months (Kruger 1981, Pierce and Cowling 1984a). In other species, moisture stress during the hot dry summer months leads to 'bimodal' growth patterns, with a second growth peak observed when autumn rains set in (Debussche et al. 2004). Shallow rooted understorey fynbos species, such as Ericaceae and Restionaceae, seem to grow whenever temperature and moisture conditions are at an optimum (Pierce and Cowling 1984a, b). Most fynbos species flower during spring and summer, but some phylogenetic groups, such as the Ericaceae, flower all year round (Johnson 1993). How flowering is controlled by temperature and rainfall patterns is not well understood.

Climate change predictions for the Western Cape, which includes most of the Cape Floristic Region, indicate warmer as well as drier future conditions (Rutherford et al. 1999). The aim of

this study is to determine the relative importance of either or both temperature and moisture as the main driver of growth and flowering patterns in fynbos. Based on the results, predictions are made on how climate change is likely to affect productivity and reproductive output in fynbos species.

A temperature and moisture gradient along a north-facing mountain slope has been selected as a phenological monitoring site. The site is characterised by increasing precipitation and decreasing temperature with increasing altitude. Monitoring of the timing and duration of growth and flowering phases in wide ranging species is expected to show specific patterns across the gradient, depending on whether temperature, moisture, or a combination of temperature and moisture controls phenophases.

In this chapter, the following climate change related hypotheses are tested, and the results verified by analysis of growth responses to climate recorded on the gradient. The expected trends in timing and duration of phenological stages, growth rate variation and biomass accumulation across altitude are schematically illustrated in Figure 1.

#### *Temperature*

Increased temperatures generally lead to extended growth seasons. Therefore, if temperature mainly controls growth and flowering, it is expected that growth and flowering phases will start earlier at the lower, warmer end of the gradient (Figure 1 AI) and that the growth season will continue longer relative to higher, colder altitudes. It is expected that higher growth rates will be maintained at lowest, warmest altitudes throughout the growth season (Figure 1 AII), and that biomass accumulation will increase with increasing temperature so that highest biomass accumulation will be recorded at the lowest end of the gradient (Figure 1 AIII).

#### *Moisture*

Discerning moisture availability as the controlling factor in fynbos phenology and growth is somewhat complex. Mortimer et al. (2003) found that irrigation leads to increased growth in a *Protea* hybrid species only up to 40% soil field capacity, with further increases in irrigation making no difference to growth. However, the study site is situated at the dry northern edge of the fynbos biome and receives relatively low rainfall of around 700 mm per year compared to other fynbos sites recording up to 2000 mm per year (Cowling and Holmes 1992), and therefore rainfall effects on phenology should be discernable.

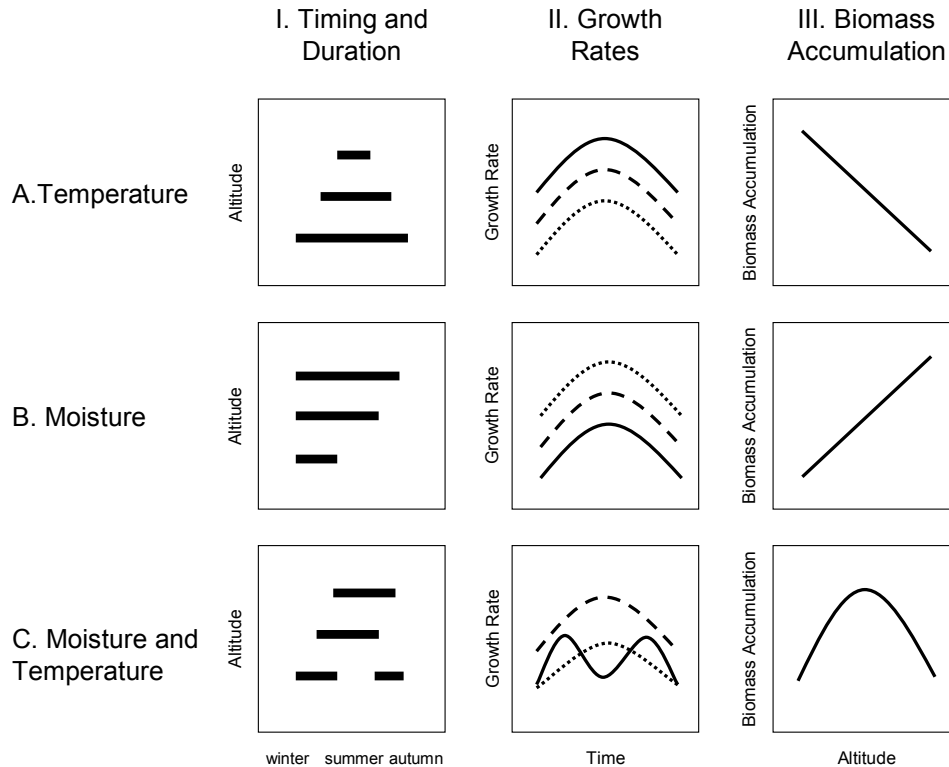


FIGURE 1. Idealized graphs of hypothesized effects of (A) temperature, (B) moisture and (C) combined temperature and moisture on (I) timing and duration of growth and flowering, (II) growth rates and (III) biomass accumulation across the gradient. Increasing altitude is associated with increasing rainfall and decreasing temperatures. (I) Timing and duration at different altitudes are indicated by the placing and length of the black bars. (II) Growth rates: solid lines (—) indicate growth rate at low altitudes, dotted lines (.....) indicate growth rates at high altitudes and dashed lines (- - -) indicate growth rates at intermediate altitudes. Lines on plots of biomass accumulation against altitude (III) indicate expected trends.

All plant species have a minimum temperature below which growth ceases (Salisbury and Ross 1992), and so even if moisture is the main driver of growth and flowering, timing of the start of spring phenological stages will possibly also show shifts across the gradient. However, the growth and flowering seasons are expected to be longer at highest altitudes, which receive a high proportion of its total annual rainfall during summer (Figure 1 BI, also Table 1 and Chapter 1), thus reducing summer drought limitations prevalent at lower altitudes. Growth and flowering seasons are expected to terminate during early summer at lowest monitoring sites.

If moisture availability is the main controlling factor of growth in fynbos plants, it is expected that above a minimum temperature threshold, growth will respond to higher rainfall rather than higher temperatures, leading to higher growth rates recorded at higher altitudes (Figure 1 BII). Similarly, it is expected that greatest biomass accumulation will be recorded at altitudes that receive the most rain, that is, the highest monitoring site (Figure 1 BIII).

### *Temperature and moisture*

If temperature and moisture availability controls phenophases in combination, it may be difficult to discern the timing and duration of growth and flowering seasons from moisture control alone. It is expected that growth and flowering will start earlier at the lowest, warmer altitudes, but that it will be maintained longer at the higher, wetter altitudes, and that a second autumn peak in growth and/or flowering will possibly be recorded at lower altitudes (Figure 1 CI). However, on the basis of growth rates and biomass accumulation clear differences from moisture patterns are expected: highest growth rates (Figure 1 CII) and greatest biomass accumulation (Figure 1 CIII) is expected in the middle of the gradient, where combined temperature and moisture conditions are likely to be at an optimum. Growth rates will show altitudinal shifts in peak growth rates during the season, with highest growth rates recorded at warmer middle to lower altitudes at the start of the growth season when moisture is plentiful, thereafter changing to highest growth rates at middle to higher altitudes later in the season when moisture becomes limiting at the lowest altitudes.

## METHODS

### *Study area*

Phenological monitoring was conducted on an altitudinal gradient on the north-facing slope of Jonaskop (33°58'00 S 19°30'00 E, altitude 1694 m) in the Riviersonderend Mountains, Western Cape. Weather stations and data loggers have been installed at selected points along the gradient, and temperatures and rainfall have been recorded on the gradient since February 2002. Temperatures decrease on average 0.38 °C with every 100 m rise in altitude (Chapter 1), while highest altitudes receive on average 404.2 mm higher mean annual precipitation than the lowest end of the gradient. See Table 1 for a summary of climate conditions across the gradient.

TABLE 1. Summary of climate on the Jonaskop gradient. Means are the result of three years of climate monitoring (2002-2004).

<b>Altitude (m)</b>		<b>545</b>	<b>953</b>	<b>1303</b>
Location	S	-33°55.053	-33°56.061	-33°57.691
	E	19°30.421	19°31.228	19°30.800
Mean annual temperature (°C)		16.7	13.8	12.3
Mean annual rainfall (mm)		315.4	411.3	719.6
Mean winter (April-September) rain (mm)		187.4	266.6	401.3
Mean summer (October-March) rain (mm)		128.1	144.7	318.3

### Study species

Common fynbos species, representing different growth forms, were selected for monitoring. At the start of the experiment, in April 2002, three Proteaceae species (*Protea amplexicaulis* (Salisb.) R.Br., *Leucadendron laureolum* (Lam.) Fourc. and *Leucadendron salignum* P.J.Bergius), one Ericaceae (*Erica plukenetti* L.) and a leaf succulent Mesembryanthemaceae species (*Erepsia gracilis* (Haw.) L.Bolus) were selected for monitoring. At the start of the second year of the experiment, from April 2003, four more species were added. These were three more Proteaceae (*Protea laurifolia* Thunb., *Protea repens* (L.) L. and *Leucadendron nervosum* E.Phillips & Hutch) and another Ericaceae (*Erica vestita* Thunb.). The Proteaceae are tall broad leaved evergreen shrubs, and the species selected dominate the emergent shrub layer of the fynbos vegetation on the gradient (Chapter 1). The Ericaceae, which have narrow leaves with rolled edges (known as ericoid leaves), and *Erepsia* are low shrubs, forming part of the vegetation ‘understorey’ (Pierce and Cowling 1984b). All nine species have fairly wide distributions across the gradient, but they do not have similar altitudinal ranges. The altitudinal distributions of the study species are indicated in Table 2.

TABLE 2. Altitudinal distributions of species selected for the study. Grey shading indicates at which monitoring sites species are found.

Species	Family	Monitoring sites (altitude)				
		744	953	1044	1196	1303
<i>Protea amplexicaulis</i>	PROTEACEAE		■	■	■	■
<i>Protea laurifolia</i>	PROTEACEAE		■	■	■	
<i>Protea repens</i>	PROTEACEAE		■	■	■	■
<i>Leucadendron laureolum</i>	PROTEACEAE		■	■	■	■
<i>Leucadendron nervosum</i>	PROTEACEAE			■		■
<i>Leucadendron salignum</i>	PROTEACEAE	■	■			
<i>Erica plukenetti</i>	ERICACEAE	■		■	■	■
<i>Erica vestita</i>	ERICACEAE	■	■	■		
<i>Erepsia gracilis</i>	MESEMBRYANTHEMACEAE	■			■	■

### Phenological monitoring

Monitoring was concentrated at five points along the gradient where weather stations or data loggers had been installed. At each monitoring site, three individuals of each of the selected species occurring at that site were marked. In the case of the three *Leucadendron* species, which are dioecious, three male and three female plants were marked for monitoring at each site. However, for *L. nervosum*, a relatively rare species, not enough female plants were found at

1044 m, and therefore only males were monitored. Initially, three unbranched terminal shoots were marked for monitoring on each marked individual plant, but this number was increased to four shoots per plant at the start of the second year of monitoring, as shoots were often damaged.

Marked shoots were measured monthly using digital callipers. Growing shoots often produced side shoots. All side shoots were considered as new growth, and therefore all side shoots forming on marked shoots were also included in monthly measurements until the end of the growth season, when new, unbranched terminal shoots were selected for the following growth season.

At each monitoring visit, growth and flowering phenophases were noted for each marked plant. The timing of the start of the growth and flowering seasons were taken when first signs of growth or first open flowers were found in the marked plant as a whole, and not just through evidence from the marked shoots. Monitoring continued until the end of the second growth season, in April 2004.

#### *Data analysis*

Monthly growth rates were calculated as the difference in shoot length between the current month and the previous month's measurements, divided by the number of days between the measurements. Mean monthly growth rates of each monitoring site were plotted against time in months to compare growth rates across the gradient.

Shoot elongation was taken as a substitute for biomass accumulation. At the end of each year of monitoring (April 2003 and April 2004), total growth per shoot, including all side shoots, was taken as the total annual growth. Total annual growth per shoot was calculated as the sum of monthly growth measurements taken across the year (May-April).

Kruskal-Wallis tests were used to test for significant differences in total annual growth between individuals of each species at different monitoring points along the gradient (N per monitoring point = 3). For the analysis of *Leucadendron nervosum* and *Leucadendron salignum*, which is found at only two points, Mann-Whitney U tests were done.

To verify evidence of temperature and moisture control from hypothesized patterns, relationships between growth and temperature and aspects of rainfall recorded at the monitoring sites, monthly data was explored further graphically and through simple regressions. Temperature recordings were converted to mean daily temperature of the month preceding each monthly measurement, and rainfall was converted to mean daily rainfall by dividing the total rainfall recorded since the previous measurement by the number of days between the measurements. Because rainfall is recorded at only three monitoring points, rainfall recorded at closest points to monitoring sites without rain gauges were taken as rainfall for that site. Therefore, rainfall recorded at 545 m, which is not a phenology monitoring site, was used for 744 m, rainfall recorded at 953 m was also used for 1044 m, and rainfall recorded at 1303 m was also used for 1196 m.

Relationships between growth and temperature/rainfall were tested across the gradient as well as at individual monitoring sites. Because physical and physiological processes regulating water availability to plants can vary over large timescales (Berger 1995), relationships between mean daily rainfall over one and two months preceding measurements were tested and the best fit selected. Cowling et al. (2005) reported the importance of rainfall reliability as a driver of plant traits in Mediterranean ecosystems. The regularity of rainfall events could be even more important to plants' ability to make use of available water, by sustaining soil moisture levels especially in summer, than the absolute amount of rainfall recorded (Porporato et al. 2004). Therefore the relationship between regularity of rainfall, which was calculated as the mean number of days between rainfall events, and growth was also investigated.

To explore growth responses to the combined effects of temperature and rainfall, and rainfall amount and variability, three dimensional contour plots with growth on the Z-axis, were constructed. The levels of contours are calculated as the average growth of points in the vicinity of a particular temperature-rainfall or rainfall amount-regularity combination, by means of distance weighted least squares. Values of mean number of days between rainfall events were log transformed to achieve a linear fit to mean monthly rainfall values.

## RESULTS

A careful analysis of climate recorded during the experiment revealed that the monitoring site at 953 m is somewhat cooler than the site directly above it at 1044 m (Figure 2a, see also Chapter



1, Table 3). This is possibly due to topographic effects, with the 953 m situated on a plateau, while the monitoring sites above 953 m are all set against the steep mountain slope, resulting in cold air drainage creating temperature inversions on the plateau during night time. Mean daily rainfall recorded during the month preceding the April 2003 measurements were extremely high due to a single very large rainfall event on 24 March 2003 (Figure 2b), and this month's data was therefore excluded from the regression analysis, as such high rainfall within such a short period is likely to be mostly lost to runoff, and plant growth would probably not show responses to it.

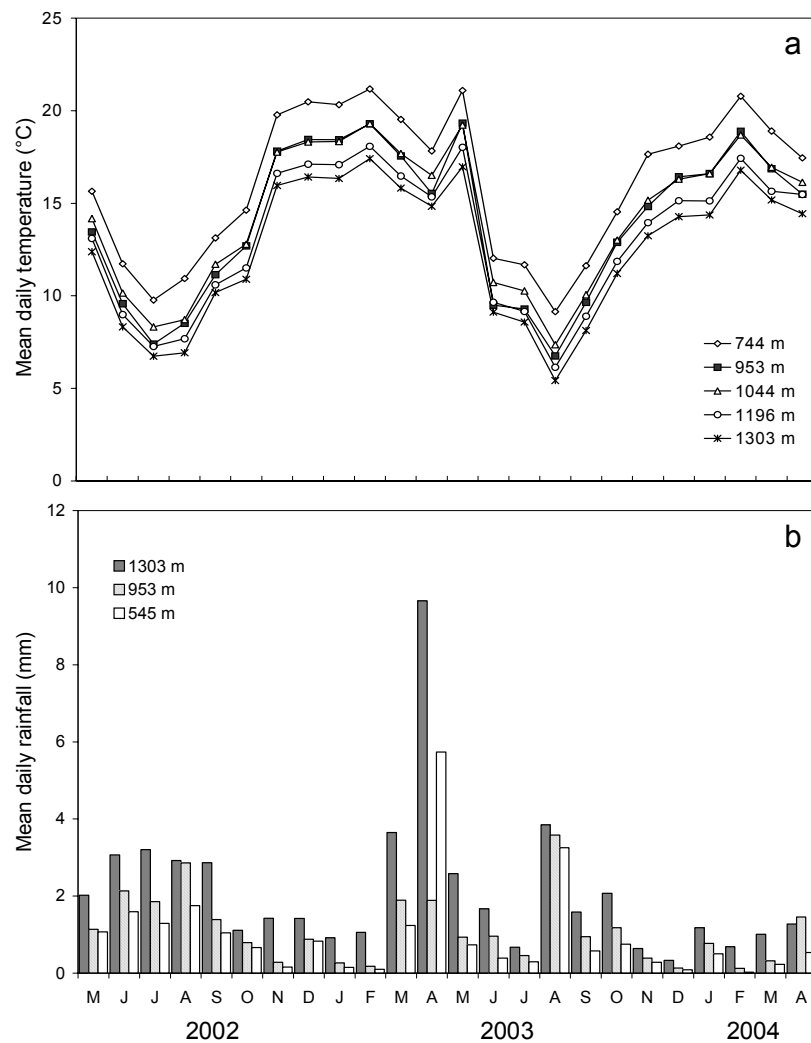


FIGURE 2. (a) Mean monthly temperatures and (b) mean daily rainfall recorded on the gradient during the experiment. Monthly temperature and rainfall values represent means of intervals between measurements, and are not necessarily aligned with the start of calendar months. Rainfall is expressed as mean daily rainfall because intervals between measurements varied between 28 and 34 days.

### *Timing of growth and flowering seasons*

The timing of growth and flowering seasons was somewhat more complex than anticipated, and often no clear signals for either temperature or moisture controls were discernable.

Timing and duration of growth seasons (Table 3) revealed distinct differences between Proteaceae and the understory shrub species, Ericaceae and *Erepsia gracilis*: all the Proteaceae species have clearly defined spring-summer growth seasons showing degrees of shifts in timing and duration with altitude, while *Erepsia gracilis* and the *Erica* species show year round growth, with some variation at different altitudes.

*Protea amplexicaulis* revealed clear temperature controlled growth patterns, with longer growth seasons recorded at the lowest altitudes of its distribution (1044 m and 953 m), due to both earlier start of growth season and later termination at these altitudes. However, *P. amplexicaulis*'s growth season ends at the highest altitude (1303 m) in February, which is generally the warmest month (Figure 2a), which may cast doubt on whether temperature is the main controlling factor in the growth of this species. *Protea laurifolia*, on the other hand, showed clear moisture controlled patterns, with the start of the growth season only slightly delayed in some plants at the highest altitude (1196 m), but with a much longer duration into late autumn at this monitoring site. The growth season gradually terminated earlier with decreasing altitude (Table 3).

*Protea repens*, *Leucadendron laurosum* males and females, and *Leucadendron salignum* females showed temperature related shifts towards an earlier start of growth season at warmer lower altitudes, but with variable patterns regarding the termination of the growth season. Growth in these species is possibly controlled by a combination temperature and moisture, but more evidence from other analyses is needed to confirm this. *Leucadendron nervosum* males as well as *Leucadendron salignum* males showed no shifts in timing of the start or termination of the growth season.

Because the *Erica* species and *Erepsia gracilis* have such extended growth seasons, it is rather difficult to discern shifts in timing and duration of the growth season across the gradient. *Erica plukenetii* shows a break in growth during August and September 2003 at 1303 m, which was an exceptionally cold month (Figure 2a). Other sites lower down also had some plants cease growth during August 2003. The break in growth between February and March 2004 at 1044 m

TABLE 3. Timing of growth seasons of nine monitored fynbos species, arranged according to altitude. Width of shaded bars indicates number of plants (out of 3) growing. Only data from second year of monitoring are shown.

Species	Alt (m)	2003					2004						
		M	J	J	A	S	O	N	D	J	F	M	A
<i>Protea amplexicaulis</i>	1303							■	■	■			
	1196						■	■	■	■	■		
	1044						■	■	■	■	■	■	
	953						■	■	■	■	■	■	
<i>Protea laurifolia</i>	1196						■	■	■	■	■	■	■
	1044						■	■	■	■	■	■	■
	953						■	■	■	■	■	■	
<i>Protea repens</i>	1303							■	■	■			
	1196						■	■	■	■	■		
	1044						■	■	■	■	■	■	
	953						■	■	■	■	■	■	
<i>Leucadendron laureolum</i> ♂	1303								■	■	■	■	■
	1196							■	■	■	■	■	■
	1044							■	■	■	■	■	■
	953						■	■	■	■	■	■	■
<i>Leucadendron laureolum</i> ♀	1303							■	■	■	■	■	■
	1196							■	■	■	■	■	■
	1044							■	■	■	■	■	■
	953						■	■	■	■	■	■	■
<i>Leucadendron nervosum</i> ♂	1303							■	■	■	■	■	■
	1044							■	■	■	■	■	■
<i>Leucadendron salignum</i> ♂	953							■	■	■	■	■	■
	744							■	■	■	■	■	■
<i>Leucadendron salignum</i> ♀	953							■	■	■	■	■	■
	744							■	■	■	■	■	■

TABLE 3. Extended.

Species	Alt (m)	2003										2004				
		M	J	J	A	S	O	N	D	J	F	M	A			
<i>Erica plukenetti</i>	1303															
	1196															
	1044															
	744															
<i>Erica vestita</i>	1044															
	953															
	744															
<i>Erepsia gracilis</i>	1303															
	1196															
	953															
	744															

is difficult to explain. It could be related to drought stress, but this trend is not noted at 744 m, which is even drier. *Erica vestita* shows similar trends of no growth during the coldest winter months at the highest end of its distribution. Moisture stress is probably the cause of the break in growth observed during late summer in individuals of this species occurring at lower altitudes (953 m and 744 m). No patterns in the timing and duration of the growth season that can be explained by temperature and moisture conditions across the gradient are apparent for *Erepsia gracilis*.

In all Proteaceae species, except for *Leucadendron nervosum*, flowering followed after the end of the growth season (Table 4). Interestingly, bud development in *Protea repens* commenced during winter before the start of the growth season, and continued all through the growth season, until flowers opened after the end of the growth season in late autumn of the following year. Le Maitre and Midgley (1991) have previously described this phenomenon in *Protea repens* and attributed it to an adaptation allowing this species to produce larger inflorescences than predicted by allometric relationships with terminal branch diameter. In some of the Proteaceae shifts towards earlier bud development at lower altitudes were observed, but because these phases occurred during late autumn to early winter, it is difficult to say whether

TABLE 4. Timing of flowering seasons of nine monitored fynbos species, arranged according to altitude. Width of shaded bars indicates number of plants (out of 3) flowering or budding, hatched shading indicates time of bud development, plain grey indicates flowering.

Species	Alt (m)	2003												2004				
		M	J	J	A	S	O	N	D	J	F	M	A					
<i>Protea amplexicaulis</i>	1303	■	■	■	■	■								■	■	■	■	■
	1196																■	■
	1044																■	■
	953																■	■
<i>Protea laurifolia</i>	1196	■	■	■	■	■	■	■	■	■	■	■	■				■	■
	1044	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Protea repens</i>	1303	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1196	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1044	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leucadendron laureolum</i> ♂	1303	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1196	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1044	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leucadendron laureolum</i> ♀	1303	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1196	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	1044	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leucadendron nervosum</i> ♂	1303																	
	1044																	
<i>Leucadendron salignum</i> ♂	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	744	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leucadendron salignum</i> ♀	953	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	744	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

TABLE 4. Extended.

Species	Alt (m)	2003										2004						
		M	J	J	A	S	O	N	D	J	F	M	A					
<i>Erica plukenetti</i>	1303																	
	1196																	
	1044																	
	744																	
<i>Erica vestita</i>	1044																	
	953																	
	744																	
<i>Erepsia gracilis</i>	1303																	
	1196																	
	953																	
	744																	

temperature plays a role (Table 4). It is possible, however, that general warmer conditions at lower altitudes allows for increased physiological activity even during winter, and that this may lead to faster development of flower buds. *Leucadendron nervosum* is an interesting exception to the other Proteaceae in the fact that this species completes flowering before the start of the growth season.

*Erica plukenetti* and *Erica vestita* continued growth throughout bud development and flowering stages. No altitudinal shifts in timing of bud development or flowering were observed in these species. *Erica vestita*, interestingly, has two flowering seasons per year, in autumn (March – May) and again in late winter (July to October). *Erepsia gracilis*, however, did cease growth during its flowering phase from mid summer to autumn. Earlier bud development and flowering were observed at the warmest site, indicating that warmer temperatures also accelerate flowering phenophases in this species.

#### Growth rates

Comparing growth rates at the various monitoring sites across the gradient proves very insightful, compared to the evidence gained from the timing and duration of growth seasons as

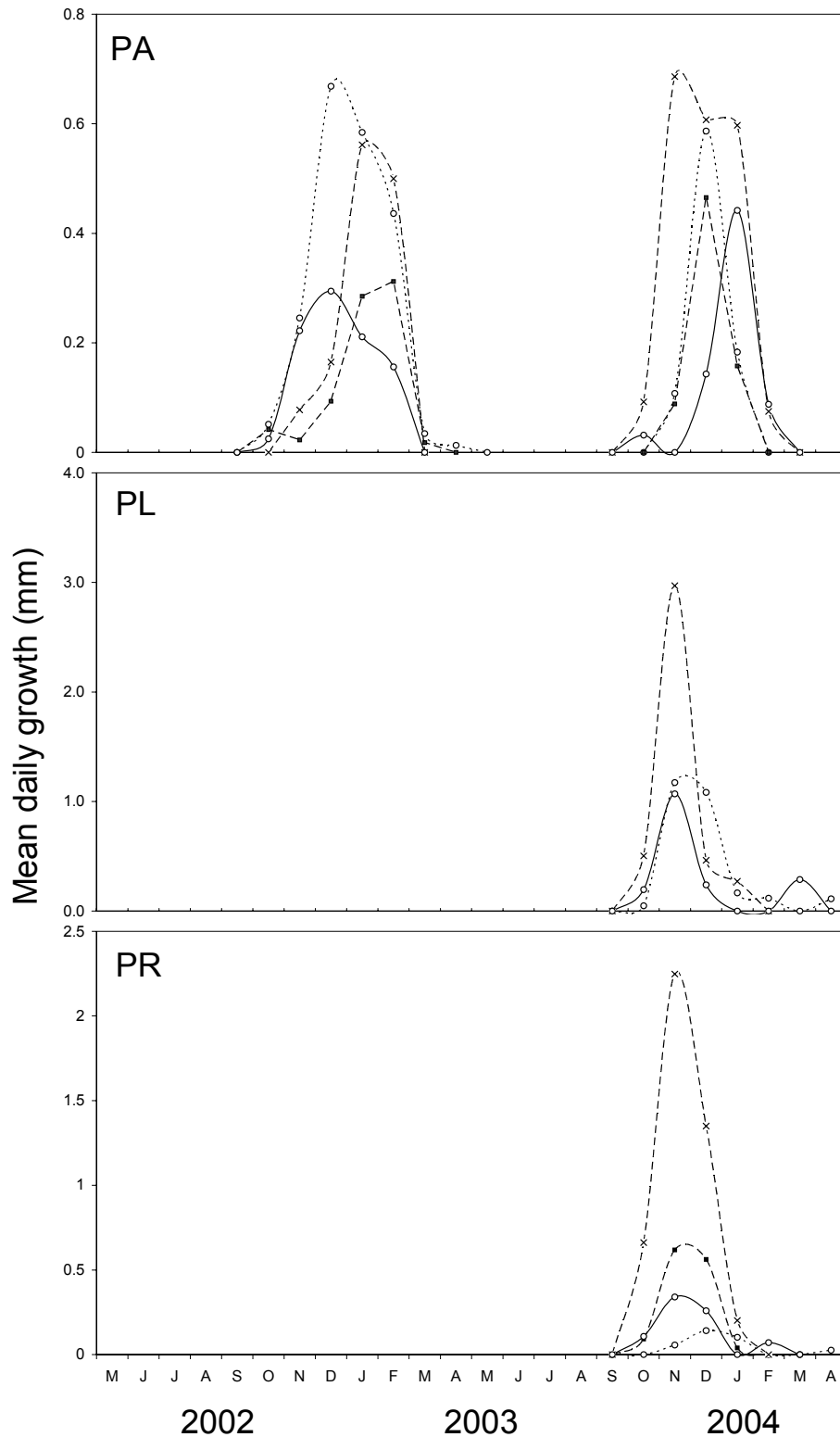
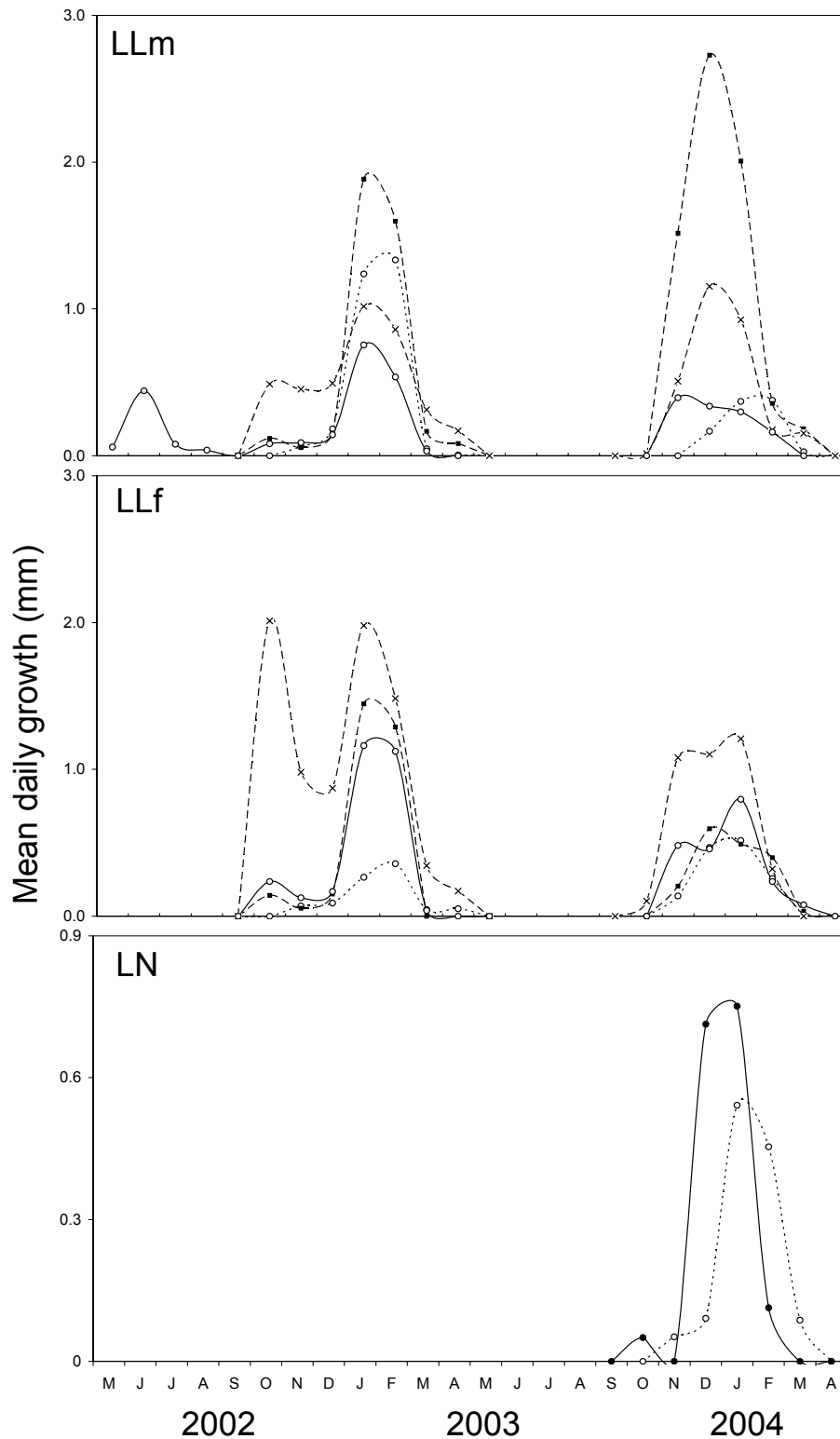


FIGURE 3. Mean daily growth rates recorded at different monitoring sites for nine fynbos species. Sites are arranged according to mean annual temperature of monitoring sites. Solid lines (—) indicate growth rate at warmest site, dotted lines (.....) indicate growth rates at coldest site and dashed lines (- - -) indicate growth rates at intermediate sites. Where species occur at four sites, two intermediate sites are distinguished by the markers x for the warmer and ■ for the colder.



colder of the two sites. Species are PA – *Protea amplexicaulis*, PL – *Protea laurifolia*, PR – *Protea repens*, LLm – *Leucadendron laureolum* males, LLf – *Leucadendron laureolum* females, LN – *Leucadendron nervosum* males, LSm – *Leucadendron salignum* males, LSf – *Leucadendron salignum* females, EP – *Erica plukenetti*, EV – *Erica vestita*, EG – *Erepsia gracilis*. *P. laurifolia*, *P. repens*, *L. nervosum* and *E. vestita* were not monitored in 2002.



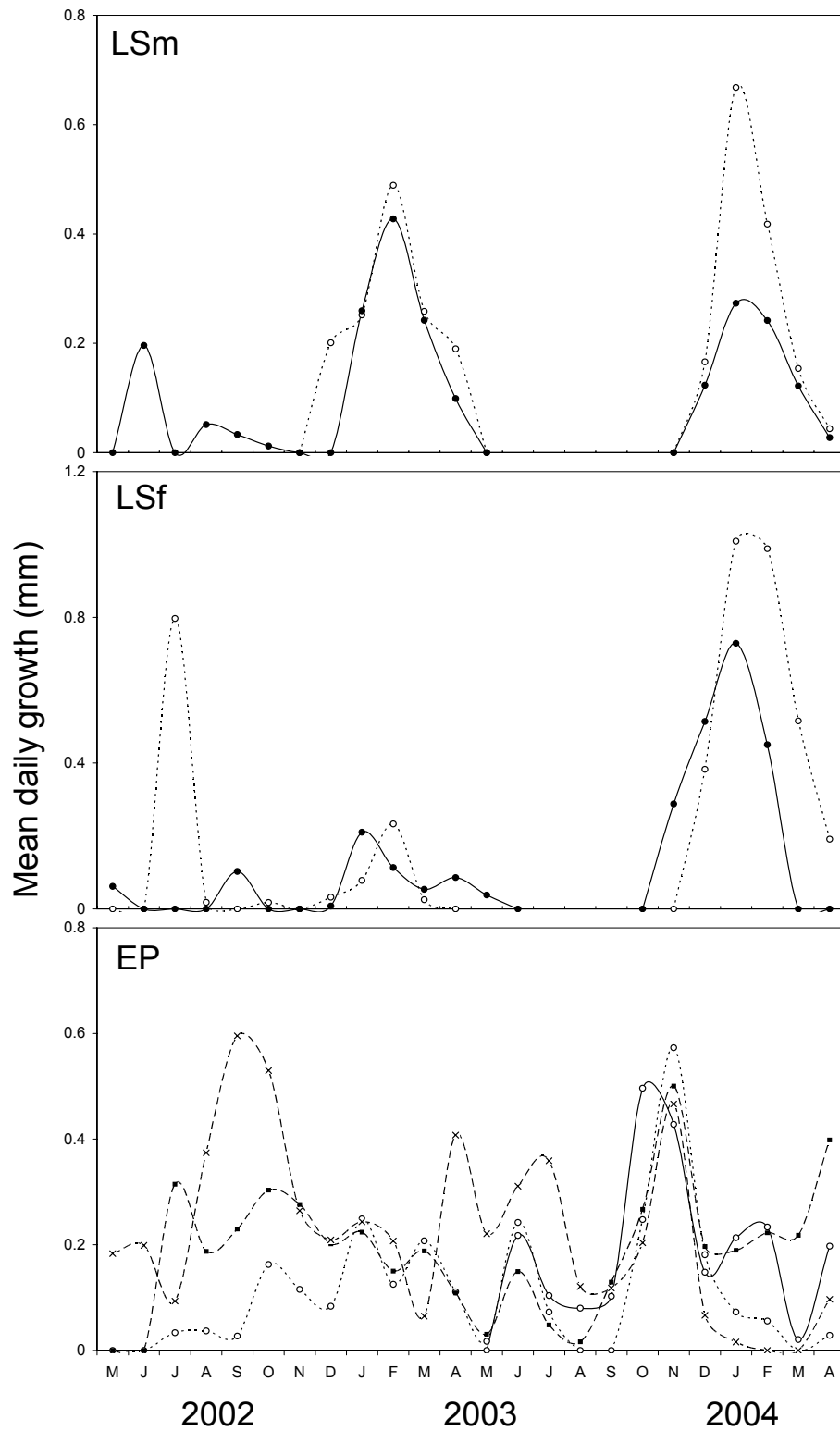


FIGURE 3. Extended

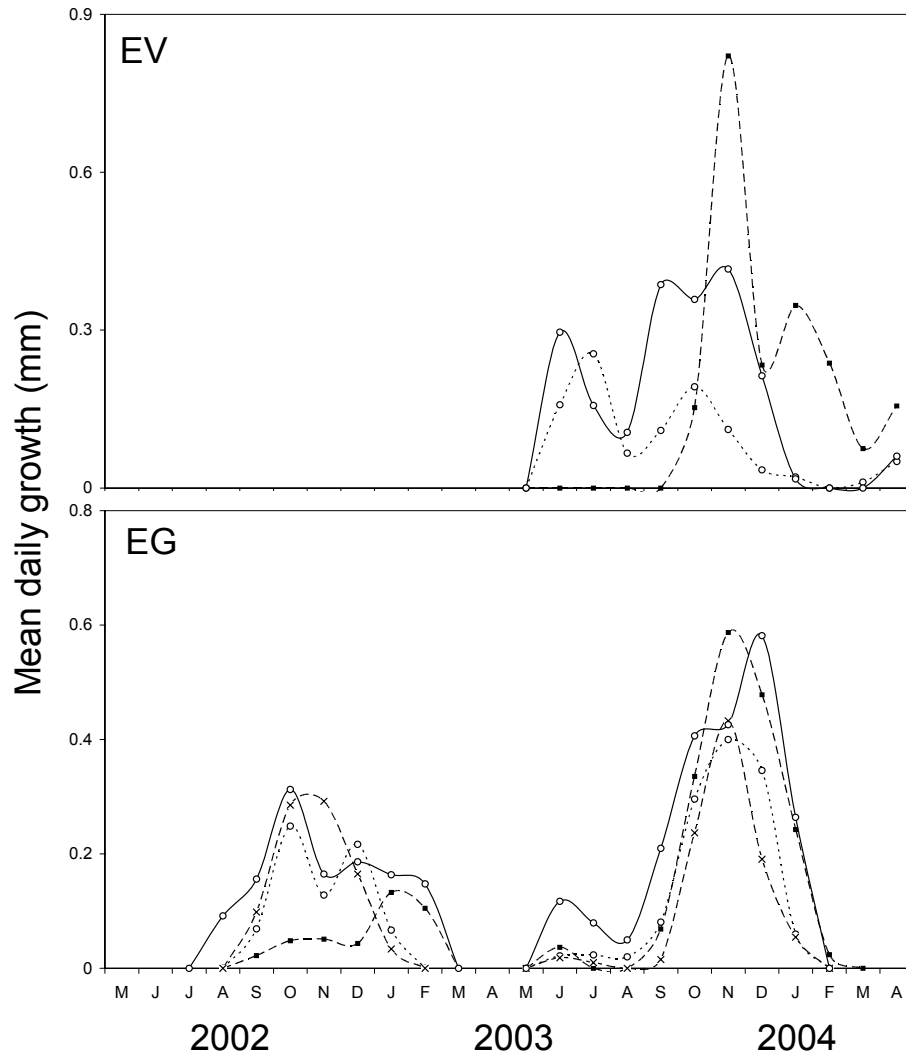


FIGURE 3. Extended

indicators of temperature and or moisture control of growth. Because temperature changes on the gradient do not exactly follow the altitudes of the monitoring sites, growth rates were compared according to mean annual temperature of the monitoring sites, rather than their altitudes. This has implications only for the Proteaceae with a lower end to their distribution ranges at 953 m (refer to Table 2). With these species, 'warmest' site refers to the monitoring site at 1044 m.

In all species except *Protea amplexicaulis*, where no trends were discernable, a combination of temperature and moisture effects control growth rates during different parts of the growth season and at different altitudes (Figure 3). In *Protea repens* and *Leucadendron laureolum* female shoots

at middle sites showed highest growth rates throughout the growth season. *Leucadendron laureolum* males also had highest shoot growth rates at middle sites, but only during the second growth season. During the first year of monitoring, growth was recorded throughout winter at the warmest site, but not at other sites. This trend was not repeated in the second year of monitoring. Interestingly, individuals at the warmest site show an earlier peak in growth rates, while the coldest site peaks later in the growth season when growth at the warmer sites has already started decreasing. This pattern was also found in *Protea laurifolia* and *Protea repens*. In many species, such as *Protea laurifolia*, *Leucadendron nervosum*, *Leucadendron salignum* females and *Erica vestita*, higher shoot growth rates are recorded at warmer/lower sites during spring, but during summer, and especially late summer, higher growth rates are recorded at cooler and moister higher sites, presumably because of moisture and perhaps high temperature stress inhibiting growth at warmer but drier sites. A bimodal growth pattern, with a second growth peak in autumn was found at the warmest site for *Protea laurifolia*.

Growth rates of *Erepsia gracilis* shoots were generally highest at the warmest site (744 m), indicating that growth rates in this species are controlled mainly by temperature (Figure 3). However, during peak summer months (November and December 2002, November 2003) growth rates of higher/cooler and moister sites were briefly higher than the warmest site, indicating that only during mid-summer moisture availability becomes somewhat limiting to growth at the warmest, driest site.

*Erica plukenetti* has extremely variable growth, as indicated by timing and duration of the growth season, as well as growth rates. During most of the year, highest growth rates were measured at middle sites (Figure 3). However, peak growth rates switch between various altitudes during different parts of the growth season. During late summer of the 2002-2003 growth season, growth decreased at the middle sites while growth increased at the coolest/highest site, so that in January as well as March 2003 growth rates were slightly higher at the coolest site than on the rest of the gradient. On the other hand, during September 2003, much higher growth rates were recorded at the warmest site, possibly because colder temperatures constrained growth elsewhere on the gradient, while peak growth rates switched back to the highest/coolest site during November 2003, while growth decreased at the middle and warmest/lowest sites.

### Shoot elongation

The fact that the monitoring site at 953 m is colder than 1044 m also caused problems for the interpretation of shoot elongation against altitude, as patterns of biomass accumulation in relation to altitude produced trends that were not explained by any of the hypotheses. However, when mean annual shoot elongation was plotted against mean annual temperature of the monitoring site, the problem was rectified (Figure 4), revealing a strong sensitivity of shoot elongation to temperature.

*Protea laurifolia*, *Protea repens* and *Leucadendron laureolum* males and females have the highest shoot elongation at intermediate temperatures, suggesting that optimum growth in these species are the result of combined optimum temperature and moisture conditions. However only the growth of *Leucadendron laureolum* male shoots were significantly different at the 0.05 level between monitoring sites (Figure 4). Interestingly, *Leucadendron laureolum* males and females show optimum growth at different temperatures, with males peaking at 13°C mean annual temperature, while females peak at 14°C. *Erica plukenetti* and *Erica vestita* recorded higher total shoot growth at warmer temperatures, but no decrease in growth was found at the warmest site in their distributions. Growth in these species was also not significantly different between monitoring sites. It is possible that growth is controlled in these species mainly by temperature at higher sites, but at the warmest site lack of moisture possibly inhibits the effects of increased temperatures on growth. Contrasting to the *Erica* species, *Erepsia gracilis* growth appears to be controlled by temperature across the entire gradient, with highest total annual shoot growth recorded at the warmest monitoring site.

*Leucadendron nervosum* responded with higher growth to higher temperatures, while *Leucadendron salignum* males and females on the other hand responded to higher rainfall. Significant differences in annual shoot growth between the 953 m and 744 m monitoring sites were found for *Leucadendron salignum* females (Figure 4). However, because these species were each monitored at only two sites, it is difficult to say with certainty whether growth in these species are controlled by a single factor only. If compared to trends in growth of other, more widely distributed species on the gradient, it seems that the point where temperature and moisture impacts on growth change in dominance is around 14°C mean annual temperature, and these two species are restricted in their distributions on the gradient to either side of this threshold.

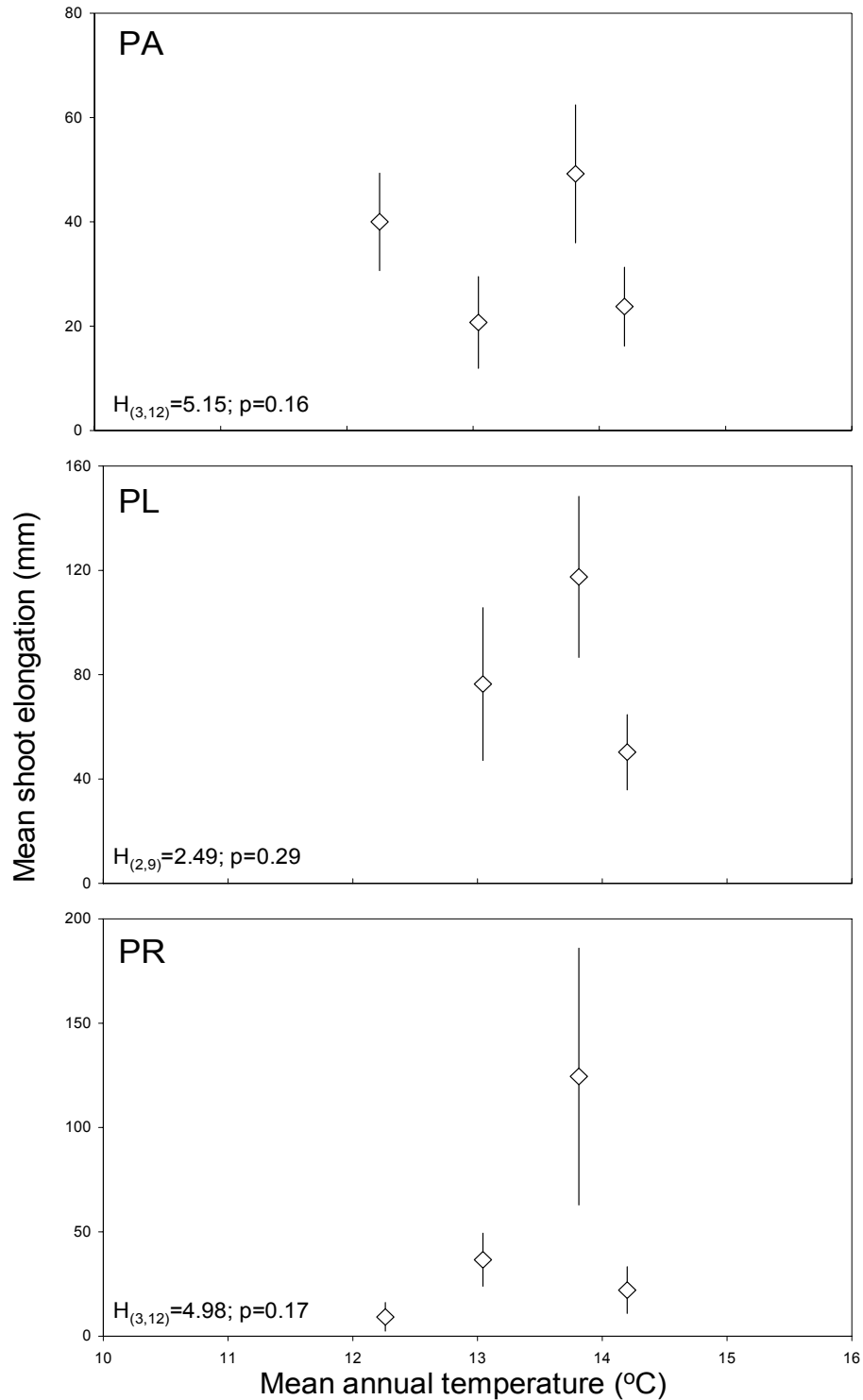
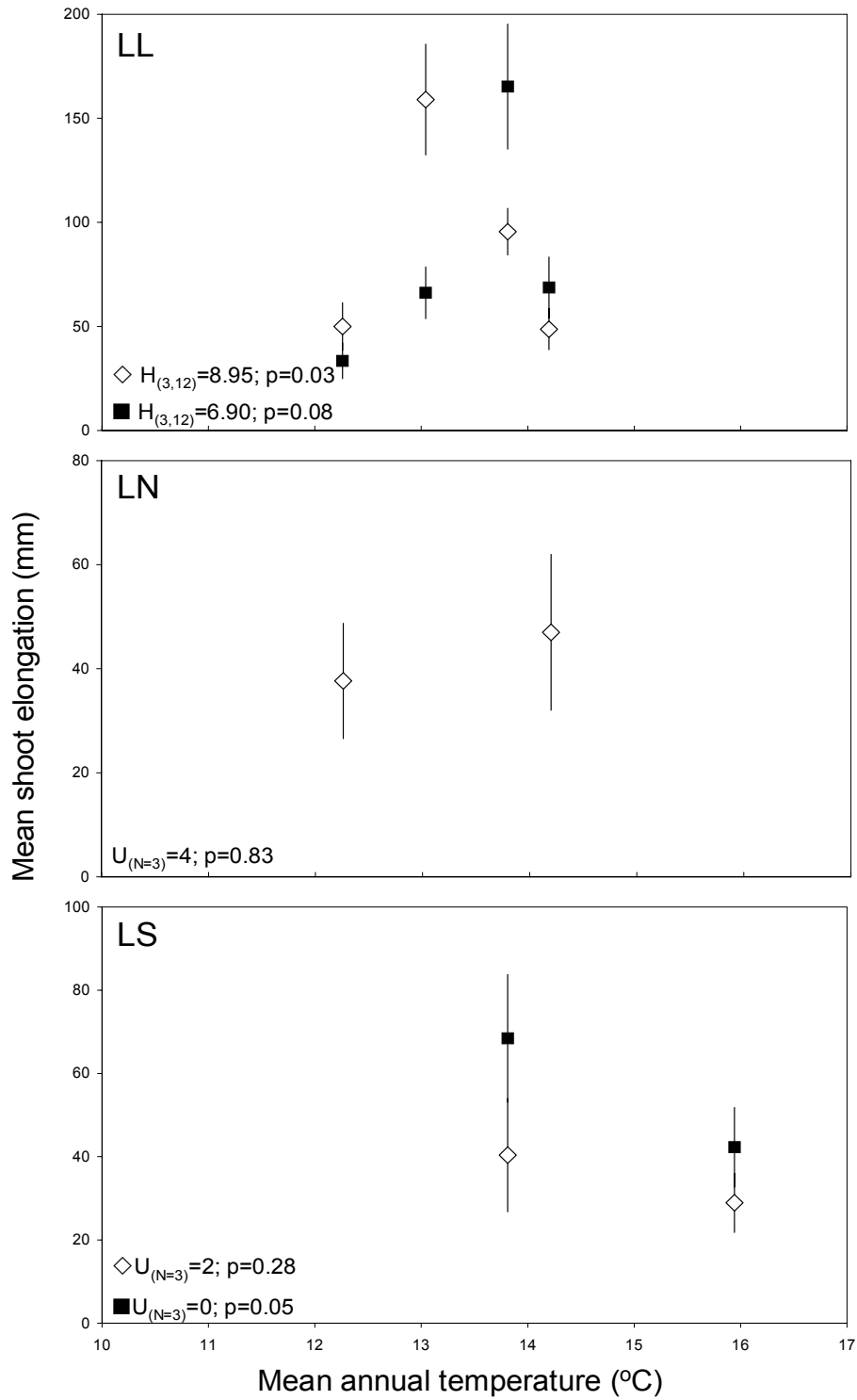


FIGURE 4. Total annual shoot elongation in relation to mean annual temperature of monitoring sites. Statistics in lower left corner indicate results of Kruskal-Wallis non-parametric analysis of variance testing for differences in shoot elongation between site for species occurring at more than two monitoring sites (H), or Mann-Whitney U tests for differences in shoot elongation for species occurring at only two sites (U).  $\diamond$  represent males in the case of *Leucadendron laureolum* and



*Leucadendron salignum*, while ■ represent females. Error bars indicate one standard error. Species are PA – *Protea amplexicaulis*, PL – *Protea laurifolia*, PR – *Protea repens*, LL – *Leucadendron laureolum*, LN – *Leucadendron nervosum* males, LS – *Leucadendron salignum*, EP – *Erica plukenetii*, EV – *Erica vestita*, EG – *Erepsia gracilis*.

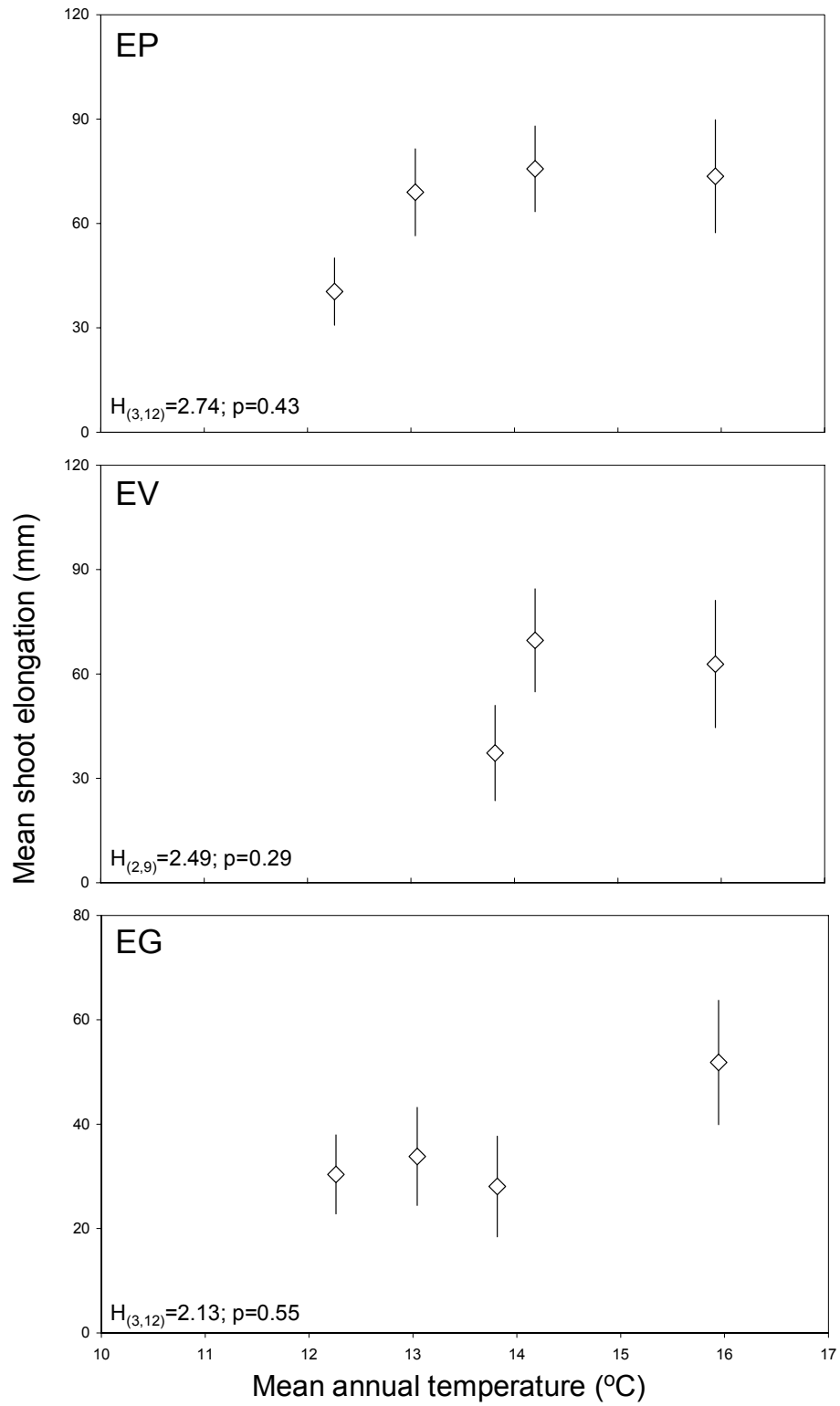


FIGURE 4. Extended

### Correlations of mean monthly growth with temperature and rainfall

The relationships between monthly shoot elongation and associated temperature and rainfall recordings were first investigated for trends across the gradient. Growth rates and biomass accumulation in all species except *Erepsia gracilis* and *Protea amplexicaulis* indicate highest growth responses in the middle of the gradient, at intermediate temperatures and rainfall, suggesting that growth responses are to optimum climate conditions, rather than linear. Therefore cubic polynomial regression analyses of growth responses to temperature and rainfall were performed in addition to linear regressions. In all instances, even growth responses of *Erepsia gracilis* to temperature, polynomials provided a better fit, with significant regressions found for most species (Table 5). However,  $r^2$  values indicate that the curves explain relatively little of the variation in the data.

TABLE 5. Results of cubic polynomial regression analysis of growth responses to temperature and rainfall. Growth values were correlated with mean temperatures of the preceding month, while mean daily rainfall of one and two months preceding growth measurements were tested and the best correlation selected. Time scale indicates whether one or two months' mean rainfall revealed the best fit. Growth and climate data from all sites at which a species occurs were included in the analyses. Values in bold indicate regressions significant at 0.05 level.

	Temperature			Rainfall			Time scale
	F	p	$r^2$	F	p	$r^2$	
<i>Protea amplexicaulis</i>	<b>7.35</b>	<b>0.0002</b>	<b>0.19</b>	<b>13.81</b>	<b>&lt;0.0001</b>	<b>0.24</b>	<b>2 months</b>
<i>Protea laurifolia</i>	2.68	0.06	0.20	1.36	0.27	0.11	1 month
<i>Protea repens</i>	1.98	0.13	0.12	2.48	0.07	0.15	1 month
<i>Leucadendron laureolum</i> ♂	<b>5.74</b>	<b>0.001</b>	<b>0.16</b>	<b>5.44</b>	<b>0.002</b>	<b>0.15</b>	<b>1 month</b>
<i>Leucadendron laureolum</i> ♀	<b>8.95</b>	<b>&lt;0.0001</b>	<b>0.23</b>	<b>12.89</b>	<b>&lt;0.0001</b>	<b>0.30</b>	<b>1 month</b>
<i>Leucadendron nervosum</i> ♂	1.94	0.16	0.23	2.45	0.10	0.28	2 months
<i>Leucadendron salignum</i> ♂	<b>5.32</b>	<b>0.003</b>	<b>0.27</b>	4.78	0.006	0.25	2 months
<i>Leucadendron salignum</i> ♀	<b>3.14</b>	<b>0.03</b>	<b>0.18</b>	2.88	0.05	0.17	2 months
<i>Erica plukenetti</i>	<b>3.35</b>	<b>0.02</b>	<b>0.08</b>	1.97	0.13	0.07	1 month
<i>Erica vestita</i>	2.48	0.08	0.19	1.30	0.30	0.11	2 months
<i>Erepsia gracilis</i>	<b>3.33</b>	<b>0.02</b>	<b>0.10</b>	<b>6.14</b>	<b>0.0008</b>	<b>0.17</b>	<b>1 month</b>

However, scatterplots of growth responses to temperature and rainfall, grouped according to monitoring site do not show clear patterns of responses to optimum temperatures (not shown). Low or no growth is generally recorded at low temperatures, while responses at higher temperatures are very erratic, explaining the low  $r^2$  values and indicating that temperatures alone do not account for the growth responses observed despite significant regression results. Scatterplots of growth responses to rainfall also indicate no clear trends (not shown), and the data was therefore further investigated for possible interactive effects of temperature and rainfall.



Contour plots of growth responses to temperature and rainfall (Figure 5) revealed interesting results. Growth trends were expressed by increasing levels of contours. However, because not all possible combinations of temperature and rainfall were recorded on the gradient during the experiment, especially in species with limited distributions and those monitored only for one year, the contour fitting procedures extrapolate growth responses where no data exists. These extrapolations are in most cases not biologically meaningful, and therefore raw data points were overlaid on the contour plots and only trends where data exists were considered.

All species recorded on average higher growth even at extremely low rainfall (Figure 5). Only in *Protea laurifolia* and *Erica plukenetti* were there indications of a lower limit of around 0.5 mm mean daily rainfall threshold, below which growth decreased slightly. However, all species except *Leucadendron laureolum* and *Leucadendron salignum* showed a temperature effect on growth, with both very high and very low temperatures affecting growth negatively, indicating that on average, sensitivity to high temperatures during summer has a stronger regulating effect on growth than rainfall.

This strong temperature effect on growth was confirmed through a simple analysis when data from Table 3, of number of plants growing per month, was plotted against mean monthly temperature (Figure 6). It was revealed that in terms of growth at the whole plant level, all the species monitored in this experiment grow best at an optimum temperature range of 10-18°C mean daily temperature. Some species, including *Protea amplexicaulis*, *Protea laurifolia* and *Protea repens*, have very narrow ranges of optimum temperatures, and these species also have the lowest optimum temperatures relative to the other species. *Erica plukenetti* and *Erica vestita* have the broadest range of optimum growth temperatures, which could explain why these species grow for such extended times during the year. However, even *Erepsia gracilis*, which in terms of growth rates and biomass accumulation showed such strong growth responses to warmer temperatures, was revealed to have a rather low and narrow range of temperatures where all plants would actively grow. *Leucadendron salignum* males and females are the most tolerant of high temperatures, with most plants growing even at around 18°C mean daily temperature.

The question still remains as to why fynbos species are able to maintain high growth rates even at extremely low rainfall, when summer moisture stress is considered such a strong limiting

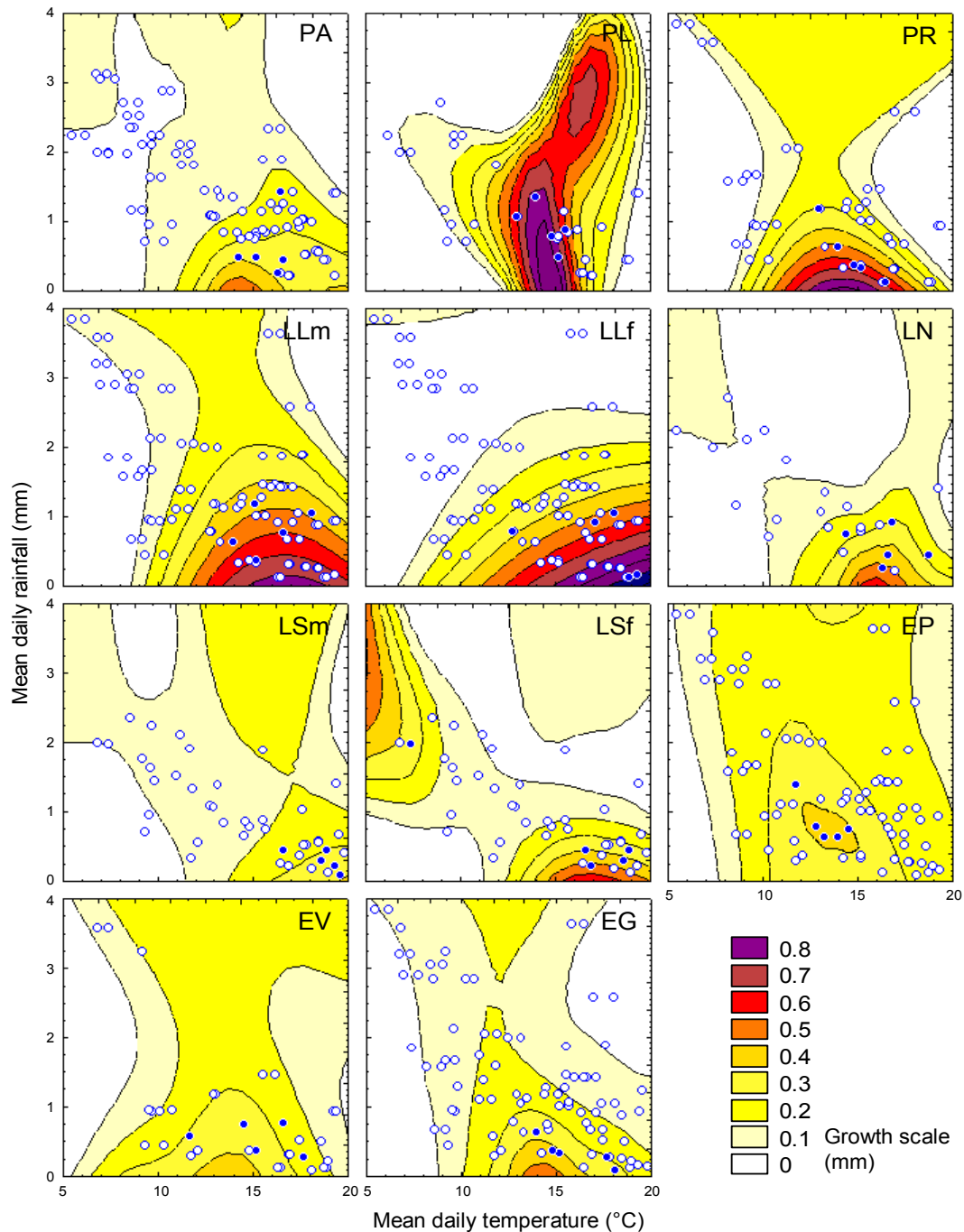


FIGURE 5. Contour plots relating mean daily rainfall and mean daily temperatures to monthly growth recorded across the gradient. Levels of contours represent mean growth in relation to particular temperature and rainfall combinations, calculated by distance weighted least squares. Raw data points were overlaid, and trends in contours should only be interpreted in areas where actual data exists. The five highest monthly growth values recorded for each species during the experiment are indicated by filled symbols. Species are PA – *Protea amplexicaulis*, PL – *Protea laurifolia*, PR – *Protea repens*, LLm – *Leucadendron laureolum* males, LLf – *Leucadendron laureolum* females, LN – *Leucadendron nervosum* males, LSm – *Leucadendron salignum* males, LSf – *Leucadendron salignum* females, EP – *Erica plukenetti*, EV – *Erica vestita*, EG – *Erepsia gracilis*.

factor to growth in Mediterranean climates (Roy et al. 1995, Spano et al. 1999). It was thought that low but regular rainfall through summer could explain summer growth rates, as such rainfall patterns would maintain soil moisture levels above stress thresholds. It was expected that a plot of growth responses to amount of rainfall combined with rainfall regularity, expressed as mean number of days between rainfall events, would reveal patterns of high growth at low rainfall, but with short intervals between rainfall events (Figure 7). This was true to some extent for most of the monitored species, with the most notable exceptions being *Protea amplexicaulis*, *Protea repens*, *Leucadendron laureolum* females and *Leucadendron nervosum*, which grew best at low rainfall combined with large intervals between rainfall events. *Erica plukenetti* and *Leucadendron salignum* males and females most clearly prefer mean daily rainfall below 1 mm falling every 4-8 days. *Protea laurifolia*, *Leucadendron laureolum* males, *Erica vestita* and *Erepsia gracilis* showed reduced growth as a result of a few rare long dry periods of on average more than twelve days.

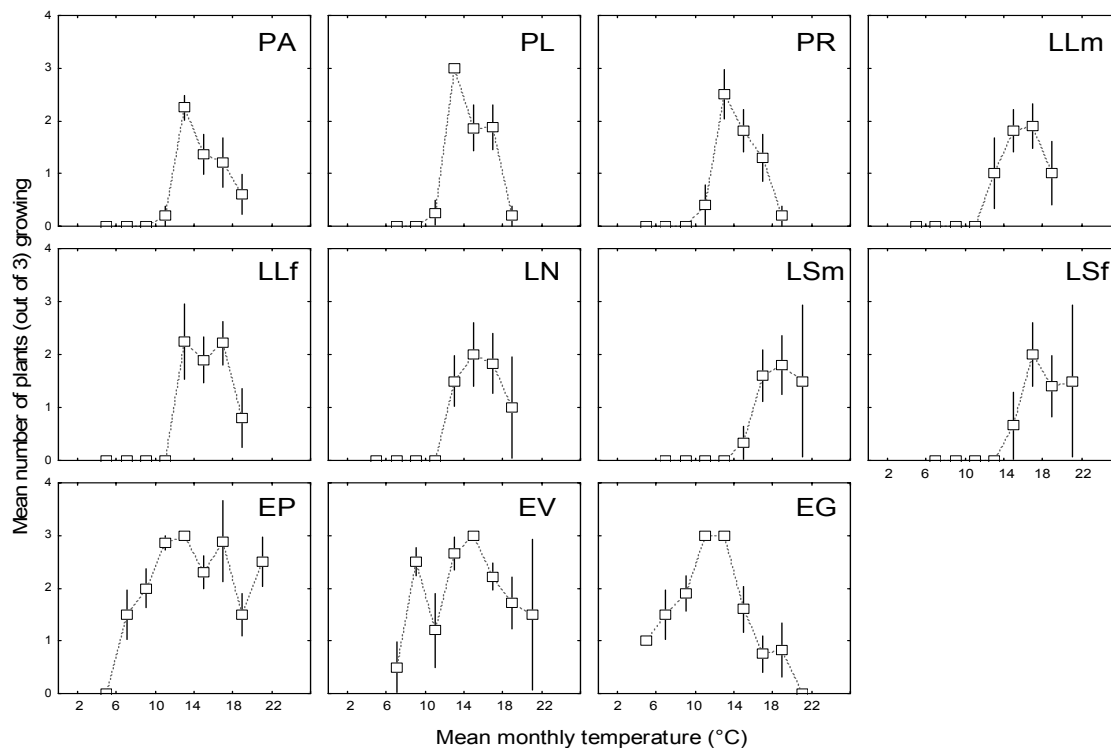


FIGURE 6. Mean number of plants growing (data from Table 3) related to mean monthly temperature, indicating ranges of optimum temperatures for growth at the plant level for the nine species monitored. Error bars indicate one standard error. Species are PA – *Protea amplexicaulis*, PL – *Protea laurifolia*, PR – *Protea repens*, LLm – *Leucadendron laureolum* males, LLf – *Leucadendron laureolum* females, LN – *Leucadendron nervosum* males, LSm – *Leucadendron salignum* males, LSf – *Leucadendron salignum* females, EP – *Erica plukenetti*, EV – *Erica vestita*, EG – *Erepsia gracilis*.

## DISCUSSION

The results of this study again highlight how phenology in Mediterranean climates is subjected to complex constraints of temperature and moisture. The environmental gradient allowed for the observation of growth responses to different temperature and moisture conditions as a result of altitudinal variation as well as the seasonal progression of shifts in temperature and moisture balances. Growth responses on a gradient provide valuable first indications of what factors could be controlling growth, but as this study showed, it needs to be followed up with specific investigations of growth responses to simultaneously recorded temperature and rainfall to verify the results of the gradient analysis.

Evidence from timing of growth and flowering seasons proved least insightful of all the analyses, with many species showing no clear signal for either temperature, moisture or combined temperature and moisture across the gradient (Table 6), which makes predictions of climate change responses based on variation in timing of phenophases rather difficult. It is therefore surprising that many phenological studies focus so strongly on timing of phenophases as indicators of climate change responses, especially since interannual variability in the timing of phenophases are often quite high (Levesque et al. 1997, Thórhallsdóttir 1998). It could be that the monitoring interval in this study was too broad to pick up subtle differences, as changes in timing are often a matter of a few days (Chmielewski and Rotzer 2001, Penuelas et al. 2002, Aerts et al. 2004), although differences in timing of flowering of up to four weeks (Thórhallsdóttir 1998) and 34 days (Levesque et al. 1997) have been found.

It was surprising that the results of the gradient hypotheses regarding timing and duration of phases, growth rates and biomass accumulation did not consistently point to either temperature, moisture or temperature-moisture combined control of growth for each individual species. Rather, various aspects of phenology seemed to be controlled by different climatic factors (Table 6). Except for *Protea amplexicaulis*, where generally no patterns were found, and *Erepsia gracilis*, which showed strong indications of temperature control across all analyses, growth rates and biomass accumulation in the other species mostly indicated combined temperature and moisture control of growth, with the location of optimum conditions varying in altitude among the species, and even between males and females of the same species, as was found in *Leucadendron laureolum*.

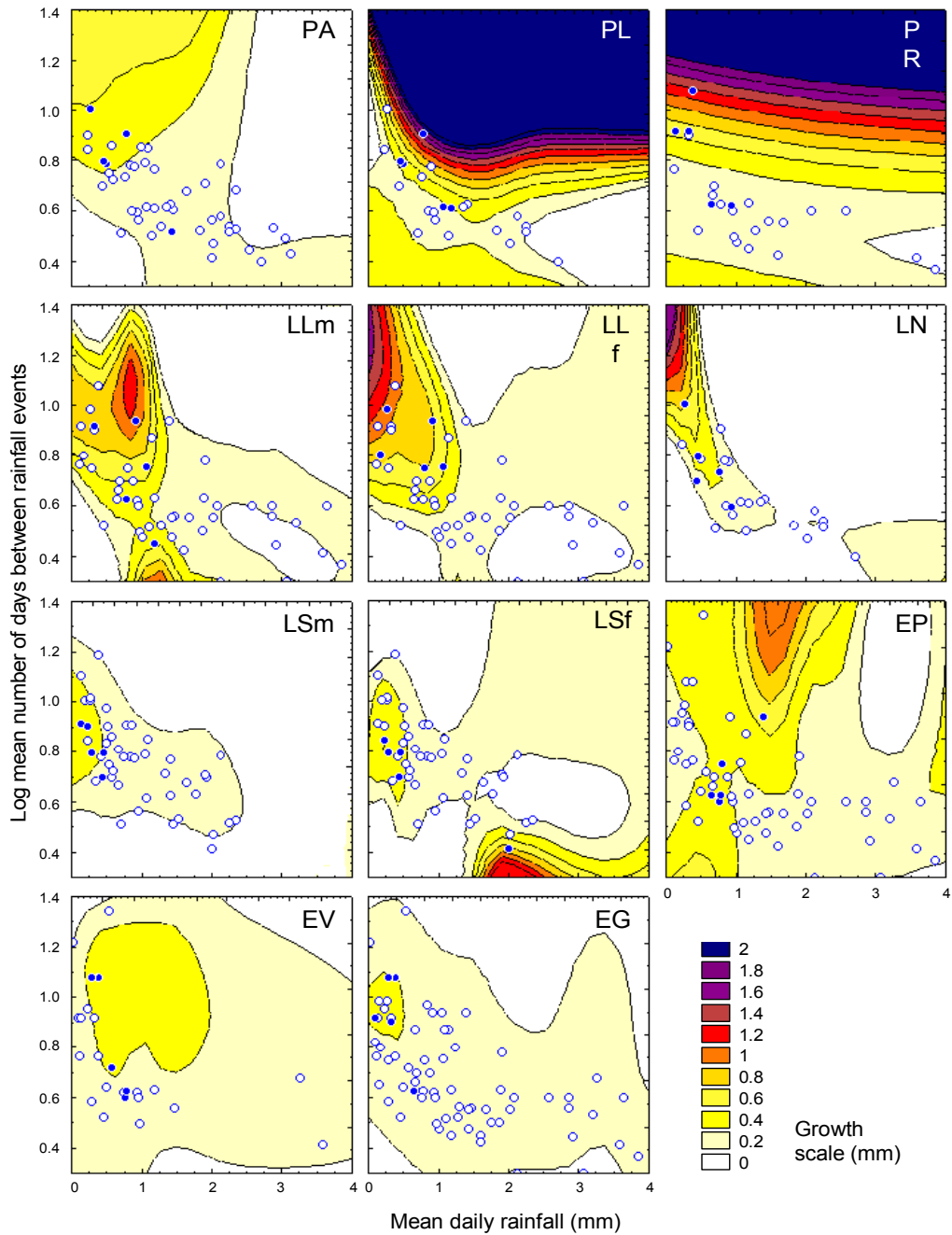


FIGURE 7: Contour plots relating mean daily rainfall and the logarithm of mean length of dry interval between rainfall events to monthly growth recorded across the gradient. Levels of contours represent mean growth in relation to particular rainfall amount and interval size combinations, calculated by distance weighted least squares. Raw data points were overlaid, and trends in contours should only be interpreted in areas where actual data exists. The five highest monthly growth values recorded for each species during the experiment are indicated by filled symbols. Species are PA – *Protea amplexicaulis*, PL – *Protea laurifolia*, PR – *Protea repens*, LLm – *Leucadendron lauroolum* males, LLf – *Leucadendron lauroolum* females, LN – *Leucadendron nervosum* males, LSm – *Leucadendron salignum* males, LSf – *Leucadendron salignum* females, EP – *Erica plukenetti*, EV – *Erica vestita*, EG – *Erepsia gracilis*.

TABLE 6. A summary of the results of the various hypotheses tested in this study.

Species	Timing and duration		Growth rates	Biomass accumulation
	Flowering	Growth		
<i>Protea amplexicaulis</i>	?	T?	?	?
<i>Protea laurifolia</i>	T+M	M	T+M	T+M
<i>Protea repens</i>	T+M	T?	T+M	T+M
<i>Leucadendron laureolum</i> ♂	M	?	T+M	T+M
<i>Leucadendron laureolum</i> ♀	?	?	T+M	T+M
<i>Leucadendron nervosum</i> ♂	T	?	T+M	T?
<i>Leucadendron salignum</i> ♂	?	?	M?	M?
<i>Leucadendron salignum</i> ♀	?	T+M	T+M	M?
<i>Erica plukenetti</i>	?	?	T+M	T+M
<i>Erica vestita</i>	?	T+M	T+M	T+M
<i>Erepsia gracilis</i>	T	?	T*	T

Notes: With regards to timing and duration of growth and flowering seasons, growth rates and biomass accumulation: T: temperature is the main controlling factor, M: moisture is the main controlling factor, and T+M indicates combined temperature and moisture effects. A question mark indicates that no clear signals were found. If M or T is followed by a question mark results indicated temperature and moisture, but there are some doubts on the validity of the conclusion. T\*, for *Erepsia gracilis* growth rates, indicates that growth rates were controlled by temperature within thresholds.

However, the fact that temperatures decrease while rainfall increases with altitude on the gradient turned out to be somewhat confounding, especially in the case where growth responses were to optimum conditions, rather than linear. Because the middle of the gradient represents intermediate conditions of both temperatures and rainfall, simple analyses of growth trends across the gradient could not distinguish whether species showing highest growth responses in the middle of the gradient were due to moisture limitations, temperature limitations or both. Thus optimum growth recorded in the middle of the gradient pointed to combined effects of optimum moisture and temperature in most species, but further analysis revealed growth responses to be the result of extreme temperature sensitivity related to a narrow range of temperatures allowing optimum growth, while rainfall had comparatively little to do with growth patterns, except for some species requiring low but regular rainfall to sustain growth during summer.

In colder climates, consistent positive responses to higher temperatures associated with decreasing altitude (James and Grace 1994, Levesque et al. 1997, Dunne et al. 2003) makes predictions relating to climate warming relatively simple. Although regressions of growth against temperature and rainfall did not prove very insightful in this study, regressions did show that growth responses are generally highly variable around high temperatures and low rainfall.

Climate change predictions for the Western Cape warn that by 2050 mean annual temperatures may increase by 0.5-1°C and annual precipitation may decrease by up to 25% (Rutherford et al. 1999). Such changes in climate are therefore likely to lead to erratic responses and making confident predictions could be difficult.

A first, very simple prediction to make is that even minor temperature increases could have severe negative effects on growth in species with relatively narrow ranges of optimum growth temperatures. Effects of altered rainfall patterns on fynbos species remain a challenge. Only two species in this study, *Protea laurifolia* and *Erica plukenetti*, responded with negative growth to rainfall of less than 0.5 mm mean daily rainfall, while other species were able to maintain high growth during the driest months recorded during the study, provided that temperatures were not too high. The range of annual rainfall on the gradient is quite wide, with the lower weather station recording on average 56% less annual precipitation than the station at 1303 m. The fact that the monitored species generally did not seem to respond to such a wide range of rainfall conditions indicate that they are possibly quite drought tolerant, or that they have other means of sustaining water supply which is not related to short term rainfall, such as extensive root systems able to tap into deep underground water sources (Chaves et al. 2002).

Another interesting aspect regarding growth responses to rainfall that emerged from this study is that many species require regular low rainfall through the summer growth period to sustain high growth rates. At this stage, climate models are only able to predict general increases or decreases in precipitation, but indications are that rainfall patterns may increase in variability and shift towards fewer but more intense rainfall events (Joubert and Hewitson 1997, Fauchereau et al. 2003). Such changes in rainfall patterns will very likely have negative effects on growth in fynbos species.

Because flowering was only investigated in terms of timing and duration, the potential effects of climate change on reproductive output remains unresolved. Climate change may have indirect effects on reproductive output in some Proteaceae species, through effects on growth. It has been shown that reduced growth, and especially reduced branching, leads to the production of less inflorescences in Proteaceae species with sympodial architecture (Bond et al. 1995). Therefore, although adult plants may survive the effects of climate change, reduced seed banks as a result of poor inflorescence production may lead to the disappearance of populations after fire.

### *Conclusion and suggestions for further study*

This study showed that growth of fynbos is very sensitive to temperature, and that even small increases in temperature, as predicted by climate change models, may have severe negative effects on growth in these species. Growth in fynbos species is possibly best explained by responses to optimum temperatures in combination with regular rainfall, rather than rainfall totals. How predicted rainfall changes might affect fynbos is however not clearly resolved yet.

Although fynbos is quite tolerant to short term summer drought, the effects of an overall reduction in annual rainfall could be severe, and attempts should be made to predict how fynbos will respond to extensive drought conditions. Possible further studies should include investigations into the effects of rainfall variability over larger timescales, such as seasonal and interannual variability of rainfall on growth, since this study revealed that short term rainfall patterns of one to two months do not relate well to observed growth responses. Since most Proteaceae have single annual growth seasons, and annual growth increments are clearly defined, these species could be well suited to retrospective growth analysis. Analysing growth patterns in relation to interannual rainfall variation could shed much light on the timescales over which fynbos species utilise water resources, and provide insights into which stages of annual rainfall patterns are most critical to successful growth.

The effects of a 25% reduction in annual rainfall on fynbos should also be tested, and experimental manipulations of rainfall in the field have proven successful in indicating how other Mediterranean species might respond to drought (Llorens et al. 2004). The response of fynbos to climate change is likely to be complex and possibly unique to individual species, but it is anticipated that once the relation between rainfall patterns and growth have been resolved, data from this study could be very useful in constructing a growth model to predict responses of the monitored species to climate change.

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## CLIMATIC CONTROLS OF GROWTH AND ARCHITECTURE IN TWO PROTEACEAE SPECIES PAIRS WITH CONTRASTING RANGE SIZES

*Abstract.* Patterns of shoot growth, branching frequency, canopy structure, and flowering were analysed in four Proteaceae species comprising two species pairs with contrasting range sizes in the genera *Leucadendron* and *Protea*. Shoot growth and branching patterns were related retrospectively to historical climate records, revealing climatic determinants of shoot growth and shrub architecture. Ecological strategies were explored, as reflected by leaf structural and whole plant architectural characteristics, and the allocation trade-offs due to age of first reproduction and investment in flowering. Narrowly distributed species did not represent similar ecological strategies or climate responses, and were not more sensitive to inter-annual climate variation than widely distributed species. Instead, fast-growing species from wide and narrow ranges were affected by climate variation in various ways, but specific responses were unique to each species.

### INTRODUCTION

Control of plant distributions, growth and performance by climatic factors has re-emerged as a central question in ecology with the rise of concern about the potential impacts of climatic change on natural ecosystems. Studies attempting to address questions regarding the effects of climate change on plant species are focused within two main fields, one concerned with climate change impacts on species' ranges (Parmesan 1996, Kleidon and Mooney 2000, Bakkenes et al. 2002, Midgley et al. 2003, Parmesan and Yohe 2003, Root et al. 2003, Thomas et al. 2004, Thuiller 2004, Parmesan et al. 2005, Thuiller et al. 2005, Wilson et al. 2005), the other attempting to use structural and physiological traits of plant species and their relationships to climate to predict vegetation responses to climate change (Woodward and Diament 1991, Box 1996, Woodward and Cramer 1996, Bond 1997, Díaz and Cabido 1997, Diaz et al. 2002, Dormann and Woodin 2002, Lavorel and Garnier 2002).

Reported shifts in species' ranges to recent increases in temperature (Parmesan 1996, Root et al. 2003) initiated a renewed interest in climatic controls of species' ranges and a frequently

asked question is whether narrowly distributed species are adapted to only a narrow range of environmental conditions, including climate, and therefore more vulnerable to climate change (Kelly 1996, Johnson 1998, Thuiller et al. 2005). Researchers working on functional traits have asked similar questions, namely whether specific traits are able to explain why some species are narrowly distributed (Kelly 1996, Ackerly et al. 2002, Lavergne et al. 2003, Lavergne et al. 2004), but no clear patterns emerged.

Thuiller et al. (2004) investigated relationships between range sizes, climatic niches and a small number of core traits in 88 *Leucadendron* taxa. Species with limited distribution ranges were found to not necessarily represent narrow climatic niches, but they did find relationships between leaf, cone and stem traits and sizes of distribution ranges. They suggested a more detailed analysis of plant biomass and canopy structure to clarify links between trait relationships and responses to climate.

The architectural analysis of plants, where growth patterns and the three dimensional structure of plants are described, has advanced a great deal since its introduction by Hallé and coworkers (Hallé et al. 1978). Many complex modelling techniques exist today (Godin 2000), while genetic and physiological processes governing plant architecture are also well understood (Reinhardt and Kuhlemeier 2002). These approaches however are mostly descriptive and mainly concerned with internal processes being expressed as growth patterns under ideal, non-limited environments. While this provides a good basis for further investigation, comparatively few plant architectural studies attempt to detect the effects of environmental factors on growth patterns in plants.

Dendrochronology, the study of annually formed growth rings in trees, on the other hand has long been used to determine the effect of climate on growth in trees through the matching of growth patterns with historical climate data, and applying this knowledge in the reconstruction of past climates from tree-ring data (Fritts 1976, Martinelli 2004). However, not all ecosystems have tree species able to provide good climate-related dendrochronological data (Fritts 1976). A relatively new discipline of retrospective growth analysis, using shoots as annual growth units and combining techniques from architectural analysis and dendrochronology, has been developed by researchers working in arctic regions (Callaghan et al. 1989, Callaghan et al. 1997). Retrospective analysis has been successfully applied to trees (Passo et al. 2002), shrubs (Callaghan et al. 1989, Bret-Harte et al. 2002), and perennial herbs (Callaghan et al. 1997).

Annual growth in shoots has been correlated successfully with historical climate records and enables researchers to make predictions of possible responses to future climate change.

Retrospective growth analysis prevents the need for intensive monitoring of plant growth, but relies however on the accurate dating of discrete growth increments. This requires annual growth to be clearly defined. Plant species that produce a single growth unit – a single, uninterrupted event of shoot elongation (definition according to Passo et al. (2002)) during a single, clearly defined, annual growth season provide the most accurate data. In the arctic it can be safely assumed that growth only takes place during summer months when plants emerge from the thick snow cover prevalent during the rest of the year. In other systems successful retrospective growth analysis however requires some knowledge of the growth phenology of the species to be investigated. Of course, longer-lived plants are able to provide longer and possibly more useful data sequences than shorter-lived species.

Many members of the Cape Proteaceae are potentially ideally suited to retrospective growth analysis. These large evergreen shrubs live as long as 50 (Midgley and Kruger 2000) to 60 years (Bond 1980a), but because fires regularly sweep through the fire-prone sclerophyll shrublands of the Cape Floristic Region, it is quite unusual to find such old individuals. Most mature stands are between 10 and 30 years old (Bond 1980a). Considering that no long term growth data for any Proteaceae species exist, retrospective analysis of even such a short time period could prove very useful. A number of phenological studies (Bond 1980b, Kruger 1981, Sommerville 1983, Le Roux et al. 1984, Pierce and Cowling 1984, Le Roux et al. 1989) indicate that most Proteaceae have a single annual growth season from late spring through summer. As a result of the Mediterranean climate of the Western Cape, plants are able to start growth once temperatures have risen sufficiently during spring. During the long dry summer months high temperatures and decreasing water availability eventually becomes limiting to growth and the growth season is terminated towards the end of summer (Chapter 2). In many species the end of the growth season is followed by the development of flower buds at the tips of shoots, or otherwise apical buds become dormant until the following year (Chapter 2). During the growth season single growth units are produced as unbranched shoots. Bud scars remain visible on branches for many years and indicate the start of annual shoots. New shoots develop either as extensions from the previous year's growth from the apical bud, or otherwise as side branches originating from axillary buds near the tip of the older shoots.



Many architectural as well as retrospective growth studies have shown age-related variation in growth patterns in many different plant species (Callaghan et al. 1989, Callaghan et al. 1997, Passo et al. 2002, Puntieri et al. 2003). It is important that changes in growth as a result of plant age are described before the impacts of climate variability on growth can be assessed (Fritts 1976, Cook and Peters 1981, Callaghan et al. 1997). It is known that Proteaceae senesce and eventually die if fire intervals are too far apart (Bond 1980a), and Midgley and Kruger (2000) have showed in an architectural study on Proteaceae how prolific branching, associated with a high canopy spread:basal diameter ratio is more likely to senesce and die due to plants breaking apart. Senescence indicates that growth probably slows down in older plants, but although there are detailed studies on Proteaceae growth during a single growth season (Heinsohn and Pammenter 1988, Dupee and Goodwin 1990, 1992), no data are available on growth and development patterns across the whole lifespan of Proteaceae shrubs.

Architectural studies on Proteaceae have focused mainly on showing allometric relationships between leaf size, inflorescence and seed size, branch diameter and branching frequency, and illustrating how these relationships contribute to sexual dimorphism in the dioecious genus *Leucadendron* (Bond and Midgley 1988, Midgley and Bond 1989, Le Maitre and Midgley 1991, Midgley 1998). Bond and Maze (1999) showed that a trade-off exists between increased floral display and viability in *Leucadendron* males producing terminal inflorescences because excessive ramification leads to an increased risk of dying due to plants breaking apart. In two other interesting studies Bond et al. (1995) reported on the important role of *Protea* architecture in chaotic post-fire regeneration dynamics, and Bond and Midgley (1995) suggested that *Protea* canopy structure may have evolved to increase flammability.

Data in Le Maitre and Midgley (1991), Bond et al. (1995) and Midgley and Enright (2000) suggest that variation in Proteaceae growth and flowering patterns, leaf longevity and degree of serotiny, and exceptions to general allometric relationships represent contrasting ecological strategies among the Proteaceae. These are clearly important functional characteristics, raising the questions: Could there be a relationship between different ecological strategies and their control by climatic factors? And as Thuiller et al.'s (2004) study suggests, might these be reflected in geographic range size? Might these be important predictors of species' potential responses to climate change?

The aims of this study were therefore firstly to explore in detail the architecture and growth patterns of selected Proteaceae species pairs with contrasting range sizes, and secondly, to retrospectively analyze growth responses to historical climate variation as an indicator of vulnerability to climate change. Patterns of ecological strategies and climate sensitivity in relation to range sizes revealed through these analyses will hopefully shed more light on whether range size or functional characteristics signify vulnerability to climate change.

## METHODS





### *Study species*

Phenological monitoring (Chapter 2, data not shown) revealed that not all Proteaceae species have single, uninterrupted annual growth seasons and not all species produce unbranched shoots during the growth season. Care was taken in this study to select species known to produce unbranched shoots during a single annual growth season as these would provide the most reliable data. Two *Protea* species, *P. laurifolia* Thunb. and *P. repens* (L.) L., as well as two *Leucadendron* species, *L. nervosum* E. Phillips & Hutch. and *L. lauroolum* (Lam.) Fourc. were selected for this study. All four of these species are seeders, which means that adults are killed during fires and post-fire recruitment is solely from newly emerging seedlings. As a result all plants within the study area should be roughly the same age, making comparisons of growth patterns and responses to climate among species much easier. All four species are broadleaved, evergreen, erect shrubs, and all have sympodial growth, with shoots terminating in a single inflorescence and further growth developing from lateral meristems. *Protea repens*, however, has a slightly modified sympodial growth pattern: although inflorescence buds terminate each year's growth, inflorescences do not fully develop until after the end of the following year's growth season (Bond et al. 1995). According to Le Maitre and Midgley (1991) this growth pattern is the reason why *P. repens* is able to escape the leaf size-inflorescence size allometric relationship and produce inflorescences far larger than predicted by its leaf size and shoot diameter.

Apart from these similarities, the four selected species represent a diversity of distribution ranges, shrub sizes, leaf and inflorescence sizes, levels of serotiny and timing of flowering. *Protea repens* is considered the most abundant sugarbush in the Cape Flora (Rebello 2001), and is found in a wide variety of habitats between 0-1500 m altitude, while *Protea laurifolia*, which is quite abundant in the western CFR, has a comparatively narrower distribution range. It

is restricted to four mountain ranges and found only on dry sandy or granite soils between 400-1200 m altitude. *Leucadendron laurosum* also has a fairly wide distribution and is found in a variety of habitats including mountains as well as coastal plains (0-1000 m) and on soils ranging from granite to sand and limestone. *L. nervosum*, on the other hand, is classified by the Red Data Book as Rare (Rebello 2001) and is found only on the northern slopes of two mountain ranges in the southern Cape. Further characteristics of the study species are summarised in Table 1.

TABLE 1. Morphological and life history characters of the study species. Data from Midgley and Enright (2000), Rebello (2001), unpublished data and Chapter 2.

		<i>Protea laurifolia</i>			<i>Protea repens</i>			
<b>Habit</b>		Erect shrub, up to 8 m tall			Erect shrub, up to 4.5 m tall			
<b>Distribution</b>		Restricted, 400-1200 m			Wide, varied habitats, 0-1500 m			
<b>Leaves</b>		Area	20.69 cm <sup>2</sup>			Area	4.05 cm <sup>2</sup>	
		SLA	2.295 cm <sup>2</sup> .g <sup>-1</sup>			SLA	2.525 cm <sup>2</sup> .g <sup>-1</sup>	
<b>Flowers</b>	Length	100-130 mm			100-160 mm			
	Width	40-60 mm			70-90 mm			
	Flowering season	April - Nov			May - Oct			
<b>Serotiny</b>		Seeds retained on plant for average 3.1 years			Seeds retained on plant for average 1.6 years			
<b>Growth season</b>		October - February			October - February			
		<i>Leucadendron nervosum</i>			<i>Leucadendron laurosum</i>			
<b>Habit</b>		Erect shrub, up to 2.5 m tall			Erect shrub, up to 2 m tall			
<b>Distribution</b>		Very restricted, 1100-1350 m			Wide, mountains and plains, diverse soil types, 0-1000 m			
<b>Leaves</b>			Male	Female			Male	Female
		Area	4.27 cm <sup>2</sup>	8.70 cm <sup>2</sup>		Area	6.45 cm <sup>2</sup>	10.21 cm <sup>2</sup>
		SLA	3.8 cm <sup>2</sup> .g <sup>-1</sup>	3.4 cm <sup>2</sup> .g <sup>-1</sup>		SLA	4.0 cm <sup>2</sup> .g <sup>-1</sup>	3.6 cm <sup>2</sup> .g <sup>-1</sup>
<b>Flowers</b>	<b>Male</b>							
	Length	24 mm			23 mm			
	Width	22 mm			21 mm			
	<b>Female</b>							
	Length	28 mm			38 – 46 mm			
	Width	25 mm			32 – 37 mm			
Flowering season	September			June				
<b>Serotiny</b>		Serotinous, retention time unknown			Seeds retained in female cones on average 3.5 years			
<b>Growth season</b>		November - April			October - April			

### Study area

Plants were sampled at two altitudes on the north facing slope of Jonaskop in the Riviersonderend Mountain Range between April and June 2003, following the end of the 2002-2003 growth season. *Protea repens*, *Protea laurifolia* and *Leucadendron laureolum* individuals were measured at 953 m altitude (S 33°56'06, E 19°31'23). *Leucadendron nervosum* does not occur at 953 m, and was therefore sampled at 1303 m (S 33°57'69, E 19°30'80), which is the only area on the northern slope where a substantial population is found.

Historical climate data from Serjeantsrivier (S 34°13'33, E 19°51'66; Altitude 366 m) were used in testing for correlations with the retrospective growth data (data provided by Agromet-ISCW, Stellenbosch). This weather station on the southern side of the Riviersonderend Mountain Range is the only station in the area of the study site with long term data (dating back to 1973) for both rainfall and temperature (Figure 1). Although north facing slopes of mountain ranges in the Western Cape are known to experience very different climatic conditions from south facing slopes, it is also true that higher altitudes of north facing slopes are influenced by southerly weather conditions (Marloth 1904, Oliver et al. 1983) and it has been shown that Jonaskop is influenced by southerly conditions bringing rain to higher altitudes, especially during summer (Chapter 1).

Monthly rainfall data were summed so that values of 'total annual' rainfall correspond with the growth phenology of the study species, rather than calendar years. The study species all grow from spring through to late summer (Chapter 2), and therefore rainfall of the winter preceding the growth season, as well as rainfall during the growth season, is most likely to influence total annual shoot growth. Thus, for example, total annual rainfall for 2002-2003 includes the rainfall for the October 2002 – March 2003 growth season, plus the preceding winter rain season (April – September 2002). 'Rainfall during the growth season' indicates the portion of the total yearly rainfall that occurred during October – March (see Figure 1). Likewise, 'temperature during the growth season' indicates the mean daily temperatures of the same period: October to March. Rainfall years were classified as average, dry or wet for some interpretations of data. Average years are years when rainfall was within 10% variation around the long term mean rainfall totals. Dry years are when rainfall is less than 10% below the long term mean, wet is when rainfall is higher than 10% above the long term mean.

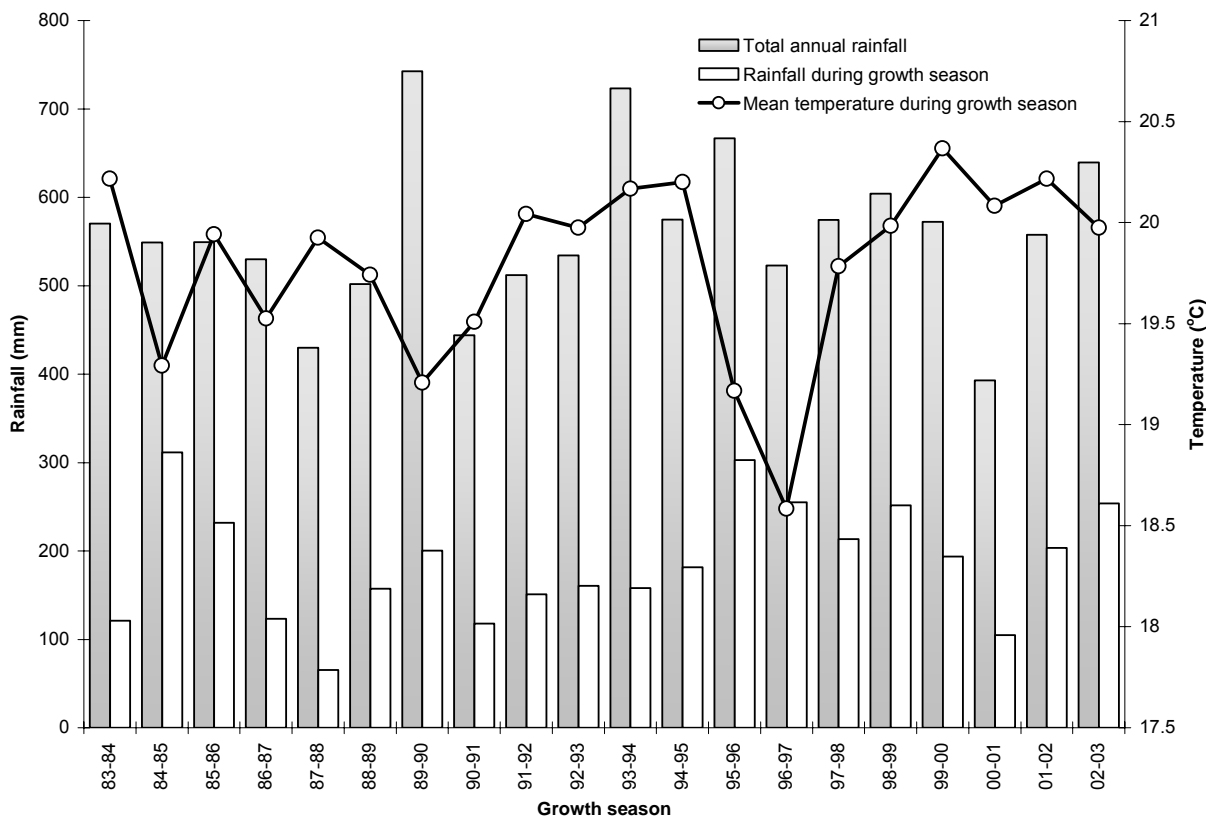


FIGURE 1. Historical climate data of Serjeantsrivier (S 34°13'33, E 19°51'66; Altitude 366 m). X axis indicates growth seasons rather than calendar years because Proteaceae grow during summer. Total annual rainfall includes rainfall during the growth season plus the preceding winter. Growth season is from October to March.

### *Sampling design and data analysis*

Phenological monitoring of the study species indicated that not all branches on Proteaceae shrubs produce new growth every year (Chapter 2, data not shown). Therefore to avoid the assignment of annual growth increments to the wrong calendar year only growth sequences on the main, vigorously growing branches originating from the base of each sampled shrub were measured, as they are more likely to produce new growth each year. This also prevented duplicate measurements of older branches. In the few instances where missing annual shoots were found, the dates of the missing growth were determined by cross-dating with complete growth sequences of other branches on the same plant, according to standard dendrochronological methods (Fritts 1976). Between 16 and 23 growth sequences were recorded for each species.

For each year's growth the length of the shoot and basal diameter was measured using digital callipers, and the number of leaves remaining on the shoot as well as the still visible leaf scars

were counted to determine the total number of leaves produced per annual shoot. On older branches leaf scars fade and are more difficult to count precisely and so annual leaf numbers were only determined as far back as accurately possible. For comparisons of shoot diameter between species only diameters of the most recent shoots were used to avoid the confounding effects of secondary growth. The number of branches emerging from a single stem of the previous year's growth was counted to determine variation in branching frequency. The locations of cones or inflorescences, or in the case of *Leucadendron* males, signs of shed cones at branch tips, were noted for every growth sequence. Measurements of shrub height and two perpendicular diameters were also taken. Canopy volumes were calculated using the formula for an ellipsoid.

Leaf longevity and leaf half lives were determined according to the methods of Witkowski et al. (1992), combining the numbers of remaining leaves and scars per annual shoot and calculating the decreasing percentage leaf survival for each following cohort.

Data from growth sequences for each plant were grouped according to the age of annual shoots and growth curves were derived for each plant individually using local regression, also known as LOESS, (Shipley and Hunt 1996, Jacoby 2000) as a smoothing function (SYSTAT® 11 software package, LOESS settings: polynomial degree:1; number of grid points: 50). The variation of shoot lengths around age related changes in growth, as predicted by the smoothed curve, is assumed to be the result of the effects of climate variation (Fritts 1976). The difference between measured growth and growth predicted by the growth curve is termed the growth deviation. Growth deviations, rather than actual shoot lengths are correlated with climate data when searching for relationships between annual growth and climate variation. Since the plants sampled were not all exactly the same age, growth deviations calculated for individual shoots grouped according to their age were then regrouped according to calendar year. Mean growth deviations for each calendar year were then used in simple and multiple linear regression analyses with various historical climate variables. A previous study (Chapter 2) revealed sensitivity to high temperatures resulting in non-linear relationships between temperature and growth. Therefore relationships between temperatures and growth deviations were also tested with curvilinear regression analyses.

General growth curves for each species were derived by combining the smoothed data for each individual plant and applying the smoothing function again. T-tests were performed on the shoot

lengths, stem diameter of the most recent shoots, branching frequency, number of leaves per shoot and leaf density of the males and females of the two *Leucadendron* species to determine whether sexual dimorphism found in the leaf sizes of these two species was also present in these architectural aspects.

Data on branching frequencies were analyzed in a similar manner. The number of branchings produced per year from single annual shoot of the previous year was grouped according to shoot age and smoothing functions were applied. The *Leucadendron* species showed age-related changes in branching frequencies but the *Protea* species did not. Deviations from the branching frequencies from values predicted by the smoothed curve were correlated with climate data.

The relationship between annual shoot length and number of leaves (leaves + leaf scars) produced per shoot was also investigated for all four species. Preliminary analyses revealed large variation around the mean for shoot length, but not for leaf production (Figure 2). Leaf numbers are possibly far more stable, since leaves are pre-formed in the apical bud before the start of the growth season, while shoot elongation on the other hand is much more flexible and responsive to climate conditions during the growth season (Chapter 2). Therefore variation in leaf density (number of leaves per unit shoot length) could also reflect the effects of climate variation. Recent developments in dendrochronology, the Needle Trace Method (NTM), designed to do reconstructions of past foliar dynamics in conifers, have found similar patterns (Sander and Eckstein 2001). Therefore, deviations of leaf densities from an expected regular linear relationship between shoot length and number of leaves were also investigated in relation to interannual climate variation.

## RESULTS

### *General growth patterns*

#### 1. Canopy structure, and its relationship to branching frequency

Canopy shapes of the four species can be roughly categorized into three groups. Females of both *Leucadendrons* are tall, narrow shrubs, while the males are shorter, rounder shrubs. *Protea laurifolia* also has a short, round shape, while *Protea repens* represents the third category: a canopy that is both the tallest and widest of all the species sampled. (Figure 3a). Contrary to

findings of Bond and Midgley (1988) and Le Maitre and Midgley (1991), shrub diameter is a better predictor of average branching frequency than shoot diameter in these species, with a significant positive correlation  $F_{1,4} = 13.38$ ,  $p = 0.022$ ,  $r^2 = 0.77$  (Log Branching Frequency =  $0.50 \times \text{Log Shrub Diameter} - 1.04$ , Figure 3b).

## 2. Species specific growth curves

All four species showed similar age-related growth patterns with annual shoot growth increasing over the first few years, and subsequently stabilizing or decreasing as the plant matures. In three species peak growth corresponds with the age when plants flower for the first time. *Protea repens* produced its first flowers at the age of 3, *Leucadendron lauroolum* at age 4 and *Leucadendron nervosum* at age 5 (Figure 4). Interestingly, *Leucadendron* males and females in both species maintained similar growth up until the age of reproductive maturity, after which females consistently produced longer shoots than males. In contrast, *Protea laurifolia* is much slower to mature, producing its first flowers only after six years, and growth reaching a peak at 10 years (Figure 4).

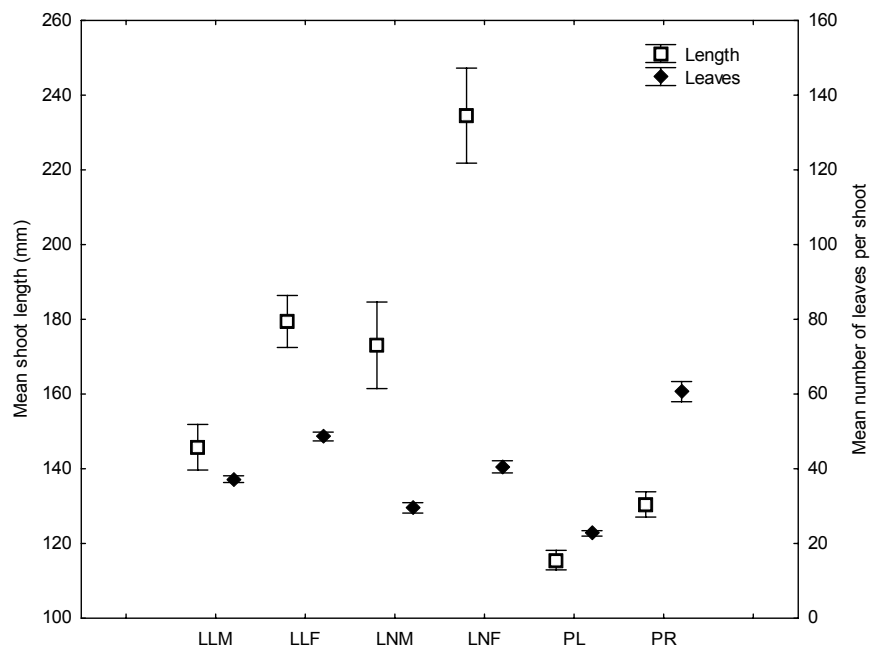


FIGURE 2. Variation in shoot lengths and number of leaves per shoot in *Leucadendron lauroolum* males (LLM), *L. lauroolum* females (LLF), *Leucadendron nervosum* males (LNM), *L. nervosum* females (LNF), *Protea laurifolia* (PL) and *P. repens* (PR). Y axes are on the same scale indicating larger variation in shoot length than leaf numbers. Error bars indicate 1 standard error.



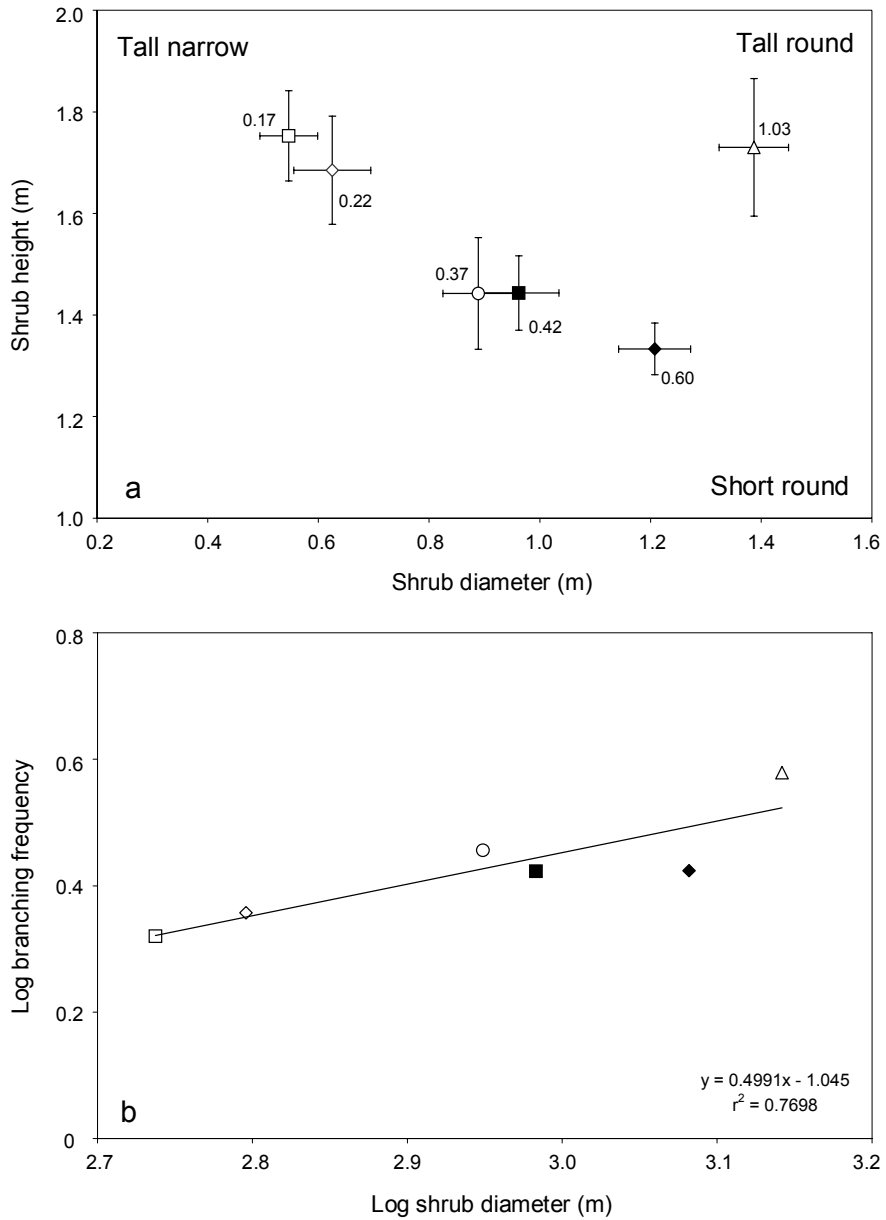


FIGURE 3. (a) Mean shrub canopy height and diameter of the selected species indicating three different canopy shapes. Error bars indicate 1 standard error, values next to data points represent shrub volumes calculated using the formula for an ellipsoid. (b) Allometric relationship between shrub diameter and branching frequency.  $F_{1,4} = 13.38$ ,  $p = 0.022$ ,  $r^2 = 0.77$ , Log Branching Frequency =  $0.50 \times \text{Log Shrub Diameter} - 1.04$ . Symbols: *Leucadendron nervosum* □ female, ■ male; *Leucadendron laurosum* ◇ female, ◆ male; *Protea laurifolia*; ○ *Protea repens*.

### 3. Relationships of branch lengths, frequencies and leaf densities

*Protea laurifolia* not only on average produced the shortest shoots of all four species, with a mean shoot length of  $115.56 \text{ mm} \pm 42.2$  standard error (S.E.), but also has the thickest shoots (mean diameter  $8.46 \text{ mm} \pm 0.36$  S.E.) and relatively low leaf density ( $0.203$  leaves per unit shoot

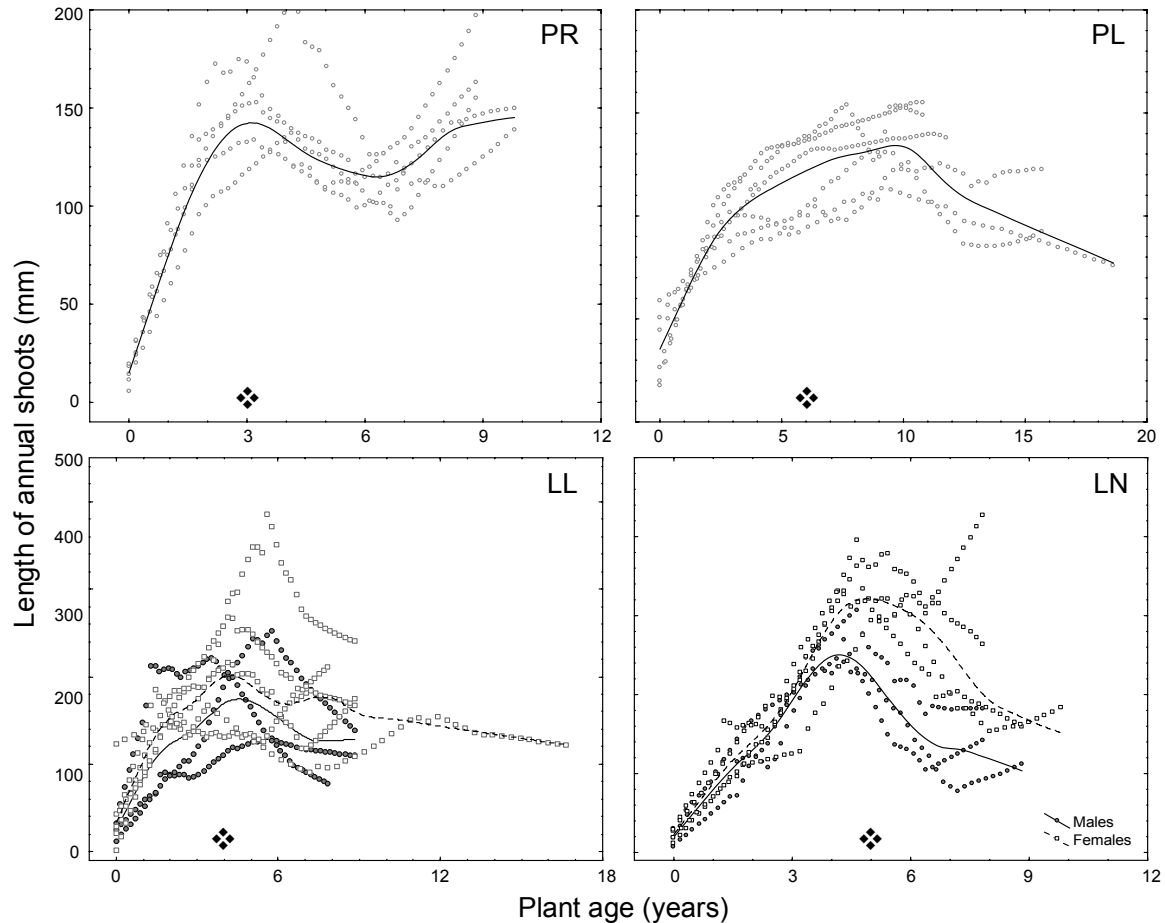


FIGURE 4. Loess-smoothed growth curves for *Protea repens* (PR), *Protea laurifolia* (PL), *Leucadendron laureolum* (LL) and *Leucadendron nervosum* (LN). *Leucadendron* males are indicated by filled symbols and solid lines, females by open symbols and dashed lines. ♠ indicates age of reproductive maturity.

length (mm)  $\pm$  0.009 S.E.). *Protea repens*, in contrast, branched far more frequently than *P. laurifolia*, and produced longer (mean length 130.45 mm  $\pm$  3.55 S.E.), but thinner (mean diameter 4.85 mm  $\pm$  0.32 S.E.) shoots than *P. laurifolia*. This is interesting, as shorter shoots are usually associated with more prolific branching, as for example in *Leucadendron* males.

Secondary growth during the growth season following inflorescence bud formation in *Protea repens* increased shoot diameter to 8.03 mm  $\pm$  0.36 S.E., which supports Le Maitre and Midgley's (1991) theory of why *P. repens* shoots can support inflorescences of similar size than those of *P. laurifolia*. *Protea repens*, with the smallest leaf area of the four species sampled, has by far the highest leaf density (0.508 leaves per unit shoot length (mm)  $\pm$  0.029 S.E.).

TABLE 2. Results of t-tests comparing means of various structural characteristics between male and female *Leucadendron* species. S.E. – standard error of means, \* 0.05>p>0.01, \*\*0.01>p>0.0001, \*\*\*p<0.0001, n.s p>0.05.

	<i>Leucadendron nervosum</i>					
	Males			Females		
	N	Mean (S.E.)	N	Mean (S.E.)	t	p
Shoot length	61	173.1 (12.2)	77	234.5 (13.4)	3.31	**
Number of leaves	57	29.5 (1.5)	77	40.53 (1.7)	4.68	***
Leaf density	57	0.190 (0.01)	77	0.194 (0.009)	0.282	n.s.
Stem diameter	8	4.04 (0.28)	9	7.45 (0.82)	3.73	**
Branching frequency before reproductive maturity	35	3.31 (0.28)	36	2.64 (0.21)	1.96	n.s.
Branching frequency after reproductive maturity	82	2.37 (0.13)	76	1.83 (0.11)	3.13	**

T-tests on mean shoot length, number of leaves per shoot, stem diameter and leaf density between male and female *Leucadendrons* revealed significant differences in mean shoot length, mean number of leaves, stem diameter and leaf density in *Leucadendron lauroolum* (Table 2). *Leucadendron nervosum* male and female mean shoot lengths, number of leaves per shoot and shoot diameter are also significantly different. Leaf density between *L. lauroolum* males and females are however not significant (Table 2).

#### *Leaf longevity*

Leaf longevity varied considerably between the species. Strong contrasts were found for the Proteas, where the oldest leaves found on *Protea repens* were 6 years old, while leaves survived up to 9 years in *P. laurifolia* (Figure 5). Similarly, the oldest leaves found on male *Leucadendron lauroolum* were only 3 years old, while female leaves remained for up to 4 years, but leaves survived up to 10 years on both male and female *Leucadendron nervosum* (Figure 5). Living leaves still outnumbered leaf scars on the basal shoots of *L. nervosum* plants, suggesting that leaves in these plants could possibly survive far beyond 10 years.

#### *Climate correlations: growth*

Growth deviations of *Protea repens* correlate negatively with mean daily temperatures during August, which is the coldest winter month at the study site (Chapter 1), but the relationship is significant only at the 0.1 level ( $F_{1,8} = 5.0956$ ,  $p = 0.054$ ,  $r^2 = 0.39$ ). Combining mean temperature during August with total rainfall during the growth season in a multiple regression analysis improved the p value only slightly for *P. repens* ( $F_{3,6} = 4.64$ ,  $p = 0.053$ ) but led to a large improvement in  $r^2$  to 0.70, indicating that, contrary to the findings of the phenological monitoring

TABLE 2. Extended.

<i>Leucadendron laureolum</i>					
Males		Females		t	p
N	Mean (S.E.)	N	Mean (S.E.)		
100	145.8 (6.4)	146	179.4 (7.3)	3.27	**
59	37.2 (0.9)	70	48.6 (1.2)	7.09	***
59	0.28 (0.01)	70	0.37 (0.01)	4.17	***
12	5.11 (0.62)	14	7.16 (0.29)	3.14	**
24	3.33 (0.32)	23	2.83 (0.26)	1.24	n.s.
97	2.49 (0.11)	89	2.14 (0.11)	2.23	*

study (Chapter 2), rainfall is important for growth in this species, but perhaps more on a longer term, cumulative scale, as opposed to short term effects. *Protea laurifolia* growth deviations had no significant correlations with any climate variables or combinations of variables.

*Leucadendron laureolum* growth also correlates negatively with mean daily temperatures during August, and the correlation is significant at the 0.05 level ( $F_{1,7} = 5.73$ ,  $p = 0.048$ ,  $r^2 = 0.45$ ). Multiple regressions with combinations of other climate variables did not present any other significant results for *L. laureolum*. *Leucadendron nervosum* growth deviations correlated positively with total annual rainfall ( $F_{1,8} = 6.69$ ,  $p = 0.032$ ,  $r^2 = 0.46$ ) and mean temperature during October ( $F_{1,8} = 4.76$ ,  $p = 0.061$ ,  $r^2 = 0.37$ ), which is the month preceding the start of the growth season of this species (Chapter 2). Warmer temperatures during October would result in an earlier start to the growth season, and warmer temperatures at high altitudes on the study site generally enhance growth rates, resulting in longer annual shoots (Chapter 2). Combining these climate variables in a multiple regression revealed a correlation significant at the 0.01 level ( $F_{2,7} = 20.05$ ,  $p = 0.0013$ ) and improved the  $r^2$  to 0.85 (Figure 6). Scatterplots of growth deviations against mean temperature during the growth season for *L. laureolum* and *L. nervosum* revealed similar patterns as was found in a phenology study (Chapter 2), namely positive responses of growth to temperature increases at low to intermediate temperatures, but highly variable growth responses at high temperatures. However, polynomial regressions did not prove significant at the 0.05 level.

Although significance is just outside of the 0.05 level, number of leaves per unit shoot length deviations are negatively correlated with total rainfall during the growth season ( $F_{1,5} = 6.49$ ,  $p =$

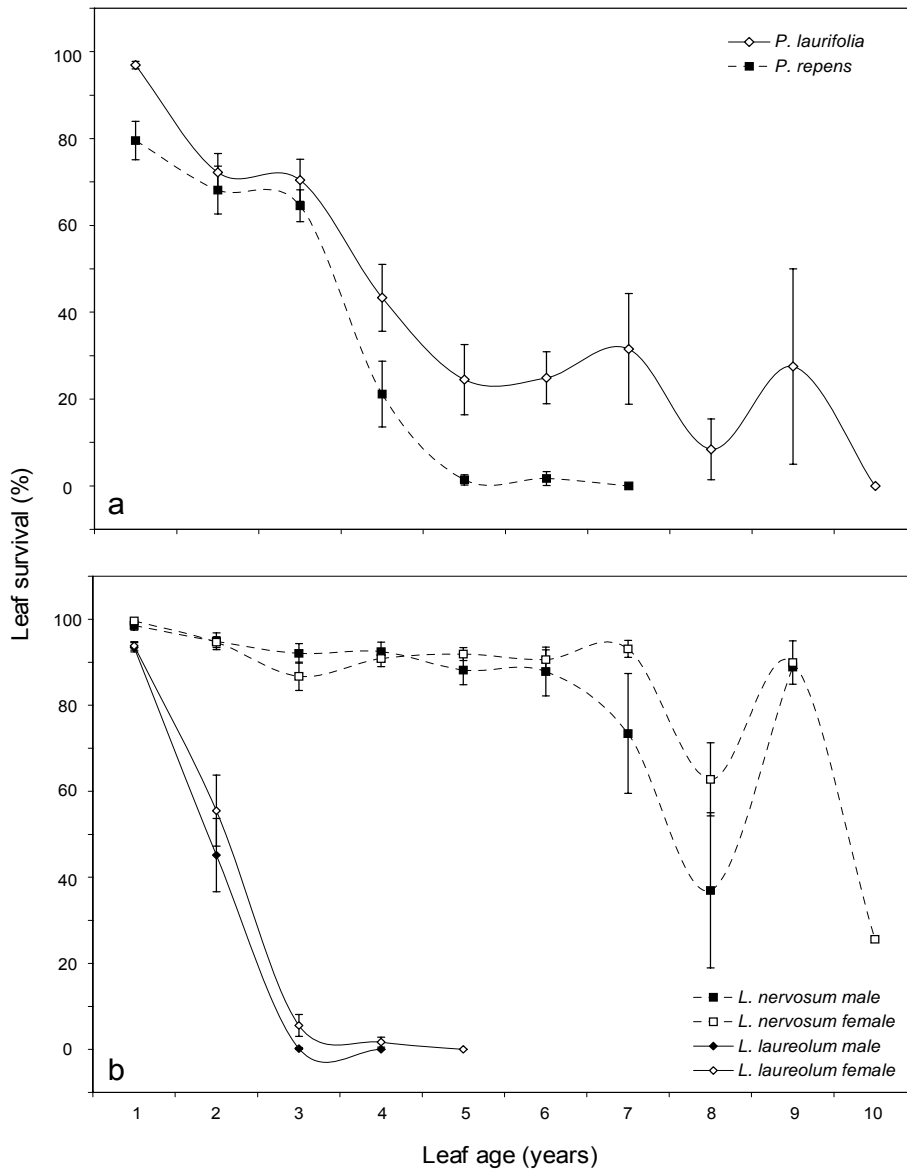


FIGURE 5. Leaf survival as a percentage of the original cohort size in (a) *Protea laurifolia* and *Protea repens* and (b) *Leucadendron laurifolia* and *Leucadendron nervosum*.

0.051,  $r^2 = 0.57$ ) in *Protea repens*. *Protea laurifolia* ( $F_{1,6} = 6.83$ ,  $p = 0.04$ ,  $r^2 = 0.53$ ), *Protea repens* ( $F_{1,5} = 5.83$ ,  $p = 0.06$ ,  $r^2 = 0.54$ ) and *Leucadendron nervosum* male ( $F_{1,6} = 7.22$ ,  $p = 0.036$ ,  $r^2 = 0.55$ ) and female ( $F_{1,7} = 5.02$ ,  $p = 0.06$ ,  $r^2 = 0.42$ ) leaf densities have significant or nearly significant positive correlations with mean temperature during the growth season, while *Leucadendron laurifolia* male and female leaf densities do not have significant correlations with any climate variables. There was however an annual increase in mean temperatures during the six years preceding the study (Figure 1), which is also the period in which the most reliable leaf records are found for most of the species investigated. Temperature seems to follow what is possibly also an age related trend. Assuming that leaf numbers remain relatively constant,

especially in *P. laurifolia* and *L. nervosum* (as shown in Figure 2, these species have very low variation in leaf numbers) and considering growth curves indicating shoots becoming shorter with age (Figures 4 and 5) it is logical to expect number of leaves per unit shoot length to increase yearly. Indeed, correlating leaf densities with simple chronological time series reveal relationships at far higher levels of significance for *P. laurifolia*  $F_{1,6} = 78.65$ ,  $p = 0.00014$ ,  $r^2 = 0.93$  and *L. nervosum* males ( $F_{1,6} = 36.97$ ,  $p = 0.0009$ ,  $r^2 = 0.86$ ) and females ( $F_{1,7} = 9.56$ ,  $p = 0.018$ ,  $r^2 = 0.58$ ). *Protea repens* leaf densities on the other hand do not correlate significantly with time ( $F_{1,5} = 5.33$ ,  $p = 0.07$ ,  $r^2 = 0.52$ ), possibly because of the fact that older *P. repens* shoots maintain a constant length rather than decreasing (Figure 4), and the leaf densities are more variable than in other species (Figure 2).

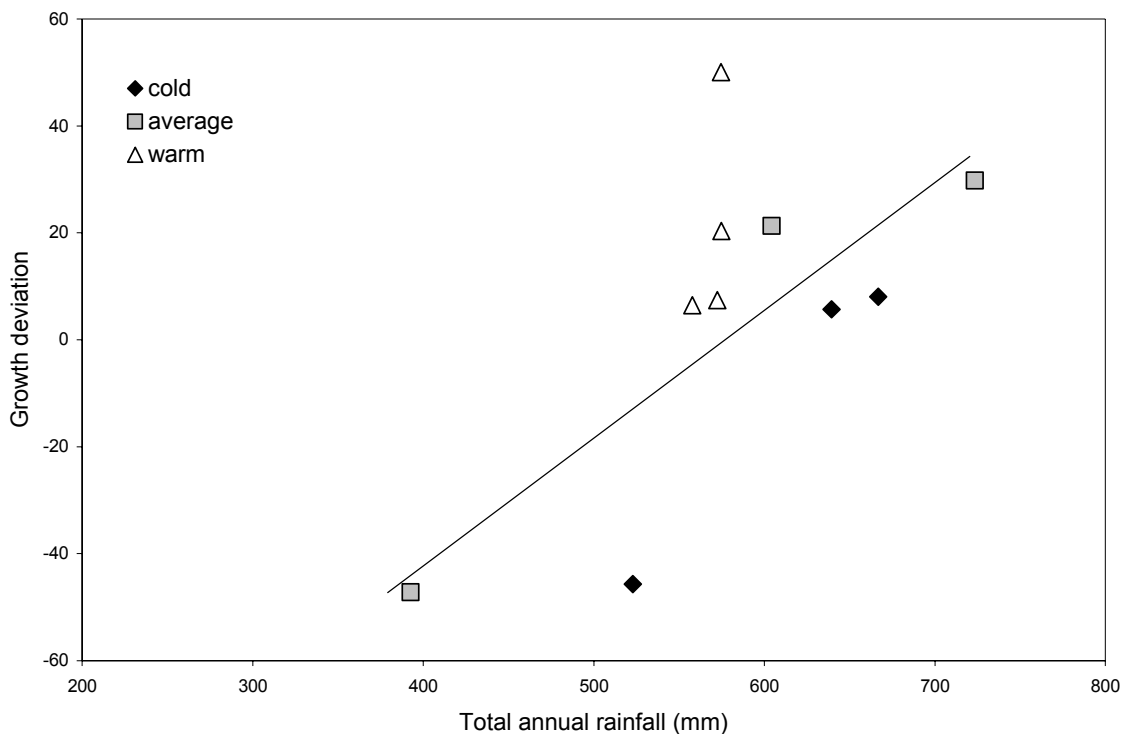


FIGURE 6. Corellation of *Leucadendron nervosum* growth deviations with total annual rainfall. Data points are categorized according to variation in mean temperature during the growth season (October to March), illustrating the interactive effects of temperature and moisture on growth.

It is however still worth considering whether temperature is influencing leaf densities in *L. nervosum* females at least. Since *L. nervosum* retains its leaves for such a long time, leaf density data is available even further back than six years. Figure 7a shows how *L. nervosum* female density deviations track a negative trend in mean temperatures from 1994 - 1997.

*Protea laurifolia* – also with long-lived leaves - density deviations is more possibly an age related trend, as Figure 87b illustrates a steady increase in leaf density from 1995 – 2003.

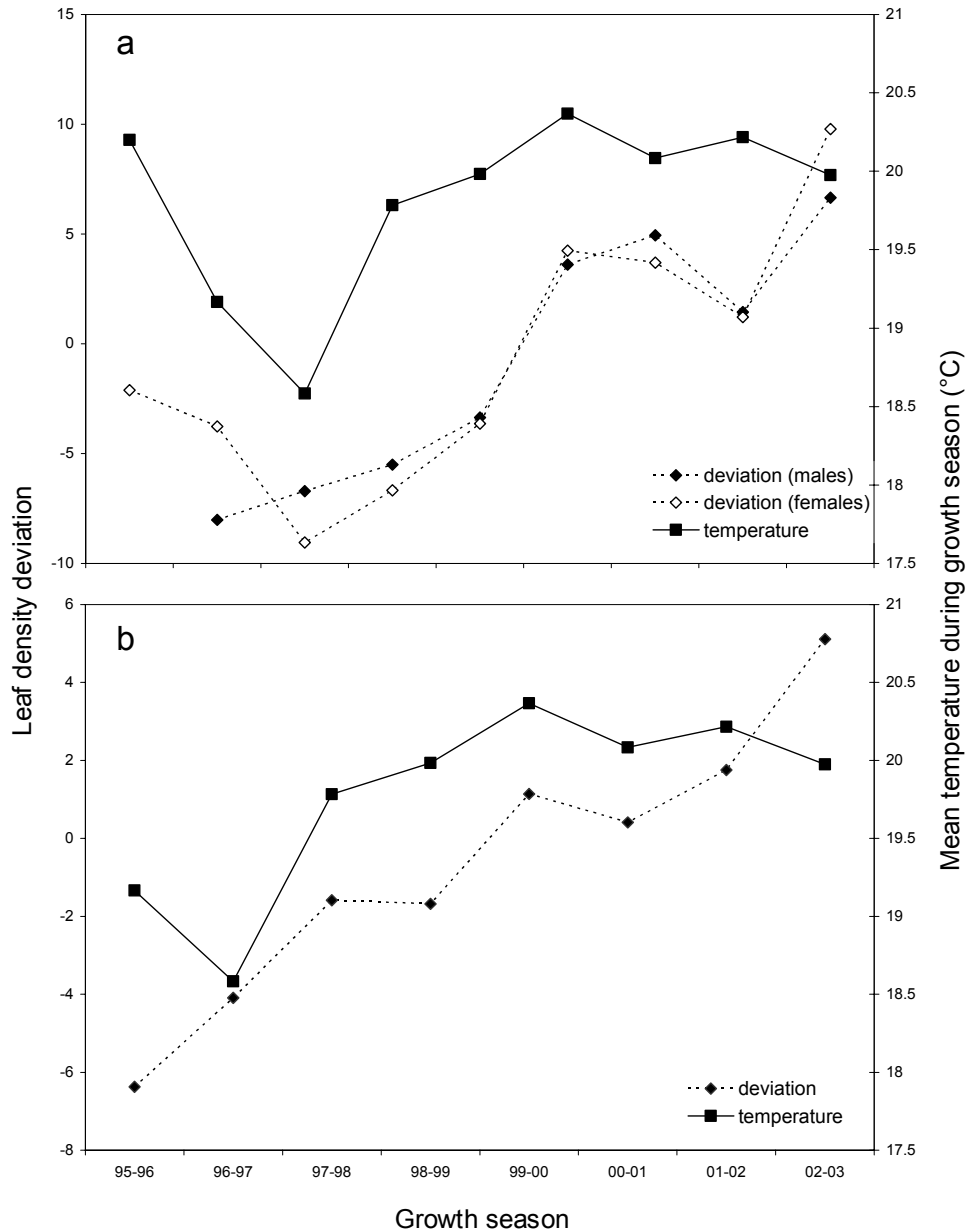


FIGURE 7. Correlations of mean temperature during the growth season with leaf density deviations in (a) *Leucadendron nervosum* males and females and (b) *Protea laurifolia*.

#### *Climate correlations: branching and flowering*

Branching and flowering patterns were very difficult to relate to interannual climate patterns. Especially in the *Protea* species, although all growth sequences in a particular plant would not flower or branch during a specific year, these occurrences were not often repeated in other plants sampled. *Protea laurifolia* growth sequences flower infrequently, with inflorescences

produced only every 3-4 years *Protea repens* growth sequences produce inflorescences every 2-3 years, although some branches flowered in two consecutive years. Some inflorescence buds formed at the end of the 1999-2000 growth season failed to develop after the 2000-2001 growth season, a particularly dry year. No age or climate related patterns in branching frequencies were found for *P. laurifolia* or *P. repens*. Instead, it seems as if branching patterns are more strongly related to flowering events within growth sequences. In both species flowering is followed by prolific branching from axillary meristems below the inflorescence, but annual growth following the year after the flowering event continues mainly from apical buds until the next flowering event.

*Leucadendron laurosum* and *L. nervosum* male and female branches are able to produce inflorescences every year. Percentage of shoots flowering increases with age, but climatic relationships with years of reduced flowering are not clear. Individuals of some species showed responses to 1996-1997, an unusually cold year (Figure 1): flowering was reduced in *Protea repens*, *Leucadendron laurosum*, and *Leucadendron nervosum*, while many growth sequences also did not produce annual shoots during this growth season. Unlike the *Proteas*, *Leucadendron nervosum* and *Leucadendron laurosum* have age related patterns in branching frequency. Again, as with shoot lengths, branching frequencies are similar in males and females before reproductive maturity, but when flowering commences, males produce consistently more shoots than females (Figure 8). T-tests revealed branching frequencies to be not significantly different between males and females before reproductive maturity in both *Leucadendrons*, but significantly different after the age of reproductive maturity (Table 2).

*Leucadendron nervosum* male and female branching frequencies have a significant negative correlation with temperature during the growth season ( $F_{1,6} = 8.86$ ,  $p = 0.02$ ,  $r^2 = 0.60$ ). *Leucadendron laurosum* female branching frequencies have a significant positive correlation with rainfall during the growth season ( $F_{1,7} = 8.11$ ,  $p = 0.025$ ,  $r^2 = 0.54$ ). Males also have a positive correlation but the relationship is not significant (Figure 9).

## DISCUSSION

There are a range of sharp contrasts as well as many similarities in architecture and ecological strategies between the species. What is most apparent from the results is that each species has its own unique range of responses to climate variation.



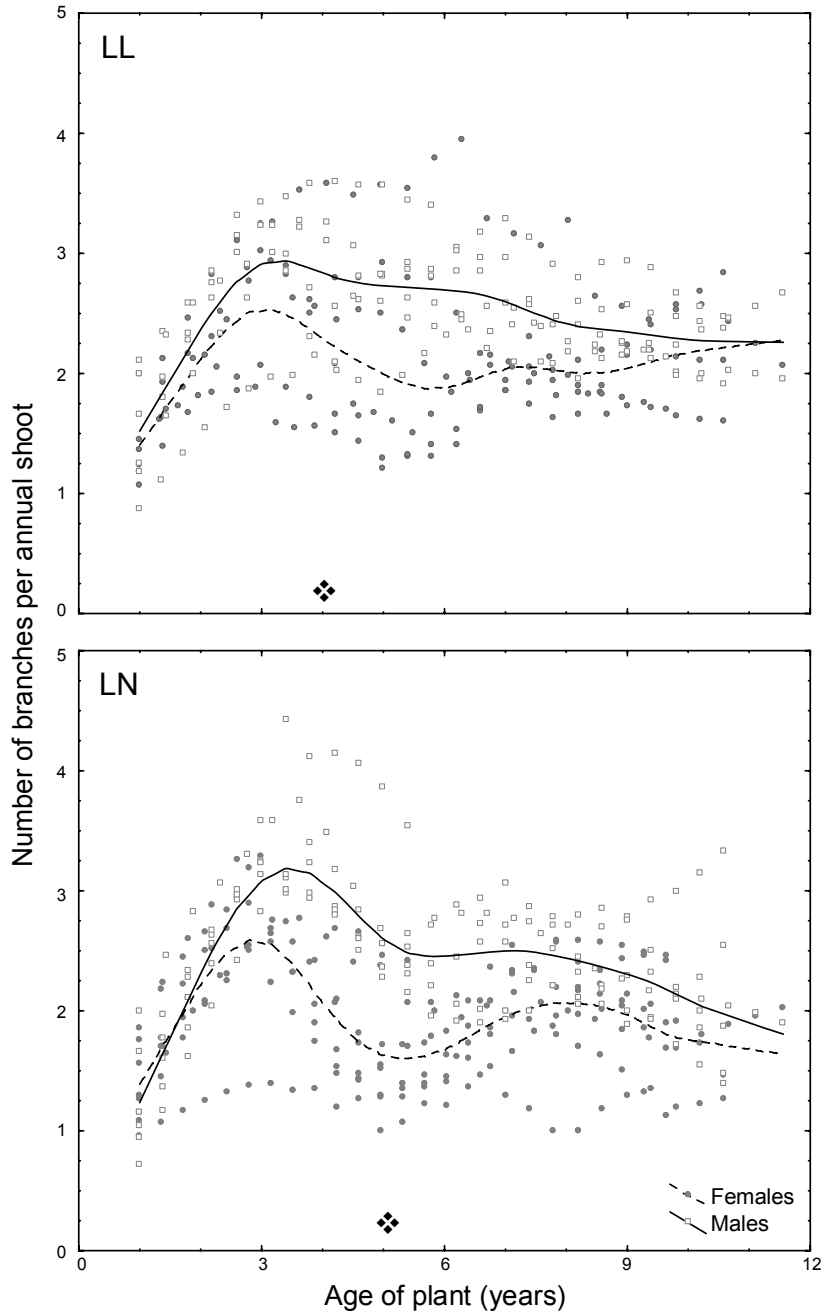


FIGURE 8. Age-related patterns in branching frequency in *Leucadendron laureolum* (LL) and *Leucadendron nervosum* (LN). ♠ indicates age of reproductive maturity.

*Protea laurifolia*, when compared to *Protea repens* represent two opposites on Grime and Hunt's (1975) classic Stress Tolerator – Competitor axis. *P. laurifolia* has short thick, infrequently branched shoots and a relatively low shrub height, large leaves and extremely low specific leaf area, which indicates slow growth (Westoby 1998, Westoby and Wright 2003). The growth curve derived for this species further points to slow growth with delayed peak growth and reproductive

maturity. In contrast, *P. repens* shrubs are tall with an extensive lateral spread, long, thin, frequently branched shoots, and a mechanism to ensure frequent and successful flowering in spite of competition (Bond et al. 1995). *Protea repens* produces high numbers of smaller, slightly higher specific leaf area (although still very low compared to the *Leucadendrons*) and shorter lived leaves and reaches reproductive maturity at the youngest age of all four species. Personal observations near the study site where sections of vegetation have escaped recent fires indicates that *P. repens* is prone to death due to mechanical failure as described by Midgley and Kruger (2000) and therefore potentially not as long lived as *P. laurifolia*.

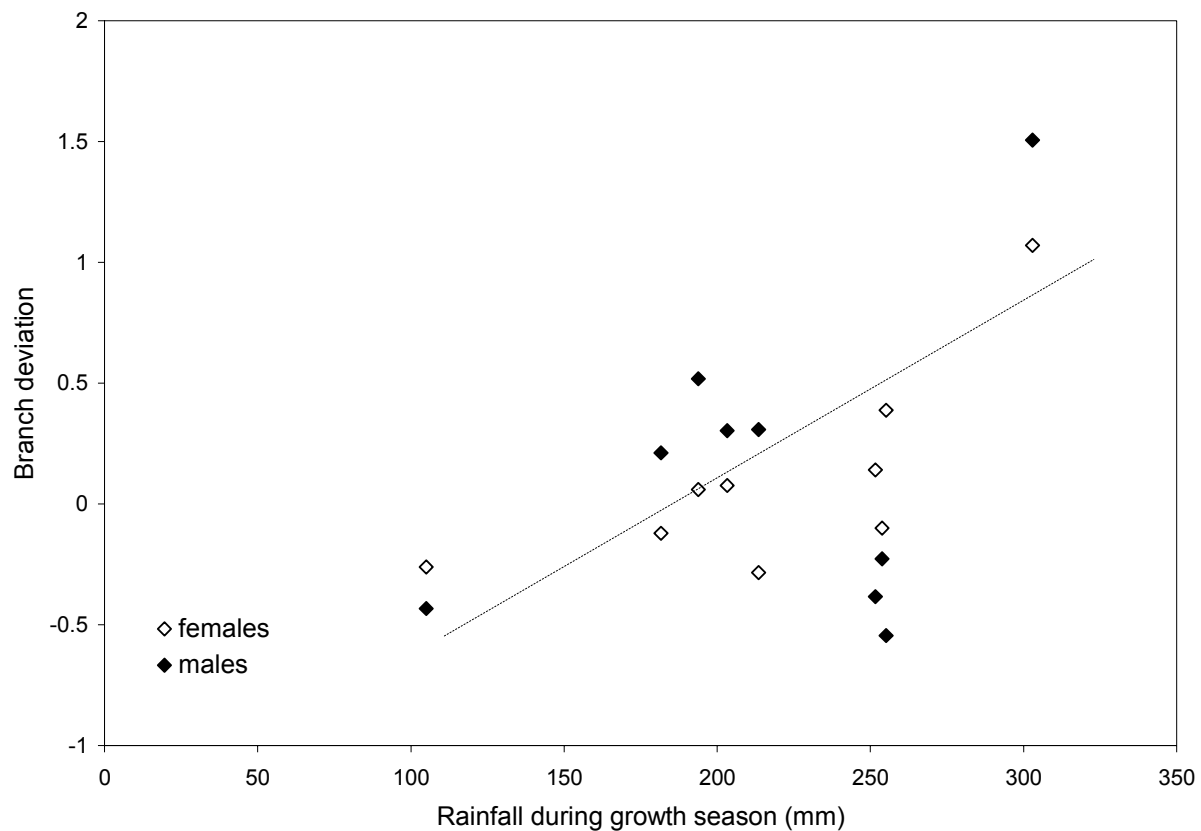


FIGURE 9. Correlations of deviations in branching frequency with rainfall during the growth season in male and female *Leucadendron laurifolia*.

The most important contrast between the two species is *P. laurifolia*'s complete lack of response to any climate variation while *P. repens* is influenced in various ways by a variety of climatic variables. Colder winter temperatures as well as high growth season rainfall promotes growth in *P. repens*, while warmer temperatures during the growth season lead to reduced shoot growth and consequently higher leaf densities. Extremely dry conditions lead to failed reproduction.

Considering climate change predictions of warmer and drier conditions for the Western Cape (Rutherford et al. 1999), *P. repens* growth as well as reproduction could be adversely affected by climate change.

Despite their large differences in altitudinal and distribution ranges, *Leucadendron nervosum* and *L. laureolum* were very similar in many respects. Both have similar canopy structures, SLA, branching frequencies, growth rates and reach reproductive maturity at a similar age. What is very difficult to explain, however, is the large difference in leaf longevity between the species. None of the regular explanations of differences in SLA (Westoby et al. 2002), differences in growth rates (Grime and Hunt 1975) or differences in canopy shape causing differential shading in older leaves (Witkowski et al. 1992) seem to apply to *L. nervosum* when compared to *L. laureolum*, as well as the *Proteas*.

What also complicates the evaluation of ecological strategies in the *Leucadendrons* is the fact that males and females are architecturally very different. Even in *L. nervosum* and *laureolum*, where sexual dimorphism is not nearly as apparent as in some other *Leucadendron* species, females of both species are more similar to each other than to males of their own species in terms of canopy shape and branching and growth patterns. It is apparent from both species that the male-female divergences set in with the reaching of reproductive maturity, indicating that, as in many other dioecious species, reproduction costs impose very different constraints on male and female growth (Obeso 2002). It is therefore quite logical to expect females to differentiate as strongly in their climate responses from males, but from the data this seems not to be the general situation, with climate responses unique to each species reflected in both males and females.

*L. nervosum* growth increases with increased rainfall and warmer temperatures during October, the month preceding the start of the growth season, which probably leads to an earlier start to the growth season (Chapter 2). Warmer temperatures however lead to a decrease in branching frequency in both males and females. Female leaf densities are affected by temperatures, but the effect on males is not significant. Therefore although climate change-related increases in temperatures could lead to an earlier start of the growth season for *L. nervosum*, growth could be adversely affected by drier conditions, and decreased branching frequencies due to warmer temperatures will constrain potential production of inflorescences.

Reproductive success in *L. laureolum* could also be constrained in this way, though in this species rainfall rather than temperature is the determining factor. Drought conditions will result in decreased branching frequencies, and more strongly so in the seed producing females. General growth in *L. laureolum* is also at risk from higher temperatures, with a negative correlation between growth and winter temperatures preceding the growth season in males and females.

### Conclusion

Are there any general conclusions to be made from this study? It was expected that widely distributed species should be more tolerant of climate variation than species with limited altitudinal and geographic ranges. This however turned out not to be true – widely distributed species such as *Protea repens* and *Leucadendron laureolum* were far more sensitive to climate variation than the more range restricted *Protea laurifolia*. Thuiller et al. (2004) found that despite their large differences in range size, *Leucadendron laureolum* and *L. nervosum* have similar, relatively wide niches in terms of rainfall, seasonality of rainfall and temperature, and that this is reflected by their similar leaf sizes and shoot and canopy structures.

Rather than distribution ranges, it generally seems that faster-growing “competitor” species are more responsive to climate variation than slow-growing “stress tolerant” species, but further studies including more stress tolerators is necessary to verify this trend. But how are stress tolerant/slow growing species to be identified in the field? It seems that very few of the indicators suggested in the literature are adequate to assess and rank these four species, in spite of their close phylogenetic relationships.

Westoby’s Leaf-Height-Seed strategy (Westoby 1998), which dictates that combined characteristics of high SLA, shorter leaf life span and tall canopies indicate competitor strategies, is particularly not well suited. SLA values in these species are all very low, possibly as a result of the extremely nutrient poor soils (Wright et al. 2002), but does not reflect leaf longevity variation, and leaf longevity variation do not indicate relative growth rates. Shrub height indicates fast growth in the tall canopies of *P. repens* and *Leucadendron* females, but in an environment such as fynbos where light is not a limiting resource, growing fast laterally is also a successful strategy as indicated by the shorter, but rounder *Leucadendron* males.

The only functional characteristic emerging from this study as a reliable indicator of climate sensitivity in Proteaceae is growth rate. However, none of the structural indicators of high

relative growth rate proposed by classic functional strategy theories (Grime 1974, Reich et al. 1997, Westoby 1998) were able to adequately rank the study species according to growth rate. Instead, age to reproductive maturity was the best indicator of growth rates, and this characteristic could prove a valuable and easily determined indicator of sensitivity to climate change in the Proteaceae.

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# FUNCTIONAL TRAITS AS INDICATORS OF SENSITIVITY OF SELECTED FYNBOS SPECIES TO DROUGHT

*Abstract.* Global circulation models predict dramatic changes in precipitation as a result of global climate change for the Cape Floristic Region (CFR), a plant biodiversity hotspot. While it is relatively simple to predict vegetation responses to temperature changes, predicting responses to reductions in rainfall, and shifts in timing and intensity of rainfall events remains a challenge. In this study, the effects of a 30% reduction in total rainfall on growth in eight fynbos species, the dominant vegetation type of the CFR, was investigated. Drought treatment was by means of rainout shelters constructed to intercept 30% of incoming precipitation. The varying responses of the study species to the drought treatment were related to functional attributes such as specific leaf area (SLA), leaf nitrogen content, relative growth rate (RGR) and water use efficiency, to explore the possibility of using plant functional types in predicting species' sensitivity to drought. It was found that the study species, despite representing various growth forms and leaf characteristics, showed strong convergence in functional attributes, possibly as a response to the extreme nutrient poor soils of the study site, and therefore a range of functional strategies that could prove useful indicators of sensitivity to drought could not be discerned. RGR, however, did show a more considerable range among the study species than other functional characteristics, and was revealed to be the best indicator of sensitivity to drought. It was found that species with high relative growth rates, such as the dominant broad leaved proteoids, were more sensitive to drought than slow growing needle leaved species of lower vegetation layers, which could lead to dramatic shifts in fynbos vegetation dynamics as a result of climate change.

## INTRODUCTION

Modelling and predicting changes in precipitation as a result of anthropogenic climate change is proving far more complex than similar estimations for temperature (Allen and Ingram 2002, Trenberth et al. 2003). On a global scale, mean land precipitation is expected to increase with rising temperatures (Allen and Ingram 2002), but trends in precipitation changes will not be uniform across the globe. Predictions of latitudinal trends indicate increases in precipitation near the equator and mid-latitudes, but decreases in precipitation in sub-tropical subsistence regions

(Allen and Ingram 2002, Weltzin et al. 2003). Generally areas that are receiving low amounts of precipitation under current climate conditions are expected to become even drier in the future. However, due to the complex dynamics of atmospheric circulation and the hydrological cycle, predicting precipitation changes at regional scales remain the least consistent and least reliable aspects of current climate models (Hulme et al. 1998, Weltzin et al. 2003).

A number of attempts have been made to predict climate conditions under increased atmospheric CO<sub>2</sub> concentrations using various general circulation models (GCMs) for southern Africa (Joubert and Hewitson 1997, Schulze and Perks 2000, Hudson and Jones 2002, Fauchereau et al. 2003), but these authors have emphasized reduced confidence in precipitation predictions compared to temperature. However, all models indicate to an extent a general southward shift of tropical, subtropical and mid-latitude circulation systems bringing about statistically significant decreases in winter rainfall over the Mediterranean-type climate areas of the Western Cape, home of the Cape Floristic Kingdom, a global hotspot of plant diversity.

Hudson and Jones (2002), using HadAM3H, a high-resolution GCM under IPCC SRES emissions scenario A2, predicts decreases in rainfall mainly as a result of decreased precipitation during mid-winter months, as well as an increase in the mean duration of the summer dry period. Joubert and Hewitson (1997) as well as Fachereau et al. (2003) predict rainfall patterns to shift toward fewer but more intense daily rainfall events, and an increase in rainfall variability. Joubert et al. (1996), focusing specifically on the occurrence of droughts over southern Africa under doubled CO<sub>2</sub> scenarios, predicts changes in frequencies and intensity of wet as well as dry years, with an increased probability of droughts. Thus far, only Schulze and Perks (2000) have made specific estimates of expected reduction of mean annual precipitation for the Western Cape: using HadCM2 and an expected atmospheric CO<sub>2</sub> concentration of 550 ppm, they predict a 25% reduction in mean annual precipitation by 2050.

Due to the hot, dry summers associated with Mediterranean climates, vegetation in these regions is known to be generally drought resilient, with a wide variety of drought avoidance strategies associated with various plant species (Chaves et al. 2002). Leaf anatomical features such as reduced leaf size, sclerophylly, trichome layers and ericoid leaves are thought to be adaptations against excessive transpirational water loss during the summer months (Dickison 2000, Lamont et al. 2002). Leaves angled to avoid high light and heat conditions during midday

(Werner et al. 1999, Gratani and Ghia 2002), and seasonal leaf dimorphism, with smaller leaves produced during mid-summer months are also found in various Mediterranean climate areas (Aronne and Micco 2001). Deep rooted Mediterranean plant species are known to maintain water pressure potentials during the driest summer months by tapping into deep underground water reserves (Chaves et al. 2002). Studies on Cape Proteaceae showed how rooting depth in various species adjusts to the depth of the water table (Manders and Smith 1992).

Studies on the effects of drought on Mediterranean plant species have showed that some species are more tolerant of drought than others (Penuelas et al. 2001, Martinez-Vilalta et al. 2002, Penuelas et al. 2004). Llorens et al. (2003a) found that two Mediterranean shrubs with contrasting water use strategies, one a drought avoiding water conservative species, the other a drought tolerating species with a water spending strategy, responded differently to experimental drought conditions on a physiological level (Llorens et al. 2003b), as well as growth (Llorens et al. 2004). Drought significantly reduced photosynthetic rates in the water conservative species, but not in the water spending species. However, both species had reduced growth due to drought – but effects were slightly stronger in the conservative species.

The combination of high photosynthetic rates, rapid growth and non-conservative water use, as opposed to low photosynthetic rates, slow growth and conservative water use have long been recognised as a trade-off in competitive resource use strategies among different plant species and have led to the establishment of categories of 'Plant Functional Types' representing various resource use strategies (Grime 1974, Grime and Hunt 1975, Reich et al. 1997, Duckworth et al. 2000, Westoby et al. 2002, Reich et al. 2003, Díaz et al. 2004, Galmés et al. 2005). Specific Leaf Area (SLA) is considered a good indicator of plant strategies, with high SLA associated with rapidly growing, competitive species, and low SLA with slow growing stress tolerating species (Wilson et al. 1999, Garnier et al. 2001, Díaz et al. 2004, Galmés et al. 2005).

How different functional types will respond and adjust to prolonged drought conditions is not yet well understood. As Llorens et al.'s (2003b, 2004) studies indicated, species with different functional strategies are likely to respond differently to drought, and this may alter species' competitive abilities and ultimately ecosystem dynamics. However, Llorens et al.'s (2003b, 2004) studies are based on only two contrasting species, which makes generalizations problematic. Galmés et al. (2005) investigated the effects of drought on relative growth rate (RGR), net assimilation rate (NAR) and specific leaf area (SLA) of eight Mediterranean species, but grouped

species according to growth forms rather than functional strategies. As Llorens et al. (2003b, 2004) have shown, species with similar growth forms could have opposing water use strategies and therefore different responses to drought. Galmés et al. (2005) did not attempt to make predictions regarding which growth forms will be most vulnerable to drought, and their results remain inconclusive.

With climate change-related threats of increased droughts it is important to know which species will be most sensitive to drought, in order to focus conservation strategies on the more vulnerable species, as well as to understand how ecosystem functioning might be impacted by changes in species productivity. The exceptional botanical diversity of the Cape Floristic Region however makes it impossible to assess each species individually. Therefore, finding similar drought responses among species of similar functional strategies, and being able to determine which functional groups will be most severely affected by drought, would aid assessments immensely. Studies on plant water relations of fynbos species have revealed distinct water use strategies among different growth forms (Stock et al. 1992). Deep rooted proteoid overstorey shrubs are considered to be water spenders as they are able to maintain constant high xylem pressure potentials throughout the year by accessing deep soil water during the dry summer and are therefore able to maintain relatively high photosynthetic rates (Van der Heyden and Lewis 1989). Shallow rooted understorey species such as restioids and ericoids have been shown to have reduced photosynthetic rates during times of water stress, with resulting reduced productivity compared to the proteoids (Stock and Allsopp 1992). This is however due to different reasons: ericoids, as well as succulents are conservative water savers, with strategies and adaptations to control excessive water loss during the dry season (Stock et al. 1992) which then negatively impact their photosynthetic rates, while restioids maintain high stomatal conductances irrespective of water availability with consequent highly variable xylem pressure potentials, low water use efficiency and a higher potential of summer stress (Van der Heyden and Lewis 1989, Stock and Allsopp 1992).

Judging from the results of Llorens et al. (2004) and existing knowledge on water relations of various fynbos growth forms, it can be hypothesized that primary productivity in water conservative understorey species might be more severely affected than in water spending overstorey species. The aim of this study, therefore, is to select a variety of fynbos species representing various life histories and growth forms, and to characterize them with regards to leaf characteristics, water-use efficiency and growth rate. These species were subjected to

experimental drought, and their performances monitored in relation to each other, undroughted conspecific individuals, and functional strategies, in order to potentially make generalized predictions regarding the drought vulnerability of a wide range of fynbos species.

## METHODS

The study site for this experiment is situated at the middle of an altitudinal gradient on the north-facing slope of Jonaskop (33°56.427 S, 19°31.541 E; 960 m) in the Riviersonderend Mountains, Western Cape, South Africa. The site was selected because of its relatively level topography, and because vegetation was still relatively young and short in structure after a recent burn in 2000. Eight fynbos species, common at the study site, were selected to be tested for responses to reduced rainfall.

Leaf material was collected of four individuals of each species during a plant functional trait survey conducted at the site during October 2002 and leaf nitrogen (N) content and  $\delta^{13}\text{C}$  carbon isotope ratios were determined by mass spectrometry (Finnigan MAT 252 mass spectrometer interfaced with a Kiel II (Bremen) Individual Acid Bath Device as well as a Carlo Erba NA1500 via a Conflo II). Leaf material was collected again during November 2005, and specific leaf area (SLA) was determined for each species according to standard methods (Garnier et al. 2001). Leaf N, SLA and leaf life span are good indicators of light saturated net photosynthetic capacity ( $A_{\text{max}}$ ), and a combination of high SLA and  $A_{\text{max}}$  is a strong indicator of the rapid growth functional strategy (Reich et al. 1997, Reich et al. 2003).  $\delta^{13}\text{C}$  isotope ratios are a good indicator of plant water use efficiency (Dawson et al. 2002).

Ten rainout shelters, each covering an area of 2m x 2m, were constructed according to the design of Yahdjian and Sala (2002), with 25 cm gaps between 11 cm wide clear acrylic bands, so as to intercept 30% of incoming precipitation, which is relative to the predictions of Schulze and Perks (2000). The rainout shelters were placed in the field during April 2003 so that five individuals of each of the selected species were covered by five different rainout shelters. Five individuals of each species growing outside of the shelters, but in the same area were also selected and marked as controls. Marked shoots on individuals under and outside the rainout shelters were monitored for two growth seasons (August 2003 – March 2004 and August 2004 – March 2005). Shoot lengths were measured monthly using digital callipers. Note was taken of any deaths among plants under the rainout shelters. A weather station at the site recorded



temperature and rainfall throughout the experiment. Annual rainfall totals are calculated according to fynbos growth phenology. Rainfall during the growth season (October – March), as well as rainfall of the preceding winter is thought to be the most directly related to growth patterns. Therefore ‘annual’ rainfall is the total rainfall from 1 April – 31 March.

Total growth per shoot, the difference in shoot length between the end and start of the growth season, was tested for significant differences between drought treated and control plants as well as between years using non-parametric Mann-Whitney U tests (STATISTICA 6, StatSoft® Inc).

Standard correlations between SLA, leaf N content and relative growth rates (RGR) of control plants were tested to establish whether the selected species confirm worldwide trends. Relationships between water use efficiency ( $\delta^{13}\text{C}$ ) and mean daily growth rate and SLA were also investigated using correlations. To compare the effects of drought on seasonal progression of changes in growth with control plants, variation in absolute growth rates across the growth season was calculated as the change in shoot length between two consecutive monthly measurements, divided by the number of days between the measurements and plotted against time. The proportional decrease in shoot growth as a result of drought, calculated as the difference between mean shoot elongation of control shoots and droughted shoots divided by the mean shoot elongation of control shoots, was then correlated with leaf traits and water use efficiency to establish whether these measurements could be used as potential indicators of drought sensitivity.

## RESULTS

Fire life history strategies - whether species regenerate after fire by means of seed germination (seeders) or by resprouting from vegetative underground structures (sprouters), leaf characteristics and water use efficiency of the eight studied species are summarized in Table 1. Specific leaf area ranged from extremely low ( $6.9 \text{ mg.g}^{-1}$  in *Serruria gremialis*) to  $34.6 \text{ mg.g}^{-1}$  in *Protea amplexicaulis*. Leaves of *Phaenocoma prolifera* are extremely small, and SLA for this species could not be determined accurately. Succulents with low SLA, despite high leaf water content, have been found in other floras and represent an alternative strategy to sclerophylly in dealing with nutrient-poor, drought prone environments (Vendramini et al. 2002), such as the Cape Floristic Region, explaining why SLA of *Erepsia gremialis* is relatively low. Very low leaf nitrogen content found in seven of the species also reflected the highly leached sandstone

derived soils on which they are found. *Podalyria* sp. has slightly higher leaf nutrient content due to free N<sub>2</sub> fixing root nodules (Musil et al. 2003). Carbon isotope ratios for all species analyzed fall within the C3 range (Dawson et al. 2002). Analysis of other succulents at the study area revealed ratios within the CAM range. *Erepsia gracilis*, which was not sampled during the 2002 survey, is most likely also CAM, which would have made comparisons with the other species problematic. *Protea repens* has the highest water use efficiency (-25.70), while *Leucadendron salignum* (-28.02) and *Serruria gremialis* (-28.07) has the lowest.

Only a few of the very smallest seedlings died as a result of the drought treatment. Deaths were found for seedlings of *Phaenocoma prolifera* and *Serruria gremialis*. Total annual rainfall recorded at the site during the first year of monitoring (May 2003 – April 2004) was 360.9 mm and during the second year (May 2004 – April 2005) 491.9 mm.

Five out of the eight species monitored showed reduced growth under the drought treatment during the first growth season (2003, Figure 1). Growth was not affected by the drought treatment in *Protea laurifolia*, *Serruria gremialis* and *Phaenocoma prolifera*. However only for *Leucadendron salignum* was growth significantly reduced (Mann-Whitney U = 3, p = 0.047) during the first growth season, while only *Protea repens* had significantly reduced growth in drought treated individuals during the second growth season (Mann-Whitney U = 0, p = 0.009).

For *Protea laurifolia*, *Serruria gremialis* and *Phaenocoma prolifera* mean daily growth in drought treated plants matched that of control plants for most of the first growth season. Only towards the end of the growth season, during late summer, did growth in the drought treated individuals decrease, while control plants maintained higher growth rates (Figure 2).

Despite higher total annual rainfall during the second year, many species had reduced growth during the second year of the experiment, compared to the first, drier year (Figures 1 and 2). Both drought treated and control plants of *Protea laurifolia*, *Serruria gremialis*, *Podalyria* sp., *Phaenocoma prolifera* and *Erepsia gracilis* showed greatly reduced growth in the second year of the experiment compared to growth during the first year (Figure 1). Two of the three species that tolerated the first year of drought with little effect on growth (*P. laurifolia* and *P. prolifera*) not only had reduced growth in all plants during the second year, but reduced growth in drought treated plants compared to control plants also became apparent (Figure 2), however growth in drought

TABLE 1. Leaf and other characteristics of the species used in this study. Values for leaf area, specific leaf area (SLA), leaf nitrogen and  $\delta^{13}\text{C}$  ratios are means of four plants  $\pm$  1 standard error.

Species	Family	Growth Form	Fire Life History	Height of Adult (m)
<i>Protea amplexicaulis</i> (Salisb.) R. Br.	PROTEACEAE	evergreen shrub	seeder	0.4
<i>Protea repens</i> (L.) L.	PROTEACEAE	evergreen shrub	seeder	4.5
<i>Protea laurifolia</i> Thunb.	PROTEACEAE	evergreen shrub	seeder	8.0
<i>Leucadendron salignum</i> P.J. Bergius	PROTEACEAE	evergreen shrub	sprouter	1.0
<i>Serruria gremialis</i> Rourke	PROTEACEAE	evergreen shrub	sprouter	0.3
<i>Podalyria</i> sp.	FABACEAE	evergreen shrub	sprouter	0.6
<i>Phaenocoma prolifera</i> (L.) D. Don	ASTERACEAE	evergreen shrub	seeder	0.5
<i>Erepsia gracilis</i> (Haw.) L. Bolus	MESEMBRYANTHEMACEAE	leaf succulent	seeder	0.3

treated plants was not significantly lower than in control plants. Reduction in growth of all plants between the first and second growth season was significant for *Protea laurifolia* (Mann-Whitney U = 23,  $p = 0.041$ ), *Serruria gremialis* (Mann-Whitney U = 23,  $p = 0.039$ ) and *Podalyria* sp. (Mann-Whitney U = 12,  $p = 0.004$ ).

Positive relationships were found between relative growth rate and SLA, leaf N content and SLA, as well as  $\delta^{13}\text{C}$  and SLA (Figure 3), but these relationships were not significant ( $p > 0.05$ ), and not as strong as reported in the literature (Reich et al. 1997, Reich et al. 1999, Lamont et al. 2002). No significant relationships between reduction in growth due to drought and SLA,  $\delta^{13}\text{C}$  or relative growth rate were found (Figure 4). Very low SLA species, such as *Serruria gremialis* and *Erepsia gracilis* were not as severely affected by drought as higher SLA Proteaceae species such as *Leucadendron salignum* and *Protea repens*. However, within the three *Protea* species, which have similar, relatively high SLAs, there was large variation in growth responses to drought between the species (Figure 4a). Water use efficiency, as indicated by  $\delta^{13}\text{C}$ , did not explain drought resistance, with both the species with the highest  $\delta^{13}\text{C}$  (*Protea repens*) and second lowest  $\delta^{13}\text{C}$  (*Leucadendron salignum*), being most severely affected by drought (Figure 4b). Relative growth rate was the strongest predictor of the severity of drought effects on growth with  $r^2 = 0.43$  (Figure 4c).

## DISCUSSION

Five species tested in this experiment, *Protea laurifolia*, *Serruria gremialis*, *Phaenocoma prolifera*, *Podalyria* sp. and *Erepsia gracilis* were more strongly affected by interannual variation in rainfall during the experiment than the drought treatment. Although total rainfall during the

TABLE 1. Extended.

Leaf Area (cm <sup>2</sup> )	SLA (cm <sup>2</sup> /g)	Leaf N (mg/g)	δ <sup>13</sup> C (‰)	Other specialized leaf characters
5.92±0.8	34.6±1.6	8.2±0.7	-26.95±0.3	sclerophyll
1.68±0.2	21.0±2.2	10.1±1.1	-25.70±0.4	none
4.76±0.4	30.5±1.7	7.3±0.5	-27.84±0.3	sclerophyll, trichome layer
0.50±0.1	20.2±0.8	4.0±0.3	-28.02±0.5	none
0.24±0.03	3.6±0.8	6.9±1.2	-28.07±0.4	branched terete
0.61±0.08	27.5±0.7	19.9±1.4	-27.04±0.4	dense trichome layer
0.003 ±0.0004	n/a	6.2 ±0.7	-26.94±0.4	very small ericoid leaves
0.06±0.005	9.6±0.7	n/a	n/a	succulent leaves, drought deciduous

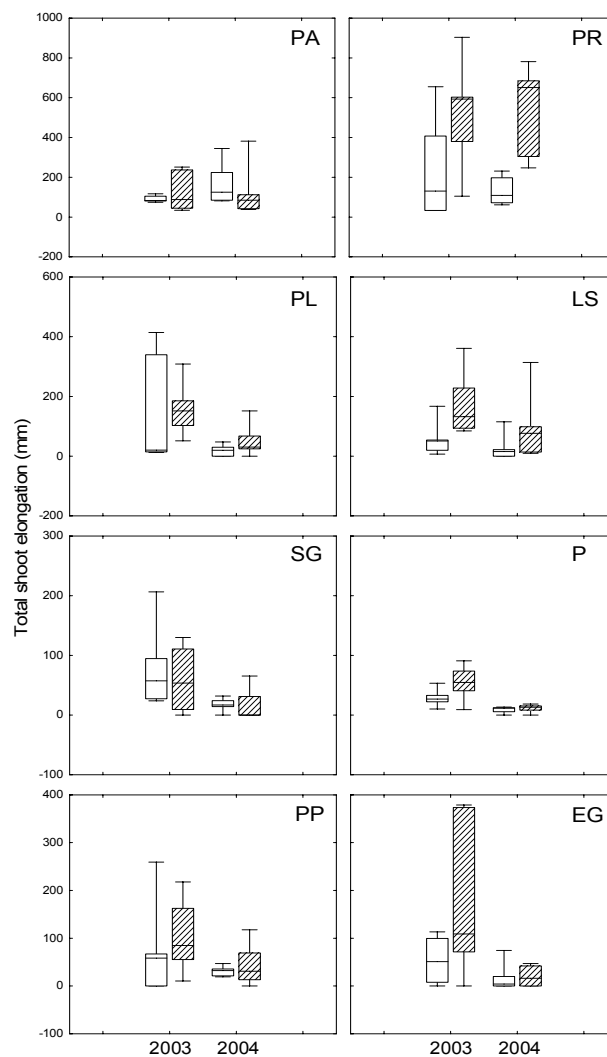


FIGURE 1. Boxplots (min-max, median and quartiles) of annual shoot elongation, comparing growth of drought treated individuals (unshaded boxes) with growth of control plants (shaded boxes) across two growth seasons, 2003 and 2004. Species are PA – *Protea amplexicaulis*, PR – *Protea repens*, PL – *Protea laurifolia*, LS – *Leucadendron salignum*, SG – *Serruria gremialis*, P – *Podalyria* sp, PP – *Phaenocoma prolifera* and EG – *Erepsia gracilis*.

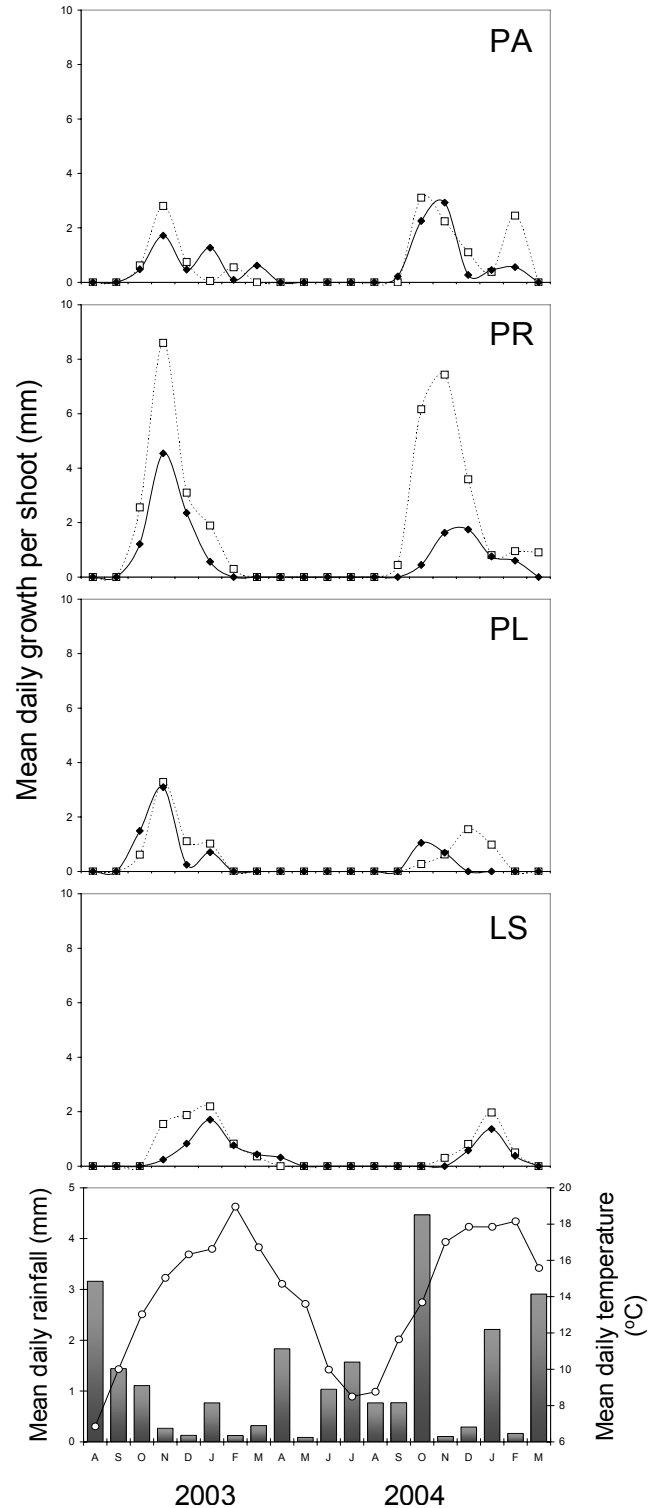


FIGURE 2. Mean monthly absolute growth rates (mm.day<sup>-1</sup>) across the duration of the experiment showing differences in growth rate between drought treated (solid lines) and control plants (dotted lines). Graphs below indicate corresponding temperatures and rainfall recorded at the site during the experiment. Species are PA – *Protea amplexicaulis*, PR – *Protea repens*, PL – *Protea laurifolia*, LS – *Leucadendron salignum*, SG – *Serruria gremialis*, P – *Podalyria* sp, PP – *Phaenocoma prolifera* and EG – *Erepsia gracilis*.

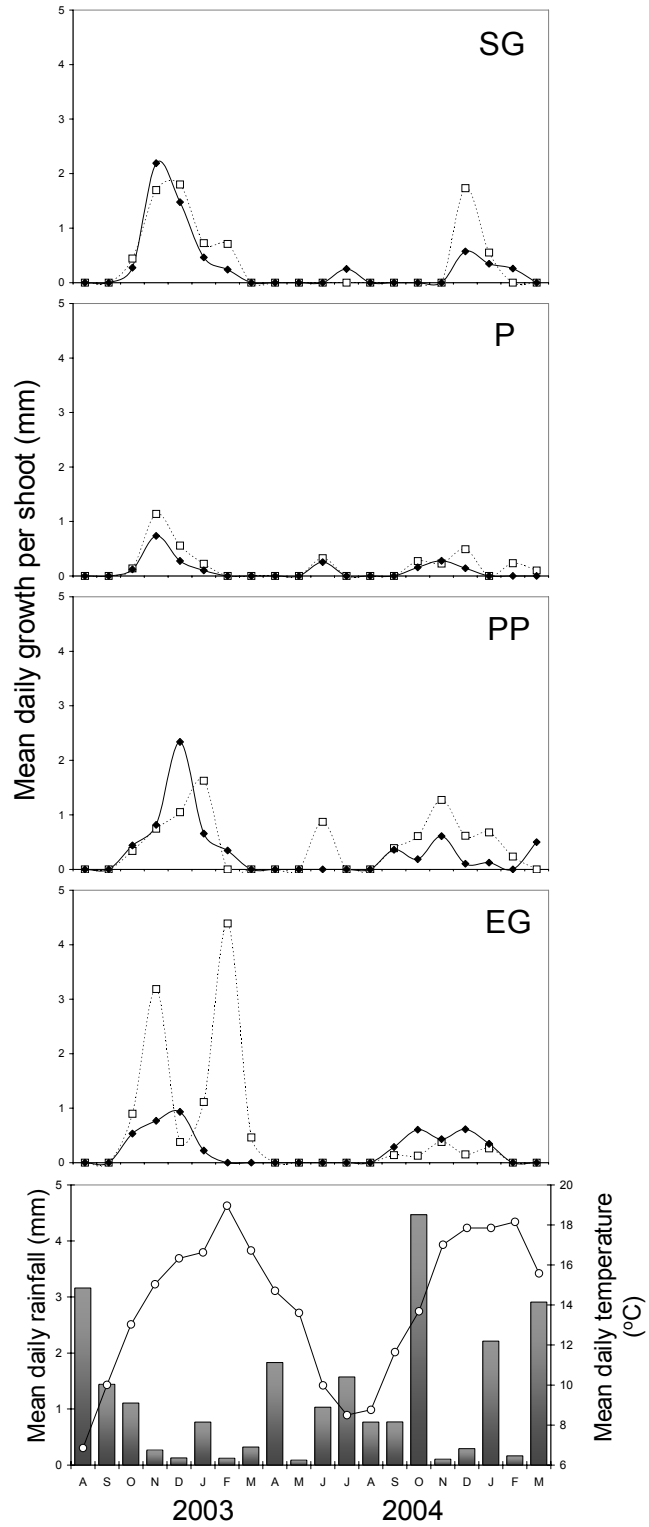


FIGURE 2. Extended.

second year was more than 100 mm higher than during the first year of the experiment, these species responded with large reductions in shoot growth. A careful analysis of monthly rainfall patterns (Figure 1) indicates that the high total rainfall of 2004-2005 is entirely due to extremely high rainfall during October, January and March, while the winter months preceding the start of the growth season were relatively dry compared to the previous year. The very dry summer of 2003-2004, which was followed by the dry winter of 2004 represented a long and likely very stressful dry period, which resulted in the overall poor growth of so many species. Although growth was monitored for only two years, responses of the study species strongly emphasize the importance of rainfall variability affecting productivity more severely than rainfall totals. Growth responses indicate that Hudson and Jones's (2002) predictions of winter droughts and Joubert and Hewitson's (1997) predictions of shifts to fewer and more intense rainfall events will have severe consequences for growth of fynbos species.

Relationships between SLA, leaf N and water use efficiency as indicators of resource use strategies have been illustrated across sites (Wright et al. 2001, Lamont et al. 2002) and biomes (Reich et al. 1997, Reich et al. 1999, Díaz et al. 2004), but at individual sites these relationships can become less clear (Ackerly et al. 2002). Especially among the species included in this study, the range of SLA's represented is very narrow, and *Serruria gremialis*, with its extremely low SLA, leaf N and RGR compared to all other species, in most cases defined trends (Figures 3 and 4). SLA and leaf N in all the species sampled in this study are so low as to place them all among needle-leaved evergreens, rather than other broad leaved evergreen species associated with nutrient poor environments, according to categorizations based on a global analysis by Reich et al. (1997). SLA, leaf N and RGR in the study species are therefore more likely representing a convergence in adaptive responses in resource use strategies, rather than indicating a range of strategies, or 'solutions' to surviving the challenges of climate and soil nutrient status of the study site.

Relative growth rate, however, is more variable among the study species compared to variation in SLA and leaf N, and it proved to be the best indicator of sensitivity to drought, with species with higher RGR's being more sensitive to drought. This confirms the findings of another study on growth responses of Proteaceae species to interannual climate variability showing faster growing species to be more responsive to variation in temperature and rainfall than slow growing species (Chapter 3). It is suggested therefore that relative growth rate is used as a measure for assessing vulnerability to drought in fynbos at the more local scale, rather than SLA.

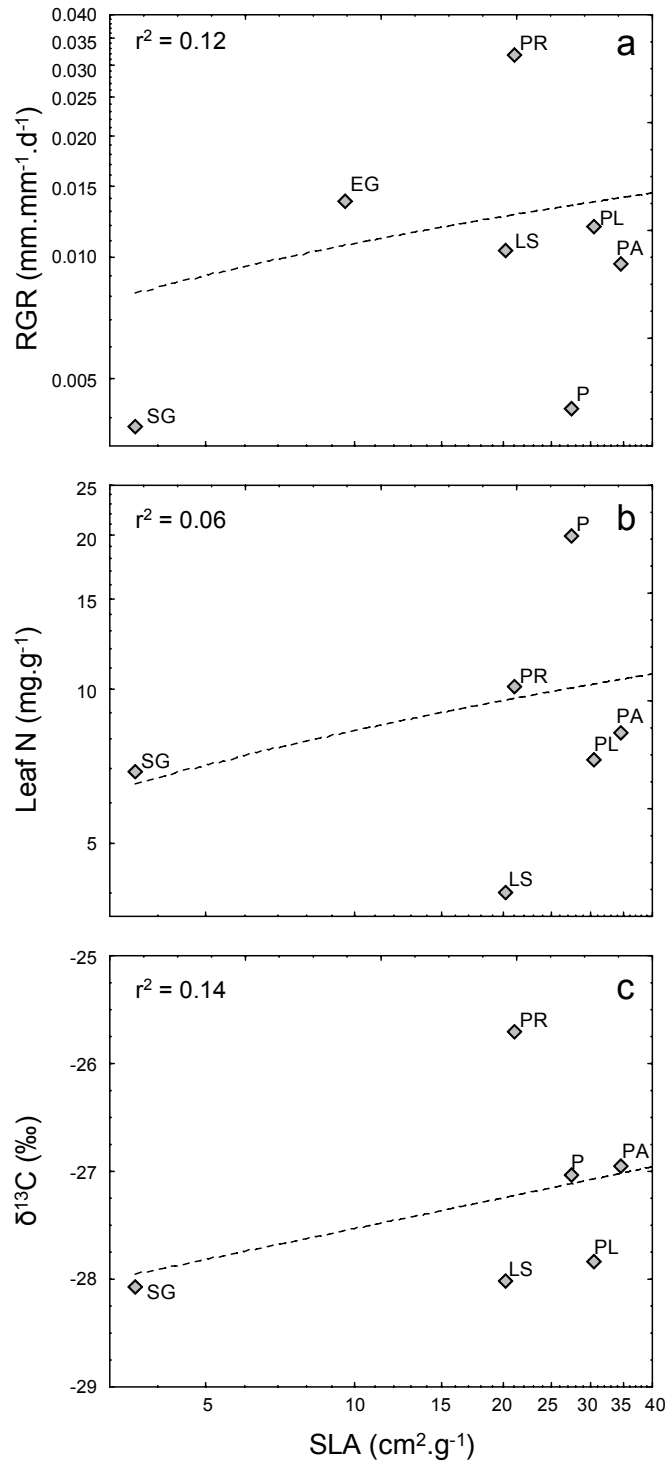


FIGURE 3. Relationships between specific leaf area (SLA) and (a) relative growth rate (RGR), (b) leaf nitrogen content and (c) water use efficiency ( $\delta^{13}C$ ) of the study species. Regression lines indicate trends, but none are significant at  $p = 0.05$ . Species are PA – *Protea amplexicaulis*, PR – *Protea repens*, PL – *Protea laurifolia*, LS – *Leucadendron salignum*, SG – *Serruria gremialis*, P – *Podalyria* sp., PP – *Phaenocoma prolifera* and EG – *Erepsia gracilis*.



Interestingly, the three species representing the lowest relative growth rates among the eight monitored species (*Serruria gremialis*, *Phaenocoma prolifera* and *Podalyria* sp.) were all among the species that showed stronger responses to the dry summer and winter preceding the second growth season than to the drought treatment, suggesting that perhaps while fast growing species are more sensitive and responsive to short term changes in climate and general reductions in rainfall, slow growing species might also be affected negatively by longer term droughts.

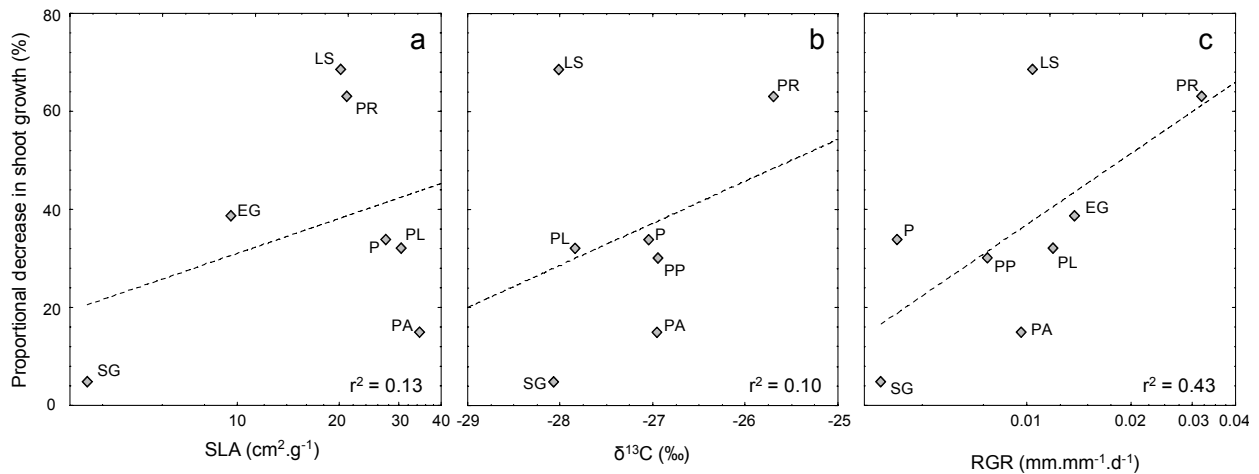


FIGURE 4. Proportional decrease in shoot growth as a result of the drought treatment in relation to (a) specific leaf area (SLA), (b) water use efficiency ( $\delta^{13}\text{C}$ ) and (c) relative growth rate (RGR). No relationships are significant at 0.05 level. Species are PA – *Protea amplexicaulis*, PR - *Protea repens*, PL – *Protea laurifolia*, LS – *Leucadendron salignum*, SG – *Serruria gremialis*, P – *Podalyria* sp, PP – *Phaenocoma prolifera* and EG – *Erepsia gracilis*.

In general, it appears that drought impacts are more likely to result from changes in rainfall sequencing, rather than from a simple 30% reduction in rainfall, and that after establishment, quite significant rainfall reductions or extreme drought durations may be necessary to result in individual plant mortalities. This highlights the difficulties of modelling species range determinants using “average” climatic conditions (e.g. Midgley et al 2003) and illustrates the importance of developing species-specific models of drought susceptibility that may not be clearly derived from simple analyses of plant functional type traits.

Contrary to the findings of Llorens et al. (2003a, 2004), in this study extremely slow growing conservative species such as *Serruria gremialis* were very resilient to the drought treatment, while highly productive, fast growing dominant overstorey species such as *Protea repens* were

most severely affected. Should this be a general trend in fynbos, fynbos vegetation dynamics will be severely altered by climate change, with shifts among dominance in the tall broadleaved proteoids from fast growing, productive species such as *Protea repens* to slower growing species such as *Protea laurifolia*, while lower vegetation layers shifts in dominance will be towards slow growing needle leaved species such as *Serruria gremialis*.

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### SOIL TYPE AND CLIMATE AS DETERMINANTS OF THE FYNBOS SUCCULENT KAROO-BOUNDARY: NEW INSIGHTS FROM A RECIPROCAL TRANSPLANT EXPERIMENT

*Abstract.* Bioclimatic modeling of the effects of climate change on biomes and species of the winter rainfall zone of the south-western Cape, South Africa, indicates that in future many areas currently occupied by the Fynbos Biome will be experiencing warmer and drier conditions similar to that currently associated with an adjacent biome, the Succulent Karoo. This raises the question whether in future fynbos vegetation, or at least some of its component species, will disappear from these areas and be replaced by succulent karoo species. The determinants of the fynbos-succulent karoo boundary are fairly well understood and are almost certainly not due to climate alone. In this study a reciprocal transplant of fynbos and succulent karoo seedlings on an elevational gradient straddling a transition between fynbos and succulent karoo vegetation allowed the investigation of three key questions regarding climate change and the fynbos-succulent karoo boundary: Firstly, whether climate, soil type or other biotic factors are the main determinants of the boundary, secondly to determine the effects of drier and warmer climate on fynbos seedlings, and thirdly to assess the potential of succulent karoo to invade fynbos as a result of climate change. Although climate had a significant effect on growth and survival of seedlings of all species, growth and survival responses were not consistent with their natural distributions, with seedlings surviving and growing well outside of their natural ranges. Soil type limited fynbos seedling survival and growth, but not karoo seedlings. Cooler and wetter climates at higher altitudes did not limit karoo species. Fynbos seedlings were tolerant of short term drought, but the effects of prolonged drought on seedling survival remain unknown. It is suggested that competition and fire, rather than climate and soil type, likely prevent succulent karoo species from intruding into fynbos, while soil type is a strong controller of the distribution of fynbos species. Marginal habitats on the northern edges of the fynbos biome are at the greatest risk of being replaced by succulent karoo species in the event of a severe post-fire drought preventing regeneration of fynbos vegetation, and should therefore be considered important monitoring sites for early signs of ecosystem changes.

## INTRODUCTION

The mountain ranges of the Cape Floristic Region are known for their extreme environmental gradients, which are reflected in the rapid turnover in floristic composition of the vegetation along the slopes of these mountains. These gradients are the result of temperature and rainfall variation, associated with aspect and altitude, as well as soil diversity (Oliver et al. 1983, Cowling and Holmes 1992, Goldblatt 1997). On the dry, north-facing slopes of the south-western and southern interior of South Africa, climatic and soil gradients lead to the intersection of the Fynbos Biome, the main vegetation type of the Cape Floristic Region, with its major neighbouring biome, the Succulent Karoo (Cowling and Holmes 1992), with high turnover of species across the fynbos-succulent karoo boundary (Chapter 1).

Both Fynbos and the Succulent Karoo Biomes are renowned for their exceptional species diversity (Goldblatt 1997, Cowling et al. 1999) and are largely associated with the winter rainfall region of the Western Cape. The Succulent Karoo is associated with drier and warmer areas, and is found on plains and lower slopes with annual rainfall between 20 and 290 mm and with summer temperatures reaching up to 40°C during summer (Hoffman 1998), while fynbos is found on sandy lowland coastal plains as well as mountains, but not in areas where annual rainfall is below 200 mm (Rebelo 1998), and seldom on shale-derived substrates.

With climate change predictions for the Western Cape indicating a 0.5-1°C increase in mean annual temperatures and a 25% reduction in annual rainfall within the next 50 years (Joubert and Hewitson 1997, Rutherford et al. 1999, Fauchereau et al. 2003), there is the possibility that extensive areas may become too dry to support fynbos, and that these areas might be invaded by succulent karoo elements. Bioclimatic modeling of biome distributions under future climate scenarios indeed indicate a contraction of fynbos and a southward shift of succulent karoo into areas currently occupied by fynbos (Hannah et al. 2002, Midgley et al. 2003). These models however consider only climatic limitations to biome distributions, while there may be many other biotic and abiotic factors involved in shaping biome boundaries. Before realistic assessments of the impacts of climate change on biome distributions can be made, it is important that the determinants of biome boundaries be well understood.

A large amount of literature exists on the determinants of southern African biomes, as well as on the boundaries of the Fynbos Biome in particular (Cowling and Holmes 1992, Rutherford and

Westfall 1994, Rutherford 1997, Lechmere-Oertel and Cowling 2001, Bond et al. 2003). Apart from climate, disturbance is considered one of the main sculptors of vegetation patterns in southern Africa (Bond 1997, Bond et al. 2003). In the Fynbos Biome fire as a disturbance is the driving force of ecological processes such as regeneration, succession and vegetation dynamics. Because tolerance of fire requires adaptive responses in plants (Bond and van Wilgen 1996), fire is likely to be a critical factor in preventing other biomes from intruding into fynbos. Succulent karoo species are intolerant of fire, but it has been found that in the absence of fire thicket species and succulents have successfully invaded fynbos (Cowling and Pierce 1988).

Soil type is another important factor to consider. The Cape Floristic Region is characterized by a diversity of geological formations and soil types. Fynbos is found on a variety of soil types, ranging from derivatives of ancient, highly leached sandstone formations in the mountains, to moderately fertile finer-grained soils derived from shales and granite (mostly on the lowlands) and complex sequences of nutrient poor acidic and alkaline sands of Aeolian and marine origin along the coast (Cowling et al. 1997). Most of the underlying geological formations of the Fynbos Biome extend beyond the biome borders (Partridge 1997), and adjacent biomes share many of the fynbos soil types. Therefore, at the biome level soil type seems relatively unimportant in delimiting biome boundaries.

However, at the level of vegetation type, many species assemblages are associated with specific soil types (Low and Rebelo 1998). Then again, many experimental studies have indicated that soil factors as determinants of community boundaries are very complex, interacting with a variety of other environmental factors, for example Richards et al. (1997a) found that soil type, rather than competition explains replacement of Proteaceae species pairs on a sandstone-limestone edaphic gradient, and further showed how community boundaries are associated with variations in soil nutrient levels (Richards et al. 1997b). Mustart and Cowling (1993), however, in a reciprocal transplant experiment found that soil type does not limit the germination and growth of seedlings and did not explain the distribution of edaphically restricted Proteaceae species on the Agulhas Plain. In a controlled greenhouse experiment specifically concerned with the fynbos-succulent karoo boundary Lechmere-Oertel and Cowling (2001) found that a combination of soil type and moisture levels controlled seedling growth and survival. Fynbos seedlings survived on sandstone as well as shale derived soils under mesic conditions, but died rapidly under xeric conditions in both soil types. Succulent karoo seedlings survived



well in both soil types and under both moisture regimes. Euston-Brown (1995) performed a reciprocal transplant between eight vegetation types in the Kouga Mountains, Eastern Cape, and found that fynbos plants survived well at all sites except in the most arid areas, which were associated with shale derived soils. Succulents grew well at all sites except at the highest elevations.

Reciprocal transplant experiments are very useful in disentangling various biotic and abiotic determinants of community boundaries (Ewanchuk and Bertness 2004, Pennings et al. 2005). Such experiments are also very valuable in testing climate change ecosystem model predictions (Newton et al. 2001). Transplanting species across elevational gradients allows the simulation of future climate change scenarios (Bruelheide 2003, Link et al. 2003). In this study a reciprocal transplant experiment on a temperature and moisture gradient comprising a natural transition between fynbos and succulent karoo was designed with three main objectives:

1. To refine existing knowledge of the exact determinants of the fynbos-succulent karoo boundary.
2. To determine the effects of future climate change on selected fynbos species.
3. To assess the invasibility of fynbos by succulent karoo under climate change conditions.

## METHODS

### *Study area*

The study area is an altitudinal gradient providing both temperature and moisture trends, on the north-facing slope of Jonaskop in the Rivieronderend Mountains, and situated in the Mediterranean climate region of the Western Cape. Succulent Karoo vegetation is found on shale derived soils on the lower warmer and drier end of the gradient (up to 600 m altitude). Between the top of the mountain (1694 m) and the middle of the gradient (800 m) Mountain Fynbos is found on sandstone derived soils. Descending further, between the Succulent Karoo and Mountain Fynbos, and directly above the transition from shale derived to sandstone derived soils, is an ecotonal zone consisting of a mixture of karoo and fynbos elements (Figure 1). Vegetation types are named according to Low and Rebelo (1998).

Climate stations placed at selected points along the gradient, which spans a change of roughly 1000 m in altitude, indicate that temperatures decrease on average by 0.38°C with every 100 m

rise in altitude. The weather station located in the succulent karoo at the lowest end of the gradient records on average 56 % less rainfall than the weather station located near the mountain summit. Data of total monthly rainfall, mean, maximum and minimum temperatures recorded during the experiment at the top, middle and lower end of the gradient are summarized in Figure 2.

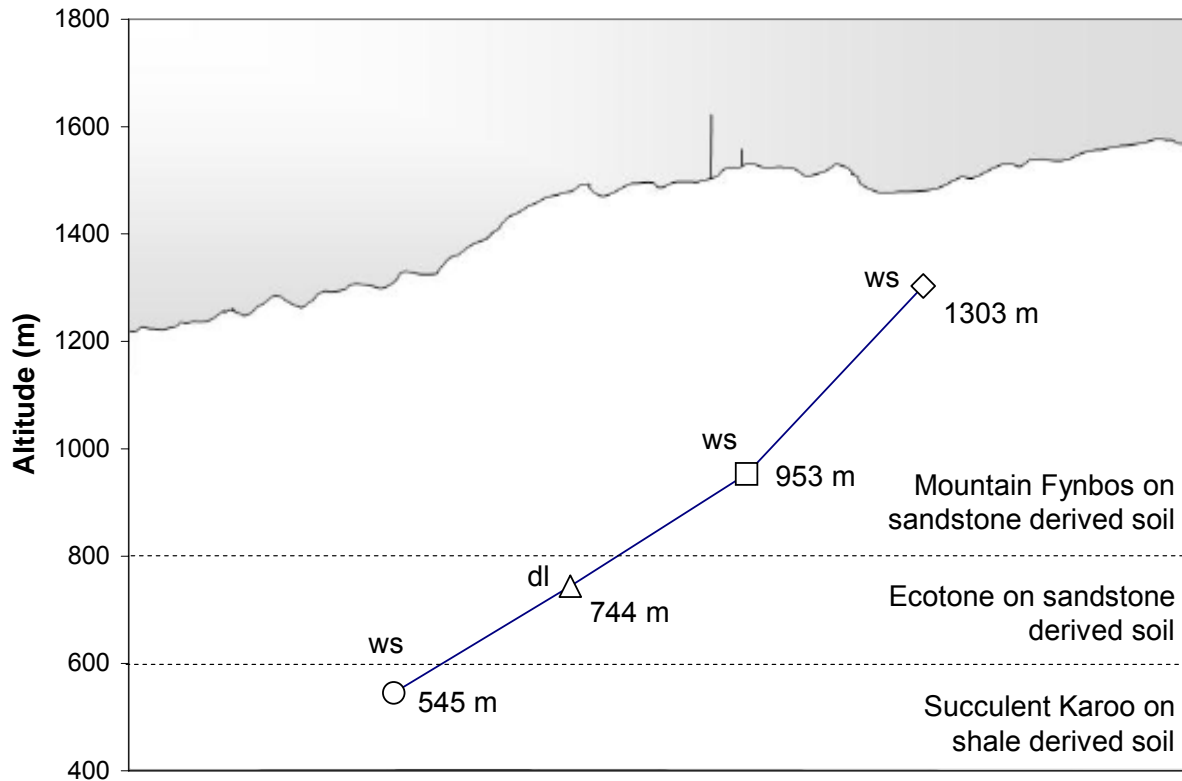


FIGURE 1. The study site, a temperature and moisture gradient on a north-facing mountain slope, showing the location of data loggers, weather stations and experimental plots. The same symbols indicating the altitudinal location of experimental plots are also used in all other figures. ws: weather station, recording temperature as well as rainfall, dl: data logger, recording only temperature.

Sandstone and shale derived soils sampled at selected altitudes on the gradient differ strongly in phosphorous and magnesium content (Figure 3), but not in terms of other nutrients (N, Ca, K and Na) and pH.

#### *Study species*

Seeds were collected on the gradient of several species representing fynbos and succulent karoo: five Proteaceae, two Ericaceae, one Restionaceae in the fynbos, and two Mesembryanthemaceae and one Asteraceae from the succulent karoo.

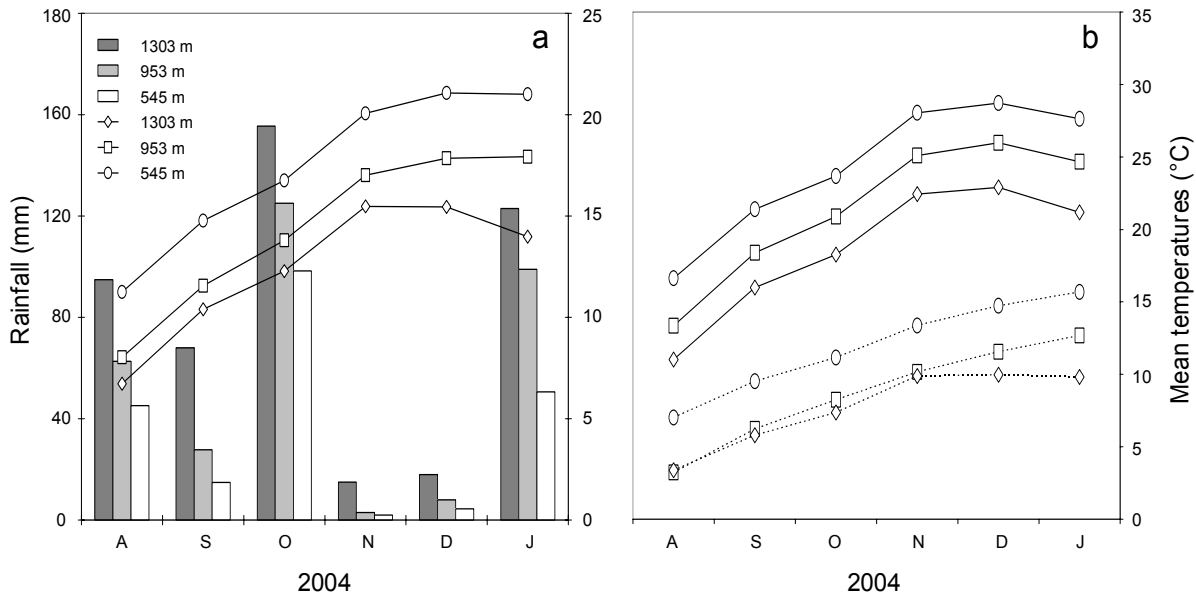


FIGURE 2. Temperature and rainfall recorded at selected altitudes during the experiment. (a) Total monthly rainfall and mean monthly temperature. (a) Mean daily maximum temperatures (solid lines) and mean daily minimum temperatures (dashed lines).

All seeds were treated with commercially available smoke primer, since it has been shown that not only fynbos species (Brown and Botha 2004), but many succulents germinate better as well in response to smoke treatment (Pierce et al. 1995). Larger seeds, such as the Proteaceae and Restionaceae were germinated first on moistened filter paper in temperature and light controlled growth chambers according to prescriptions by Mustart and Cowling (1991) before being planted into seedling trays. Smaller seeds (Asteraceae, Ericaceae and Mesembryanthemaceae) were sown directly into seedling trays containing either sandstone or shale derived soils collected on the gradient. All seeds were germinated during April 2004.

Only six species germinated in sufficient numbers to be used in the experiment. They were *Protea magnifica* Link (Proteaceae), *Protea amplexicaulis* (Salisb.) R. Br. (Proteaceae), *Protea humiflora* Andrews (Proteaceae), *Drosanthemum speciosum* (Haw.) Schwantes (Mesembryanthemaceae), *Ruschia lineolata* (Haw.) Schwantes (Mesembryanthemaceae) and *Pteronia incana* (Burm.) DC. (Asteraceae).

*Protea magnifica* is generally found on hot dry slopes near the snow line (1200-2700 m) on mountain ranges in the western and southern Cape (Rebello 2001). On the Jonaskop gradient *P. magnifica* is found from 1200 to 1400 m a.s.l. *Protea amplexicaulis* and *Protea humiflora* are

both low sprawling shrubs pollinated by rodents. *Protea amplexicaulis* is very common on dry north-facing slopes of mountain ranges in the Western Cape, and found on sandstone soils from 180-1600 m, while *P. humiflora* is typically found near the fynbos-succulent karoo ecotone on very hot and dry north-facing slopes (450-1200 m). It has a slightly more eastward distribution than *P. amplexicaulis*, intruding into the Anysberg, Rooiberg and Gamka Mountains of the western Little Karoo (Rebello 2001). On Jonaskop *P. amplexicaulis* is found from 1400 m down to 900 m, whereafter it is replaced by *P. humiflora* which occurs from 900 m down to 600 m.

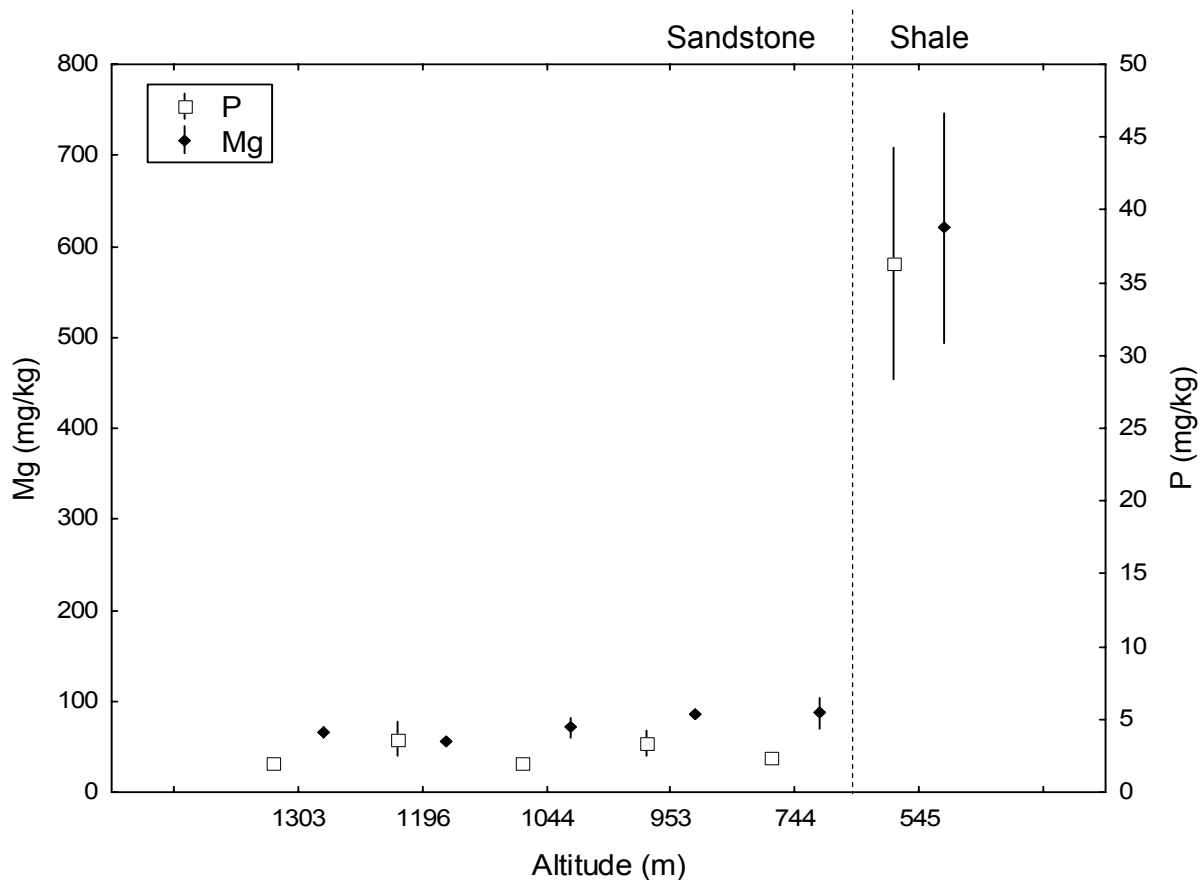


FIGURE 3. Phosphorous (P) and magnesium (Mg) content of soil collected at selected altitudes on the gradient, indicating differences in nutrient levels between sandstone and shale derived soils.

*Drosanthemum speciosum* is a perennial succulent shrub endemic to the Worcester-Robertson Karoo Centre. *Ruschia lineolata*, a dwarf perennial succulent shrub is associated with succulent karoo as well as fynbos, found from Caledon to as far east as Humansdorp, as well as in the Little Karoo from Worcester to Barrydale (Chesselet 2003). *Pteronia incana* is a finely branched unpalatable shrub and very widespread, occurring from the north of Namaqualand to the south-

western Cape, and eastwards as far as the Fish River in the Eastern Cape. It is found in Succulent Karoo as well as Nama Karoo habitats (Bond and Goldblatt 1984), and can become dominant in vegetation degraded by overgrazing (Kakembo 2001). On the Jonaskop gradient *P. incana* and *R. lineolata* are restricted to the succulent karoo, while *D. speciosum* is found in the succulent karoo as well as the ecotone.

Seedlings were kept under greenhouse conditions for roughly two months after germination and watered daily. About three weeks before planting into the field, seedlings were moved into direct sunlight and watering was gradually reduced to twice a week to harden seedlings in anticipation of field conditions. Seedlings were planted into the field site during late July 2004.

#### *Experimental design and statistical analysis*

Field plots were prepared at four selected altitudes (Figure 1): 1. 1303 m, near the top of the mountain; 2. 953 m, near the middle of the gradient and lower edge of fynbos; 3. 744 m, in the ecotone; and 4. 545 m, in the succulent karoo. These sites were selected because vegetation analysis (Chapter 1) and a phenological study (Chapter 2) indicated these points as important climatic thresholds controlling growth and distributions of species on the gradient. A nested design was used, where each plot consisted of 14 containers, each 0.6 m wide, 0.64 m long and 0.3 m deep. Containers were placed on top of the soil surface, and 7 containers were filled with sandstone derived soil collected from the 953 m site, while the other 7 were filled with shale derived soil collected from the lower end of the gradient, in a randomized design. The bottoms of the containers were left open, but were isolated from the soil below with a layer of coarse gravel and plastic sheeting with regularly spaced holes to facilitate drainage. An outer frame filled with sand provided insulation around the outer perimeter of the experimental plots.

Depending on germination success, either two (*Protea amplexicaulis*), three (*Protea magnifica*, *Pteronia incana*) or four (*Protea humiflora*, *Drosanthemum speciosum*, *Ruschia lineolata*) seedlings per species were planted in each container, again to randomly assigned positions in the containers. Seedlings were watered after transplanting and again two days later, but after that were left to grow under natural climate conditions.

Geographic distribution data for each species was used to derive ranges of climatic conditions under which each species is found. Herbarium records (PRECIS database) were used for *Ruschia lineolata*, *Drosanthemum speciosum* and *Pteronia incana*, while more systematically

collected field census data from the Protea Atlas Project (Rebello 2001) were used for the *Proteas*. Climate data associated with each locality were interpolated from the South African Atlas of Agrohydrology and –climatology (Schulze 1997). This method has been used to construct three dimensional climatic niche spaces for plant species (Westman 1991). Climate variability associated with the transplanted species' geographical ranges was characterized in two ways: Mean annual temperature vs. mean annual precipitation, as an indicator of the species' ranges of general temperature and moisture requirements, and mean minimum temperature of the coldest month ( $T_{\min}$ ) vs. mean maximum temperature of the warmest month ( $T_{\max}$ ), as a specific indication of the temperature ranges associated with the species' distributions. Number of records rather than proportion of total distribution area associated with each combination of temperatures or temperature and rainfall were used to construct response surfaces. Climate data related to the selected species' natural ranges were compared to climate data recorded by weather stations on the gradient before and during the experiment, in order to make predictions of how seedlings are expected to perform at the various altitudes. Climate conditions associated with the highest frequencies of records for each species were considered as optimum conditions, and temperature and rainfall data recorded on the gradient were placed in context of both the extent of climate variability under which each species is found as well as in relation to optimum conditions.

Seedling sizes were measured monthly for six months (height and diameter measurements were taken) to include a winter (wet) as well as summer (dry) period. Seedling sizes were calculated by a simple multiplication of height (mm) with diameter (mm). At the end of the experiment, total seedling growth was calculated as the difference in seedling size between the last and first measurements, taken on the day the seedlings were transplanted. If seedlings died during the experiment, total growth was calculated as the difference in size between the last measurement taken before seedling death and the first measurement. Mean total growth for each container was used in a main effects ANOVA to test separately for the effects of categorical factors climate (site 1-4) and soil type on seedling growth. Interactive effects of climate and soil type were further tested using ANCOVA (homogeneity of slopes general linear model, substituting site number with altitude to create a continuous covariate, STATISTICA 6, StatSoft® Inc).

## RESULTS

Constructed climate niches indicated that the karoo site (545 m) is too dry for *Protea magnifica* and *P. amplexicaulis* (Figure 4), falling outside of climate ranges under which these species are found. The karoo site is also too hot for *P. magnifica*, and very close to the extremes of temperature conditions for *P. amplexicaulis* (Figure 5). Performance of seedlings at this site could possibly indicate how these two species might respond to future climate change. Seedlings for these two species were expected to perform best at the middle (953 m) and highest (1303 m) sites. The middle site (953 m) also represents optimum conditions for *P. humiflora* and while the karoo site (545 m) is not outside of this species' modeled climatic range, it is very near the extremes, especially in terms of maximum and minimum temperatures (Figure 5) and therefore seedling growth at this site could also give some indication of response to climate change.

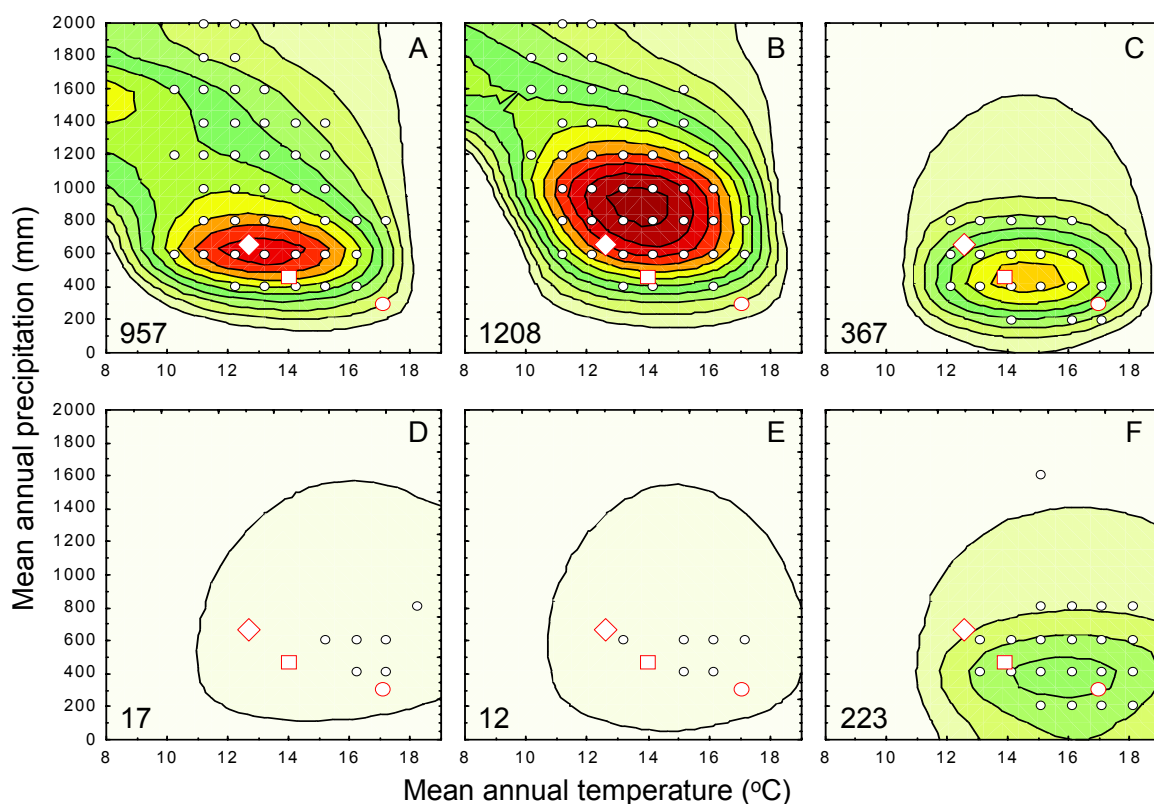


FIGURE 4. Climate niches of the study species in terms of mean annual precipitation and mean annual temperature. Darker colours on contour surfaces represent higher frequencies of records, with actual data points overlaid. Numbers in bottom left corners indicate total number of records per species. Fynbos species: A *Protea magnifica*, B *Protea amplexicaulis*, C *Protea humiflora*. Karoo species: D *Drosanthemum speciosum*, E *Ruchia lineolata*, F *Pteronia incana*. Climate data recorded during the experiment as well as the preceding six months were used to plot climate conditions at the experimental plots in relation to each species's climate niche.  $\diamond$  1303 m,  $\square$  953 m,  $\circ$  545 m.

Scant records for *Drosanthemum speciosum* and *Ruschia lineolata* made it difficult to interpret bioclimatic data. It is clear that the highest site is too cold in terms of mean, maximum as well as minimum temperatures for these two species as well as *Pteronia incana*. The middle (953 m) and ecotonal (744 m) sites are closer to optimum conditions for the karoo species, but they were expected to perform best in their native karoo site (545 m). In fact, it is interesting to note that for all six species the altitudes at which they occur naturally on the gradient are also the altitudes with climate characteristics closest to optimum conditions as indicated by their climatic niches.

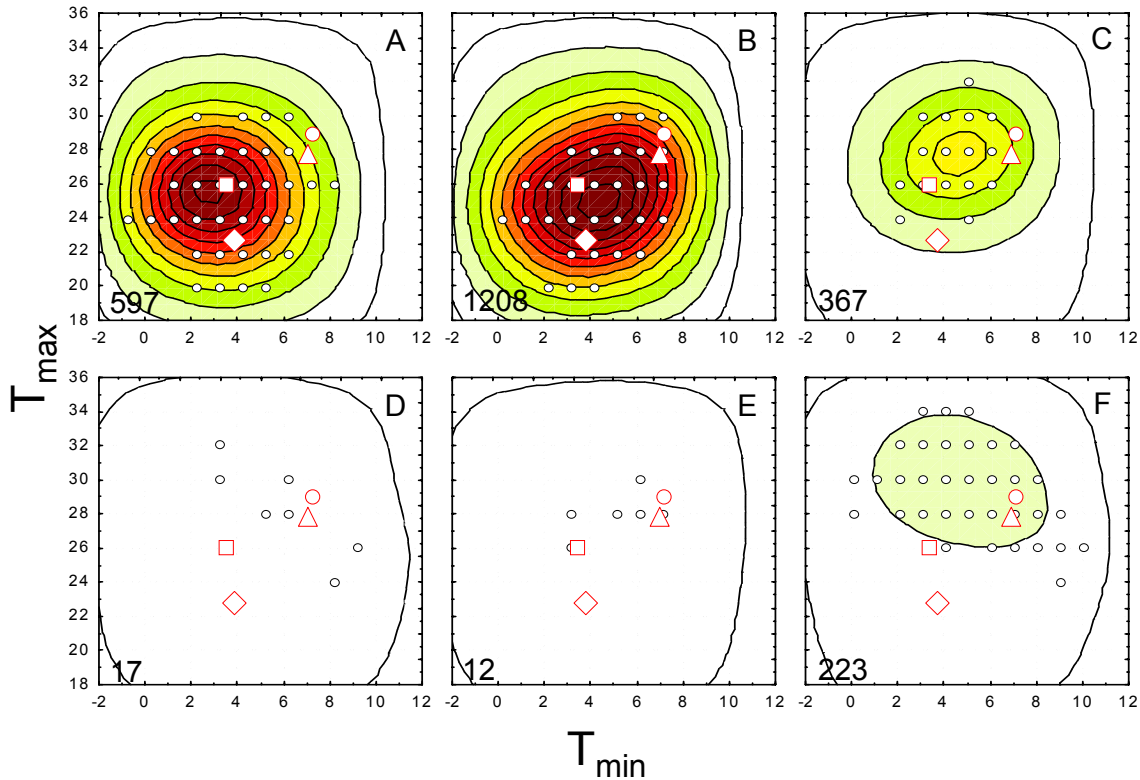


FIGURE 5. Climate niches of the study species in terms of mean daily minimum temperatures of the coldest month ( $T_{\min}$ ) and mean daily maximum temperatures of the warmest month ( $T_{\max}$ ). Darker colours on contour surfaces represent higher frequencies of records, with actual data points overlaid. Numbers in bottom left corners indicate total number of records per species. Fynbos species: A *Protea magnifica*, B *Protea amplexicaulis*, C *Protea humiflora*. Karoo species: D *Drosanthemum speciosum*, E *Ruschia lineolata*, F *Pteronia incana*. Climate data recorded during the experiment were used to plot climate conditions at the experimental plots in relation to each species's climate niche.  $\diamond$  1303 m,  $\square$  953 m,  $\triangle$  744 m,  $\circ$  545 m.

Seedling growth and survival data, however presented some interesting contradictions to expectations, especially during the first (winter) phase of the experiment. Initially all *Protea seedlings* grew fastest in the karoo site (545 m), but when the dry summer season commenced, growth rates declined greatly at this site, while growth rates of seedlings at the middle and higher sites increased rapidly so that at the end of the experiment *P. magnifica* seedlings were



largest at the highest site (1303 m), *P. humiflora* seedlings at the middle site (953 m) and *P. amplexicaulis* at the ecotonal site (744 m). *Protea* seedlings grew rapidly in their native soils from the beginning of the experiment, while remaining small in karoo soils throughout the experiment (Figure 6).

Soil distinctions were not found in the growth of *Drosanthemum speciosum* and *Ruschia lineolata* seedlings. *Pteronia incana* performed better in native karoo soil, but this trend only became apparent during summer (Figure 6). Contrary to the patterns found in fynbos seedlings, karoo seedlings grew little during winter, and growth rates increased rapidly as temperatures rose during spring months. *Drosanthemum speciosum* and *P. incana* grew best at the middle site (953 m), which is within natural fynbos vegetation, while *R. lineolata* performed best at the karoo site (545 m). A reduction in mean size of *Pteronia incana* seedlings at the ecotonal site (744 m) was due to 9 seedlings dying between November and December 2004 (Figure 7).

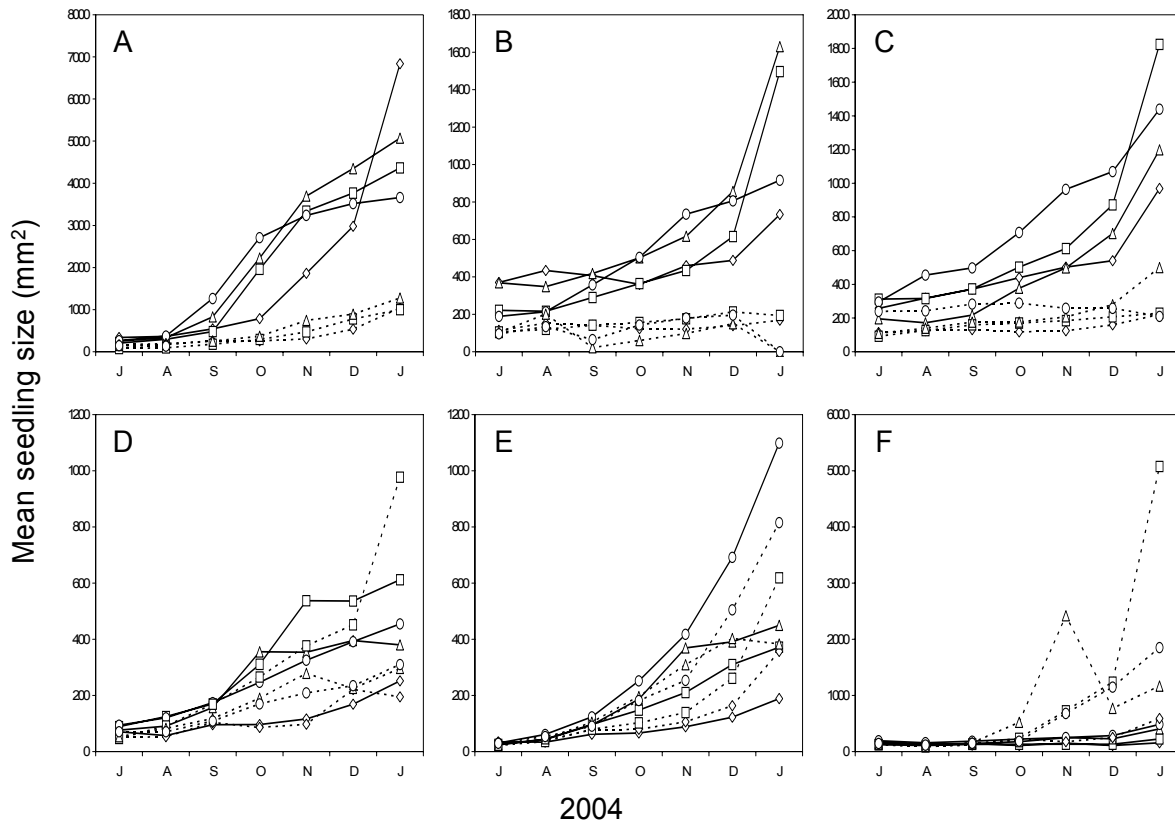


FIGURE 6. Seedling growth during the experiment as indicated by mean seedling size (height x diameter) at each monthly measurement. Fynbos species: A *Protea magnifica*, B *Protea amplexicaulis*, C *Protea humiflora*. Karoo species: D *Drosanthemum speciosum*, E *Ruschia lineolata*, F *Pteronia incana*.  $\diamond$  1303 m,  $\square$  953 m,  $\triangle$  744 m,  $\circ$  545 m, solid lines: seedlings growing on sandstone (fynbos native soil), dashed lines: seedlings growing on shale (karoo native soil).

*Protea* seedlings died rapidly in karoo soil at all altitudes, but generally survived well in their native soils, with only a few deaths at the end of the dry summer period at the lower sites (744 and 545 m). *Protea amplexicaulis* and *P. humiflora* seedlings in fynbos soil at the highest site (1303 m) also died rapidly after transplanting (Figure 7). No general patterns emerged in succulent karoo seedling survival. *Drosantherum speciosum* seedlings in both soil types survived poorly at the highest site (1303 m), but otherwise no clear altitudinal pattern or soil preference is apparent (Figure 7). *Ruschia lineolata* seedlings initially survived well at all sites and in both soil types, but some seedlings died during summer. *Pteronia incana* had poorest survival in karoo soil at the highest site (1303 m) and survived best in fynbos soil at the lowest site (545 m). At the middle and ecotone sites (953 and 744 m) no clear soil or altitudinal patterns in survival were found (Figure 7).

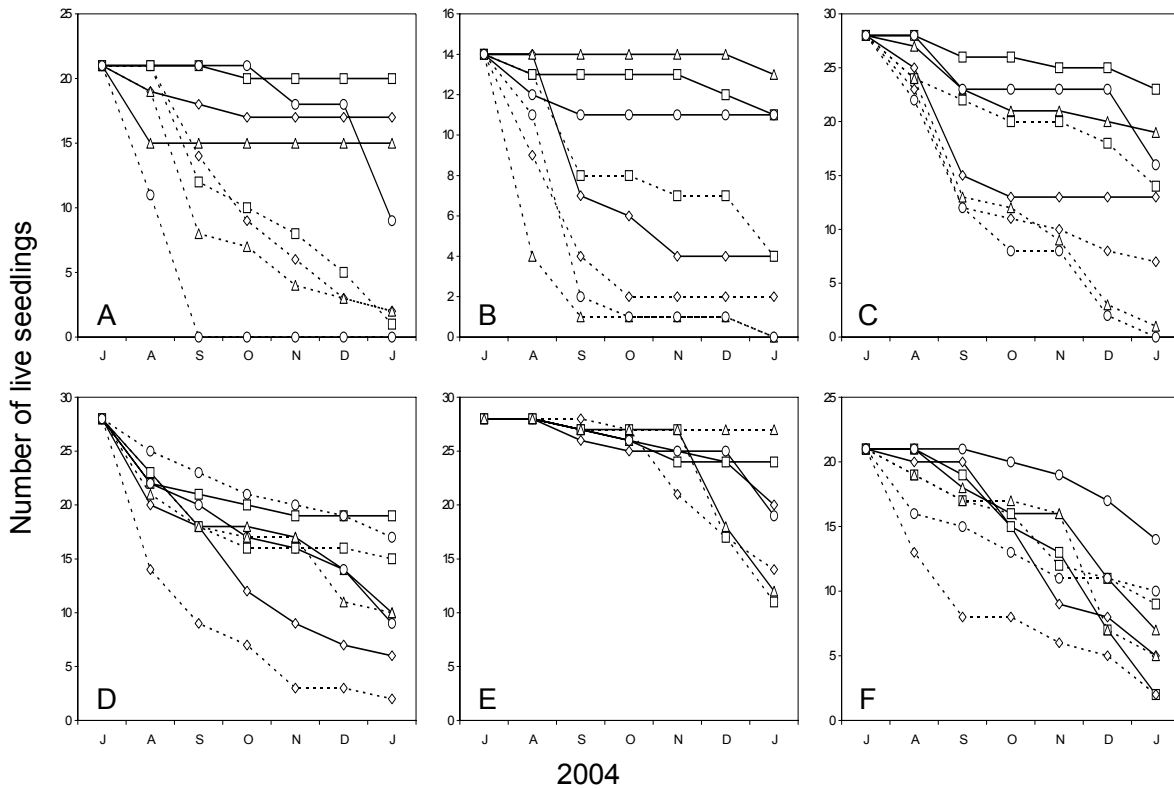


FIGURE 7. Seedling survival during the experiment as indicated by number of surviving seedlings at each monthly measurement. Fynbos species: A *Protea magnifica*, B *Protea amplexicaulis*, C *Protea humiflora*. Karoo species: D *Drosantherum speciosum*, E *Ruschia lineolata*, F *Pteronia incana*.  $\diamond$  1303 m,  $\square$  953 m,  $\triangle$  744 m,  $\circ$  545 m, solid lines: seedlings growing on sandstone (fynbos native soil), dashed lines: seedlings growing on shale (karoo native soil).

Growth data for *Protea magnifica*, *P. amplexicaulis* and *P. humiflora* were normally distributed and no large differences in variance were found. *Drosanthemum speciosum* and *Ruschia lineolata* growth data were not normally distributed, due to a few exceptionally large seedlings skewing the data towards the right. Cube root transformations of the data were done to achieve normality. *Pteronia incana* growth data was also not normally distributed, but log transformation of the data did result in a normal distribution.

Climate had a significant effect on seedling growth in all species except *P. magnifica*. Soil type had a significant effect on seedling growth for all three *Protea* species, as well as *Pteronia incana*, but not in the Mesembs (Table 1). In all cases of significant soil effects, seedlings performed best on their native soils.

TABLE 1. Main effects ANOVA testing the effects of climate (associated with different altitudes at which experimental plots were placed) and soil type on the growth of fynbos and karoo seedlings. \* 0.001<p<0.01, \*\* 0.001<p<0.0001, \*\*\* p<0.0001, ns p>0.01.

	Climate		Soil	
	F <sub>3,51</sub>	p	F <sub>1,51</sub>	p
<i>Protea magnifica</i>	1.07	ns	264.04	***
<i>Protea amplexicaulis</i>	5.07	*	54.5	***
<i>Protea humiflora</i>	6.68	**	87.84	***
<i>Drosanthemum speciosum</i>	9.77	***	2.18	ns
<i>Ruschia lineolata</i>	19.68	***	0.95	ns
<i>Pteronia incana</i>	8.29	**	15.20	**

Tukey's HSD test was used in post-hoc comparisons of growth responses in all species where climate had a significant effect. Regardless of their natural distributions on the gradient, seedlings of all five species were significantly smaller at the top site (1303 m, Table 2). Non significant differences in growth between sites for *Protea magnifica* are probably due to large variances around the mean for each site (Table 2). The large variances are the result of large differences between seedlings on the different soil types. However, retesting the effects of climate on growth of *P. magnifica* seedlings using a one way ANOVA and including only seedlings on native fynbos soil also did not reveal significant results.

Table 2 also indicates how all seedlings grew well at sites well outside their natural ranges and that three species (*Protea magnifica*, *P. amplexicaulis* and *Drosanthemum speciosum*) showed optimum growth outside of their natural ranges. In the other three species, growth at sites

outside their natural ranges was not significantly different from growth within their natural ranges, except at the very extreme top site (1303 m).

TABLE 2. Post-hoc analysis of the effects of climate (associated with different altitudes at which experimental plots were placed) on seedling growth. Mean values of changes in seedling size (height in mm x diameter in mm) between the end and beginning of the experiment, marked with b are significantly larger than values marked with \*. Values in bold indicate altitude at which most successful growth occurred. Shading indicates altitudes at which each species is found naturally at the experimental site. Values in parentheses are one standard error.

	1303 m	953 m	744 m	545 m
<i>Protea magnifica</i>	1518.8 (±459.5)	<b>2092.7 (±549.9)</b>	1836.8 (±513.3)	1513.0 (±544.4)
<i>Protea amplexicaulis</i>	97.9 (±25.5)*	576.1 (±190.9) <sup>b</sup>	<b>616.2 (±185.1)<sup>b</sup></b>	417.6 (131.8)
<i>Protea humiflora</i>	212.7 (±58.7)*	<b>768.4 (±206.8)<sup>b</sup></b>	445.4 (±128.0)	448.32 (±144.0)
<i>Drosanthemum speciosum</i>	20.0 (±0.10)*	<b>250.5 (±0.31)<sup>b</sup></b>	191.4 (±0.11) <sup>b</sup>	131.3 (±0.06) <sup>b</sup>
<i>Ruschia lineolata</i>	137.7 (±0.03)*	403.23 (±0.03) <sup>b</sup>	407.0 (±0.004) <sup>b</sup>	<b>705.5 (±0.14)<sup>b</sup></b>
<i>Pteronia incana</i>	18.6 (±1.7)*	147.9 (±1.7) <sup>b</sup>	229.1 (±1.8) <sup>b</sup>	<b>309.0 (±1.4)<sup>b</sup></b>

Post-hoc analysis of seedling growth revealed non-linear responses to altitude in *Protea amplexicaulis*, *P. humiflora* and *Drosanthemum speciosum*. Although not significantly different, size differences in *Protea magnifica* seedlings were also not linearly related to altitude (Table 2). In all instances the break in the linear relationship occurred either at the highest site (1303 m) as in *P. magnifica*, *P. humiflora* and *D. speciosum*) or at the karoo site (545 m) as in *P. amplexicaulis*. Therefore, to meet assumptions of linearity for ANCOVA, sites where breaks in the linear relationship occurred were removed for the analysis. Significant interactions of soil and climate were found only for *P. amplexicaulis* and *P. humiflora* (Table 3).

## DISCUSSION

### *What controls the fynbos-succulent karoo boundary?*

Although climate controls growth of seedlings in five of the six species tested, it does not explain the geographical distributions of these species. All six species grew and survived well outside of their natural ranges on the gradient. Even when considering climate niches at the much coarser scale of the species' entire ranges, seedling performance did not always match expectations. While *Protea humiflora*, *Drosanthemum speciosum*, *Ruschia lineolata* and *Pteronia incana* were expected to perform poorly at the highest site, low growth and persistence of *Protea amplexicaulis* at this site is explained neither by its distribution on the gradient nor its climate niche. Furthermore, this species showed no significant difference in growth between the middle

site and the karoo site, which is far outside of its natural range on the gradient as well as its climatic niche in terms of mean annual precipitation and temperature.

TABLE 3. Results of ANCOVA testing for interactive effects between soil and climate on seedling growth. Sites removed represents either the highest or lowest experimental sites on the gradient which had to be removed from the data set to achieve linear relationships between the dependent variable (growth) and the covariate (altitude).

	Sites removed	df	F	p
<i>Protea magnifica</i>	1303 m	1,38	0.11	0.74
<i>Protea amplexicaulis</i>	545 m	1,38	15.15	0.0004
<i>Protea humiflora</i>	1303 m	1,38	4.98	0.03
<i>Drosanthemum speciosum</i>	1303 m	1,38	2.70	0.11
<i>Ruschia lineolata</i>	none	1,52	0.74	0.39
<i>Pteronia incana</i>	none	1,52	0.27	0.60

*Protea magnifica* seedling growth results were also surprising in many ways. The fact that it is found only within such a narrow altitudinal range points to a possible very narrow range of climate tolerance, and yet its climatic niche is very similar in extent to the more widely distributed *P. amplexicaulis*. The coarse scale at which climate interpolations are made are often to blame for overestimating niche width in species which are found within narrow altitudinal ranges in areas of high topographic variability and associated steep climatic gradients. However, concentrating on the finer scale of a specific gradient, the expected climate sensitivity of *P. magnifica* is also not found, with growth and survival across the gradient indicating that the distribution of this species is more strongly controlled by factors other than climate. According to Rebelo (2001), *P. magnifica* is sensitive to too frequent fires and is therefore often confined to rocky areas on very steep slopes where individuals are able to escape fire.

Soil type is obviously a strong controlling factor for fynbos species, but not for at least some succulent karoo species. Studies on root physiology of Australian Proteaceae, which are also found on highly leached, extreme nutrient poor soils indicate that Proteaceae species suffer from phosphorous toxicity when growing in soils containing only marginally higher levels of P due to an inability of the roots to control P uptake (Shane et al. 2004). Preliminary studies indicate that Cape Proteaceae are similarly sensitive to increases in soil P levels (Cramer et al. 2005), possibly explaining why the *Protea* species in this study did not grow and survive well on relatively more nutrient rich shale derived soil. The interactive effects of soil and climate found for *Protea amplexicaulis* and *P. humiflora* indicate that these species could grow and survive relatively better on shale derived soils under moister conditions, which is consistent with the

findings of Lechmere-Oertel and Cowling's (2001) greenhouse study. This interaction however is probably not biologically significant considering that seedlings of these species were so much larger on their native soils even under more mesic conditions.

The fact that neither soil type nor climate is limiting the two Mesembryanthemaceae species from intruding into fynbos raises the question why are they not in fynbos? Fire is an obvious factor to consider – these two species are possibly not fire adapted. However, life histories of other Mesembryanthemaceae species such as *Erepsia* which are associated with fynbos could possibly hint at an additional factor. *Erepsia* species are often highly abundant in early post-fire regeneration stages of fynbos but disappear as the vegetation matures and becomes denser and taller. Fynbos species are very likely superior competitors over Mesembryanthemaceae and possibly other succulent karoo species as well, marginalizing their realized niches into more stressful arid environments. Such patterns of low competitive ability associated with wider tolerance of environmental conditions have been found for other species (Parmesan et al. 2005).

#### *How will climate change affect fynbos species?*

The karoo site was considered to represent possible future climate conditions. Warmer winter conditions at this site initially caused seedlings of all three *Protea* species to grow much faster and larger at this site than anywhere else on the gradient, suggesting that warmer temperatures predicted by climate change might actually enhance species' growth. Drier conditions however impaired growth to such an extent that seedlings at moister but cooler sites outgrew seedlings in the karoo site towards the end of summer. Only 6.4 mm rain was recorded at the karoo site from November to December 2004, and the effect of this was evident on seedling growth as well as survival, with many *P. magnifica* and *P. humiflora* seedlings that have survived well at that site up until then dying during January 2005. However only *P. magnifica* had higher seedling mortality at the karoo site than anywhere else on the gradient, suggesting that mortality might not be such a serious concern and that these three *Protea* species might actually be quite resilient to warmer and drier conditions. A study by Midgley (1988) also indicated that seedlings of several other Proteaceae species are remarkably resilient to summer drought.

A point to consider is that seedlings in this experiment were not established under drought conditions. Midgley (1988) found slightly, but not significantly higher mortalities in seedlings that were less than four months old at the start of summer due to fires occurring during winter rather than autumn. Drought sensitivity in *Protea* seedlings is probably apparent only in the very early

stages, and once the seedlings have become established they are able to tolerate even severe drought stress. Furthermore neither this study nor that of Midgley (1988) assessed the effects of prolonged drought on fynbos seedling survival. Had the karoo site not received relatively high rainfall (50.6 mm) during January 2005, survival patterns recorded in this experiment might have been very different, with possibly many more seedling deaths recorded at the last measurement at the end of January 2005.

*Will succulent karoo invade fynbos?*

Palaeo-ecological studies concerning vegetation responses to past changes in climate have indicated that changes happen most rapidly in marginal habitats while vegetation tends to persist in the most favourable habitats for a very long time after the climate change has taken place (Cole 1985). Dry north-facing slopes within the fynbos biome, especially in areas where fynbos intersects with succulent karoo such as the case with the study site of this experiment, are therefore probably most at risk of being replaced by succulent karoo, while fynbos in other, higher rainfall areas such as south-facing mountain slopes will probably be able to persist as a vegetation type in spite of the effects of climate change.

Nonetheless, with fynbos species being very long lived, and should further studies confirm their competitive superiority over succulent karoo, fynbos is likely to display considerable biological inertia (Von Holle et al. 2003) against invasion by succulent karoo even in marginal habitats. Von Holle et al (2003) suggests that competitively inferior but environmentally more tolerant invaders require openings in the more competitive resident vegetation before they are able to establish. In the fynbos context, fires are likely to provide such openings: should a fire be followed by a prolonged and severe drought, fynbos species could fail to re-establish and such areas could be opened up for invasion by adjacent more drought tolerant succulent karoo.

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## CHAPTER SIX

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### SYNTHESIS

Plant functional types are strongly promoted in global climate change literature as a solution to generalize ecosystem processes in order to simplify predictions of the consequences of climate change for biodiversity. Therefore, in this study, a number of attempts were made to incorporate plant functional concepts in experiments and empirical measurements. While I do not disagree that correlations between functional traits and environmental factors such as resource availability and disturbances exist and are very useful ecological concepts, I think that they have limited use in the global climate change context for the following reasons:

Firstly, conservationists, who have to implement the results of global change research in conservation policies, are asking questions at a local scale, such as ‘Which areas will be most vulnerable to climate change?’, ‘which species are threatened with extinction?’, and ‘how should management practices be adapted to mitigate the effects of climate change?’ Correlations of plant functional characteristics with variations in resources and disturbance have generally been derived across large spatial scales. This study showed that functional trait relationships are weak at the local scale because trait ranges are too narrow to establish clear trends (Chapter 4), and species do not rank consistently among various traits (Chapters 2,4). Therefore, the functional trait approach is likely to not be very useful in answering important local scale conservation questions relating to climate change.

Secondly, and more generally, because plant functional characteristics are correlated with spatial variation in resources and disturbance, they are unable to tell us how plant communities, characterized by a set of functional attributes assumed to represent adaptations and responses to their current environment, will be affected by changes in resources and disturbances over *time*. This is the central concern when predicting the effects of global climate change. This is possibly the reason why reviews of functional traits in relation to global change research (for example Lavorel and Garnier (2002)) deal only with theoretical overviews of functional concepts but stop short of making actual predictions based on functional trait theories of the consequences of climate change for biodiversity and ecosystem dynamics. It is clear that more

experimental work is needed within the functional type conceptual framework, perhaps at a broader scale than this study, to actively test how changes in the environment will lead to changes in plant community structures and dynamics, and how this relates to functional trait theories.

This study relied strongly on predictions of global circulation models regarding changes in temperature and rainfall as a result of increased atmospheric CO<sub>2</sub> in guiding experimental designs. This field-based ‘testing’ of the potential effects of predicted changes in climate revealed many interesting and unexpected results, that could not have been foreseen by modelling exercises, emphasizing the importance of the need for experimental work to follow up on modelling predictions. The limitations of modelling species’ distribution shifts by means of bioclimatic envelopes were highlighted by the results of the reciprocal transplant experiment (Chapter 5), where climate niches based on species’ ranges were unable to explain species’ performances in the experiment. The performance of the succulent karoo and fynbos seedlings especially pointed to the important fact that soil type and competition can be more important shaping factors of species distributions than climate. However, one should remain cautious about extrapolating results based on a few species to generalizations about shifts in biomes or vegetation types. Results were broadly similar to those found in previous boundary determinant experimental studies, which do add further confidence to the results as possibly representing a general pattern. This study indicated that more climate change experimental studies considering the climatic variation of species’ geographical distribution in the experimental design is urgently necessary to make more accurate predictions regarding species’ responses to climate change.

The drought experiment (Chapter 4) on the other hand revealed the limitations of climatic modelling exercises based on climatic averages, with many species responding more strongly to rainfall variability such as a naturally occurring prolonged dry season than to the treatment of an average reduction in precipitation. Therefore this study confirms that while ecological theories such as functional strategies and modelling studies provide useful first insights, and do serve an important purpose in refining research questions, they do not negate the need for experimental work. This experiment probably could be improved by including more study species and continuing monitoring on a long term basis, which could result in more clear significant results.

Two main themes regarding the potential effects of climate change on fynbos emerged from this study. Firstly, at the start of the study it was thought that temperatures predicted to rise by only a

small margin as a result of climate change is of a lesser concern than the predictions of a large reduction (25%) in rainfall, a seemingly much more serious threat to fynbos biodiversity. However, despite very individualistic responses among study species to experimental and natural climate variation, this study revealed a general sensitivity among fynbos species to temperatures higher than a very narrow optimum range. Early indications are that even minor increases in temperatures could have severe consequences for primary productivity (Chapter 2) and reproductive output (Chapter 3). On the other hand, seedlings (Chapter 5), immature vegetation (Chapter 4) and mature individuals (Chapter 2) seemed to be able to grow and survive well at extremely low rainfall. The key aspect regarding the effects of drought on fynbos was revealed to be far more complex than simple rainfall reductions in Chapters 2 and 4: timing of rainfall events is far more crucial than rainfall totals, and fynbos species that are able to tolerate reductions in mean rainfall still require regular rainfall to maintain growth. A critical limitation of monitoring species within their natural habitats, as seen in this study, is that natural climate conditions provide a somewhat limited variation in temperatures and rainfall, with too few extreme events to make any clear conclusions as to the potential effects of climate change. Another limitation was the fact that temperatures and rainfall tend to covary: high temperatures are generally associated with dry conditions and vice versa, and so it was very difficult to distinguish whether growth responses were to temperature, rainfall or a combination of factors. Therefore, clear conclusions regarding the effects on plant growth of increased temperatures and decreased rainfall, as predicted by climate change models, can only be made after this study has been supplemented with experiments where temperature and moisture conditions are strictly controlled. Experiments where the effects of the timing of rainfall on plant growth can be determined will also be beneficial.

A second theme that emerged from more than one study is that in fynbos, species' growth rates are a good indicator of sensitivity to climate variation in general (Chapter 3) and sensitivity to drought (Chapter 4). It was concluded that shifts in dominance from fast growing productive species to slower growing conservative species is likely to occur as a result of climate change. It must be noted, of course, that 'fast growing' is used relatively among fynbos species, and that fynbos species all have very low relative growth rates compared to plant species in high resource environments.

Climate change is likely to cause dramatic changes in fynbos vegetation structure and dynamics, especially if changes in temperature and rainfall are considered alongside another key driver of

fynbos dynamics, fire. This study did not find evidence of any species that are likely to undergo local extinctions as a result of temperature and rainfall changes, even from such a marginal fynbos habitat as the study site, but it is thought that fire is likely to play an important role in the shifting of species and biome boundaries. Only seedlings died as a result of experimental treatments (Chapters 4,5), and therefore it seems that the post-fire regeneration stage is likely to be the most vulnerable to severe climate change related consequences. High temperatures and drought conditions following a fire could lead to failed germination, mass mortalities and possibly local extinctions, especially in species relying solely on seedbanks for post-fire regeneration. This might open up areas for invasion by succulents and other species from neighbouring biomes, and colonization is likely to occur first in habitats near biome boundaries. It is suggested that marginal habitats such as gradients involving fynbos-succulent karoo transitions should be monitored carefully for signs of shifts in species assemblages, especially after fires.

#### LITERATURE CITED

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**:545-556.

OPPOSITE PAGE: APPENDIX I. Phytosociological table of species recorded during a survey of the Jonaskop study site. Soil type codes: SHM – shale derived soils, from mima-like mound. SH – shale derived soils, off mound, SA –sandstone derived soil. Growth form codes are explained in Table 2, Chapter 1.

# Jonaskop phytosociological survey October 2003

		KAROO				ECOTONE									
	Releve number	6A	6B	6C	6D	5.5A	5.5B	5.5C	5A	5B	5C	4A	4B	4C	3A
	Altitude (m)	545	545	545	545	690	690	690	744	744	744	953	953	953	1044
	Aspect (°)	325	320	320	330	3	355	355	255	332	330	195	140	10	320
	Slope (°)	11	16	12	7	24	16	23	14	18	12	4	3	4	25
	GRID S														
		33.55.053	33.55.059	33.55.068	33.55.109	33.55.222	33.55.235	33.55.234	33.55.312	33.55.314	33.55.272	33.56.061	33.56.097	33.56.128	33.56.563
	GRID E														
		19.30.421	19.30.417	19.30.407	19.30.441	19.31.041	19.31.057	19.31.057	19.30.599	19.30.592	19.31.035	19.31.228	19.31.183	19.31.294	19.30.539
	Rock cover (%)	0	0	0	0	25	50	30	5	35	5	35	1	2	5
	Vegetation cover (%)	80	50	40	75	75	50	70	70	60	55	60	95	68	80
	Soil type	SHM	SH	SH	SH	SA	SA	SA	SA	SA	SA	SA	SA	SA	SA
	Soil depth (range in cm)	14-31	5-23	13-32	10-21	0-33	0-17	0-12	3-38	0-37	0-36	0-10	4-53	0-37	0-39

SPECIES		FAMILY	GFM														
	<i>Galenia africana</i> L.	AIZOACEAE	LES	3													
	<i>Schismus barbatus</i> (Loefl. ex L.) Thell.	POACEAE	GRA	2M													
	<i>Galium tomentosum</i> Thunb.	RUBIACEAE	LES	2													
	<i>Ehrharta delicatula</i> (Nees) Stapf	POACEAE	GRA	1													
	<i>Aloe microstigma</i> Salm-Dyck	ASPHODELACEAE	LSS	O													
-	<i>Helichrysum revolutum</i> (Thunb.) Less.	ASTERACEAE	LES	R													
	<i>Oligocarpus calendulaceus</i> (L.f.) Less.	ASTERACEAE	AH	R													
	<i>Vellereophyton dealbatum</i> (Thunb.) Hilliard & B.L.Burti	ASTERACEAE	PH	R													
	<i>Euclea</i> sp.	EBENACEAE	MES	O													
	<i>Ornithogalum dubium</i> Houtt.	HYACINTHACEAE	GEO	R													
	<i>Bromus hordeaceus</i> L. subsp. <i>molliformis</i> (J.Lloyd) Maire & Weiller	POACEAE	GRA	R													
	<i>Ruschia lineolata</i> (Haw.) Schwantes	MESEMBRYANTHEMACEAE	DSS	1	2A	+	1										
	<i>Euphorbia burmannii</i> E.Mey. ex Boiss.	EUPHORBIACEAE	LSS	2A	1	O											
	<i>Pteronia incana</i> (Burm.) DC.	ASTERACEAE	LES	2A	O		+										
=	<i>Tylecodon paniculatus</i> (L.f.) Tölken	CRASSULACEAE	LSS	2A	O												
	<i>Oxalis pes-caprae</i> L.	OXALIDACEAE	GEO	R			R										
	<i>Sutera caerulea</i> (L.f.) Hiern	SCROPHULARIACEAE	AH	+				R									
	<i>Rhus undulata</i> Jacq.	ANACARDIACEAE	MES	O	1												
	<i>Pteronia fasciculata</i> L.f.	ASTERACEAE	LES	O	+												
	<i>Dicerotheramnus rhinocerotis</i> (L.f.) Koekemoer	ASTERACEAE	LES		+	1	3										
	<i>Oedera squarrosa</i> (L.) Anderb. & K.Bremer	ASTERACEAE	LES		1	2A	+										
	<i>Pteronia paniculata</i> Thunb.	ASTERACEAE	LES		2B	2B	2										
	<i>Crassula atropurpurea</i> (Haw.) D.Dietr. var. <i>atropurpurea</i>	CRASSULACEAE	LSS		1	1	+										
	<i>Indigofera porrecta</i> Eckl. & Zeyh.	FABACEAE	LES		R	+	R										
	<i>Phyllobolus splendens</i> (L.) Gerbault subsp. <i>splendens</i>	MESEMBRYANTHEMACEAE	LSS		+	O	O										
	<i>Chrysocoma ciliata</i> L.	ASTERACEAE	LES		R	+											
≡	<i>Ruschia caroli</i> (L.Bolus) Schwantes	MESEMBRYANTHEMACEAE	DSS		R	1											
	<i>Oxalis</i> sp.	OXALIDACEAE	GEO		+	1											
	<i>Ischyrolepis gaudichaudiana</i> (Kunth) H.P.Linder	RESTIONACEAE	GRA		O		O										
	<i>Thesium patulum</i> A.W.Hill	SANTALACEAE	PH,P		O	1	+										
	<i>Oedera genistifolia</i> (L.) Anderb. & K.Bremer	ASTERACEAE	LES			R	2A										
	<i>Aspalathus</i> sp.	FABACEAE	LES			O	+										









RECORDED IN SINGLE RELEVES ONLY

Nebelia sphaerocephala (Sond.) Kuntze	BRUNIACEAE	MES							
Tetraria bromoides (Lam.) Pfeiff.	CYPERACEAE	GRA							
Tetragonia spicata L.f.	AIZOACEAE	LES	O						
Crassula capensis (L.) Baill.	CRASSULACEAE	PHS		R					
Aspalathus alpestris (Benth.) R.Dahlgren	FABACEAE	LES		O					
Merxmuellera arundinacea (P.J.Bergius) Conert	POACEAE	GRA		O					
Crassula nudicaulis L.	CRASSULACEAE	PHS			O				
Crassula sp.	CRASSULACEAE	DSS			R				
Antimima hamatilis (L.Bolus) H.E.K.Hartmann	MESEMBRYANTHEMACEAE	DSS			O				
Drosanthemum sp.	MESEMBRYANTHEMACEAE	LSS			O				
Muraltia muraltioides (Eckl. & Zeyh.) Levyns	POLYGALACEAE	DES			O				
Polygala scabra L.	POLYGALACEAE	LES			O				
Viscum sp.	VISCACEAE	S,P			R				
Stoeboe nervigera (DC.) Sch.Bip	ASTERACEAE	DES			R				
Aspalathus hirta E.Mey.	FABACEAE	LES			+				
Pelargonium rapaceum (L.) L'Hér	GERANIACEAE	GEO			R				
Merxmuellera stricta (Schrad.) Conert	POACEAE	GRA			O				
Ursinia rigidula (DC.) N.E.Br.	ASTERACEAE	DES				+			
Adenocline pauciflora Turcz.	EUPHORBIACEAE	AH				R			
Pelargonium alchemilloides (L.) L'Hér.	GERANIACEAE	DES				O			
Pelargonium caucalifolium Jacq. subsp convulvulifolium	GERANIACEAE	LES				R			
Aristea africana (L.) Hoffmanns	IRIDACEAE	PH				+			
Geissorhiza confusa Goldblatt	IRIDACEAE	GEO				R			
Linum acuticarpum C.M.Rogers	LINACEAE	PH				+			
Cullumia sulcata (Thunb.) Less.	ASTERACEAE	LES					+		
Wahlenbergia sp.	CAMPANULACEAE	LES					R		
Cassytha ciliolata Nees	LAURACEAE	HV					1		
Lobelia capillifolia (C.Presl) A.DC.	LOBELIACEAE	LES					R		
Eriocephalus sp.	ASTERACEAE	LES						0	
Ursinia paleacea (L.) Moench.	ASTERACEAE	LES						+	
Aspalathus linearis (Burm.f.) R.Dahlgren	FABACEAE	LES						R	
Aspalathus tridentata L.	FABACEAE	LES							
Paranomus dispersus Levyns	PROTEACEAE	LES							R
Rafnia acuminata (E.Mey.) G.J.Campbell & B.-E. van Wyk	FABACEAE	DES							
Drosanthemum flammeum L.Bolus	MESEMBRYANTHEMACEAE	DSS							R
Crassula pubescens Thunb.	CRASSULACEAE	DSS							O
Pelargonium longifolium (Burm.f.) Jacq.	GERANIACEAE	GEO							
Satyrium odorum Sond.	ORCHIDACEAE	GEO							
Cliffortia sericea Eckl. & Zeyh.	ROSACEAE	LES							R
Lachnaea pudens Beyers	THYMELEACEAE	LES							+
Struthiola myrsinites Lam.	THYMELEACEAE	LES							R
Acrosanthes teretifolia Eckl. & Zeyh.	AIZOACEAE	LSS							R
Arctotis incisa Thunb.	ASTERACEAE	PH							R
Senecio burchellii DC.	ASTERACEAE	DES							R
Cliffortia ruscifolia L.	ROSACEAE	LES							+
Gazania ciliaris DC.	ASTERACEAE	PH							
Syncarpha gnaphaloides (L.) DC.	ASTERACEAE	DES							+
Heliophila subulata Burch. ex DC.	BRASSICACEAE	PH							R
Lightfootia sp.	CAMPANULACEAE	DES							+
Clutia alaternoides L.	EUPHORBIACEAE	LES							R
Sebaea exacoides (L.) Schinz	GENTIANACEAE	AH							R
Gladiolus sp.	IRIDACEAE	GEO							R

XIV RARE SPECIES R

Protea neriifolia R.Br.	PROTEACEAE	MES
Agathosma stipitata Pillans	RUTACEAE	LES
Protea lorifolia (Salisb. ex Knight) Fourc.	PROTEACEAE	LES
Adenandra uniflora (L.) Willd.	RUTACEAE	LES
Senecio acaulis (L.f.) Sch.Bip.	ASTERACEAE	PHS
Aspalathus fusca Thunb.	FABACEAE	LES
Elytropappus sp.	ASTERACEAE	MES
Syncarpha flava (Compton) B.Nord.	ASTERACEAE	DES
Ficinia deusta (P.J.Bergius) Levyns	CYPERACEAE	GRA
Dilatrix ixiooides Lam.	HAEMODORACEAE	GEO
Lobelia sp.	LOBELIACEAE	DES
Ehrharta rupestris Nees ex Trin.	POACEAE	GRA
Cliffortia sp.	ROSACEAE	LES
Erica coccinea L.	ERICACEAE	LES
Willdenowia teres Thunb.	RESTIONACEAE	GRA
Tritoniopsis lata (L.Bolus) G.J.Lewis	IRIDACEAE	GEO
Willdenowia sp.	RESTIONACEAE	GRA
Haplocarpha lanata (Thunb.) Less.	ASTERACEAE	PH
Arctotis flaccida Jacq.	ASTERACEAE	PH
Corymbium sp.	ASTERACEAE	PH
Gazania rigida (Burm.f.) Roessler	ASTERACEAE	PH
Clutia laxa Eckl. ex Sond.	EUPHORBIACEAE	LES
Clutia polifolia Jacq.	EUPHORBIACEAE	LES
Pelargonium hermanniifolium (P.J.Bergius) Jacq.	GERANIACEAE	LES
Pelargonium sp.	GERANIACEAE	DES
Aristea juncifolia Baker	IRIDACEAE	PH
Gladiolus debilis Sims	IRIDACEAE	GEO
Cyphia volubilis (Burm.f) Willd.	LOBELIACEAE	HV
Lobelia pinifolia L.	LOBELIACEAE	DES
Ehrharta ottonis Kunth ex Nees	POACEAE	GRA
Ehrharta rehmannii Stapf subsp rehmannii	POACEAE	GRA
Pentaschistis colorata (Steud.) Stapf	POACEAE	GRA
Anthospermum sp.	RUBIACEAE	DES
Pseudoselago serrata (P.J.Bergius) Hilliard	SCROPHULARIACEAE	LES
Syncarpha variegata (P.J.Bergius) B.Nord.	ASTERACEAE	DES
Erica lateralis Willd.	ERICACEAE	LES
Askidiosperma paniculata (Rottb.) Desv.	RESTIONACEAE	GRA
Erica taxifolia Bauer	ERICACEAE	LES
Cliffortia juniperina L.f.	ROSACEAE	LES
Pelargonium elegans (Andrews) Willd.	GERANIACEAE	DES
Stipagrostis zeyheri (Nees) De Winter	POACEAE	GRA
Lobelia jasionoides (A.DC.) E.Wimm.	LOBELIACEAE	PH
Metalasia montana P.O. Karis	ASTERACEAE	DES
Erica embothriifolia Salisb.	ERICACEAE	LES

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<b>TOTAL NUMBER OF SPECIES:</b>	<b>286</b>	<b>21</b>	<b>21</b>	<b>26</b>	<b>30</b>	<b>39</b>	<b>48</b>	<b>38</b>	<b>41</b>	<b>31</b>	<b>29</b>	<b>50</b>	<b>44</b>	<b>44</b>	<b>29</b>
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FYNBOS								SUMMIT		
3B	3C	2A	2B	2C	1A	1B	1C	0A	0B	0C
1044	1044	1196	1196	1196	1303	1303	1303	1576	1576	1576
20	35	335	325	45	355	10	15	25	0	10
14	4	3.5	2	4.5	6	18	13	18	22	22
33.56.560	33.56.589	33.57.283	33.57.287	33.57.287	33.57.691	33.57.694	33.57.743	33.58.224	33.58.203	33.58.130
19.30.525	19.31.000	19.31.007	19.31.011	19.31.106	19.30.800	19.30.777	19.30.823	19.30.306	19.30.266	19.30.249
40	20	2	1	55	40	20	70	80	75	70
60	30	85	90	30	60	80	30	20	25	30
SA	SA	SA	SA	SA	SA	SA	SA	SA	SA	SA
4-30	5-50+	12-50+	4-50+	10-50+	0-23	0-34	0-23	0-49	0-46	0-16

+	+	R		R	R	+	+
R	R	R	R	R	1	O	+
	R		O	R	O	2M	2A
		O			+	R	
		O			R	+	1
	2A	2A	+	2B	2A	2A	2B
		O	O		O		
	R					+	+
1						+	+







+	O
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## APPENDIX II

Checklist of vascular plant species on the Jonaskop gradient, including growth form classification, local abundance and altitudinal distribution on gradient for each species. Growth form classification is as follows: AH – annual herb; DES – dwarf evergreen shrub, less than 0.25 m in height; DSS – dwarf succulent shrub, less than 0.25 m in height; DS,P – dwarf shrub, parasite; GEO – geophyte; GRA – graminoid; HV – herbaceous vine; LES – low evergreen shrub, 0.25-1 m height; LSS – low succulent shrub, 0.25-1 m height; LS,P – low shrub, parasite; MES – mid-high evergreen shrub, 1-2 m height; PH – perennial herb; PHS – perennial herb, succulent leaves; PH,P – perennial herb, parasite. Taxonomy follows Germishuizen and Meyer (2003).

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo		ecotone		fynbos		
				400	600	800	1000	1200	1400	1600
<b>AIZOACEAE</b>										
	<i>Acrosanthes teretifolia</i> Eckl. & Zeyh.	LSS	rare							
	<i>Galenia africana</i> L.	LES	abundant	■	■					
	<i>Tetragonia spicata</i> L.f.	LES	rare	■	■					
<b>ANACARDIACEAE</b>										
	<i>Rhus dissecta</i> Thunb.	LES	frequent			■	■			
	<i>Rhus lucida</i> L.	LES	rare					■	■	
	<i>Rhus rosmarinifolia</i> Vahl	LES	rare			■	■			
	<i>Rhus undulata</i> Jacq.	MES	occasional	■	■					
<b>APIACEAE</b>										
	<i>Centella triloba</i> (Thunb.) Drude	HV	rare			■	■			
	<i>Centella</i> sp.	PH	rare			■	■			
<b>ASPHODELACEAE</b>										
	<i>Aloe microstigma</i> Salm-Dyck	LSS	rare	■	■					
	<i>Trachyandra muricata</i> (L.f.) Kunth.	GEO	rare			■	■			
<b>ASTERACEAE</b>										
	<i>Anaxeton asperum</i> (Thunb.) DC. subsp. <i>pauciflorum</i> Lundgren	DES	occasional			■	■	■	■	
	<i>Arctotis acaulis</i> L.	PH	rare						■	■
	<i>Arctotis flaccida</i> Jacq.	PH	rare						■	■
	<i>Arctotis incisa</i> Thunb.	PH	rare					■		
	<i>Arctotis</i> sp.	PH	rare			■	■			
	<i>Chrysocoma ciliata</i> L.	LES	rare	■	■					

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient														
				karoo		ecotone		fynbos										
				400	600	800	1000	1200	1400	1600								
	<i>Corymbium glabrum</i> L.	PH	rare															
	<i>Corymbium</i> sp.	PH	rare															
	<i>Cullumia sulcata</i> (Thunb.) Less.	LES	rare															
	<i>Dicerotheramnus rhinocerotis</i> (L.f.) Koekemoer	LES	frequent															
	<i>Edmondia sesamoides</i> (L.) Hilliard	PH	frequent															
	<i>Elytropappus</i> sp.	MES	rare															
	<i>Eriocephalus africanus</i> L.	LES	rare															
	<i>Eriocephalus</i> sp.	LES	occasional															
	<i>Euryops abrotanifolius</i> (L.) DC.	MES	rare															
	<i>Felicia filifolia</i> (Vent.) Burtt Davy	LES	rare															
	<i>Gazania ciliaris</i> DC.	PH	rare															
	<i>Gazania rigida</i> (Burm.f.) Roessler	PH	rare															
	<i>Haplocarpha lanata</i> (Thunb.) Less.	PH	rare															
	<i>Helichrysum revolutum</i> (Thunb.) Less.	LES	rare															
	<i>Helichrysum zwartbergense</i> Bolus	DES	occasional															
	<i>Lachnospermum fasciculatum</i> (Thunb.) Baillon	LES	frequent															
	<i>Metalasia montana</i> P.O. Karis	DES	rare															
	<i>Metalasia muricata</i> (L.) D.Don.	LES	frequent															
	<i>Metalasia</i> sp.	DES	frequent															
	<i>Oedera genistifolia</i> (L.) Anderb. & K.Bremer	LES	frequent															
	<i>Oedera squarrosa</i> (L.) Anderb. & K.Bremer	LES	occasional															
	<i>Oligocarpus calendulaceus</i> (L.f.) Less.	AH	rare															
	<i>Osteospermum polygaloides</i> L.	DES	rare															
	<i>Osteospermum polygaloides</i> L. var. <i>polygaloides</i>	DES	rare															
	<i>Othonna quinquedentata</i> Thunb.	MES	rare															
	<i>Othonna ramulosa</i> DC.	LSS	occasional															
	<i>Phaenocoma prolifera</i> (L.) D.Don	LES	frequent															
	<i>Pteronia fasciculata</i> L.f.	LES	rare															
	<i>Pteronia incana</i> (Burm.) DC.	LES	frequent															
	<i>Pteronia paniculata</i> Thunb.	LES	frequent															
	<i>Senecio acaulis</i> (L.f.) Sch.Bip.	PHS	rare															
	<i>Senecio burchellii</i> DC.	DES	rare															
	<i>Senecio paniculatus</i> P.J.Bergius	PH	occasional															
	<i>Seriphium incanum</i> (Thunb.) Pers.	LES	occasional															

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient													
				karoo		ecotone		fynbos									
				400	600	800	1000	1200	1400	1600							
	<i>Seriphium plumosum</i> L.	LES	rare														
	<i>Stoeboe aethiopica</i> L.	LES	occasional														
	<i>Stoeboe capitata</i> P.J.Bergius	LES	rare														
	<i>Stoeboe montana</i> Schltr. ex Levyns	DES	rare														
	<i>Stoeboe nervigera</i> (DC.) Sch.Bip	DES	rare														
	<i>Stoeboe</i> sp.	PH	frequent														
	<i>Syncarpha flava</i> (Compton) B.Nord.	DES	rare														
	<i>Syncarpha gnaphaloides</i> (L.) DC.	DES	rare														
	<i>Syncarpha paniculata</i> (L.) B.Nord.	LES	occasional														
	<i>Syncarpha variegata</i> (P.J.Bergius) B.Nord.	DES	rare														
	<i>Ursinia anthemoides</i> (L.) Poir. subsp. <i>anthemoides</i>	AH	rare														
	<i>Ursinia paleacea</i> (L.) Moench.	LES	rare														
	<i>Ursinia rigidula</i> (DC.) N.E.Br.	DES	rare														
	<i>Ursinia</i> sp.	DES	rare														
	<i>Vellereophyton dealbatum</i> (Thunb.) Hilliard & B.L.Burt	PH	rare														
	<i>Zyrphelis lasiocarpa</i> (DC.) Kuntze	DES	rare														
	<i>Zyrphelis microcephala</i> (Less.) Nees	DES	rare														
<b>BORAGINACEAE</b>																	
	<i>Lobostemon fruticosus</i> (L.) H.Buek	LES	occasional														
	<i>Lobostemon gracilis</i> Levyns	LES	rare														
<b>BRASSICACEAE</b>																	
	<i>Heliophila scoparia</i> Burch. ex DC.	LES	rare														
	<i>Heliophila subulata</i> Burch. ex DC.	PH	rare														
<b>BRUNIACEAE</b>																	
	<i>Nebelia laevis</i> (E.Mey.) Kuntze	MES	rare														
	<i>Nebelia sphaerocephala</i> (Sond.) Kuntze	MES	rare														
<b>CAMPANULACEAE</b>																	
	<i>Lightfootia</i> sp.	DES	rare														
	<i>Wahlenbergia neorigida</i> Lammers	LES	rare														
	<i>Wahlenbergia</i> sp.	LES	rare														

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo	ecotone		fynbos			
				400	600	800	1000	1200	1400	1600
<b>CRASSULACEAE</b>										
	<i>Crassula atropurpurea</i> (Haw.) D.Dietr. var <i>atropurpurea</i>	LSS	occasional	█	█					
	<i>Crassula capensis</i> (L.) Baill.	PHS	rare	█	█					
	<i>Crassula fascicularis</i> Lam.	PHS	rare			█	█	█	█	
	<i>Crassula nudicaulis</i> L.	PHS	rare	█	█					
	<i>Crassula pubescens</i> Thunb.	DSS	rare				█			
	<i>Crassula subaphylla</i> (Eckl. & Zeyh.) Harv.	LSS	occasional	█	█	█				
	<i>Crassula</i> sp.	DSS	rare	█	█					
	<i>Tylecodon paniculatus</i> (L.f.) Tölken	LSS	frequent	█	█					
<b>CYPERACEAE</b>										
	<i>Ficinia deusta</i> (P.J.Bergius) Levyns	GRA	rare				█			
	<i>Ficinia monticola</i> Kunth	GRA	occasional					█	█	█
	<i>Ficinia nigrescens</i> (Schrad.) J.Raynal	GRA	frequent			█	█	█	█	
	<i>Ficinia oligantha</i> (Steud.) J.Raynal	GRA	frequent			█	█	█	█	
	<i>Ficinia stolonifera</i> Boeck.	GRA	rare				█	█		
	<i>Ficinia</i> sp.	GRA	frequent						█	█
	<i>Tetraria bromoides</i> (Lam.) Pfeiff.	GRA	rare						█	█
	<i>Tetraria fasciata</i> (Rottb.) C.B.Clarke	GRA	rare						█	
	<i>Tetraria flexuosa</i> (Thunb.) C.B.Clarke	GRA	occasional				█			
	<i>Tetraria sylvatica</i> (Nees) C.B.Clarke	GRA	rare							█
	<i>Tetraria ustulata</i> (L.) C.B.Clarke	GRA	frequent		█	█	█	█	█	
<b>EBENACEAE</b>										
	<i>Euclea</i> sp.	MES	rare	█	█					
<b>ERICACEAE</b>										
	<i>Erica anguliger</i> (N.E.Br.) E.G.H. Oliv.	DES	frequent			█	█			
	<i>Erica axillaris</i> Thunb.	LES	frequent						█	
	<i>Erica cerinthoides</i> L.	LES	rare				█	█	█	
	<i>Erica corifolia</i> L.	LES	occasional				█	█	█	
	<i>Erica coccinea</i> L.	LES	rare					█	█	
	<i>Erica embothriifolia</i> Salisb.	LES	rare							█
	<i>Erica equisetifolia</i> Salisb.	LES	frequent						█	

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo		ecotone		fynbos		
				400	600	800	1000	1200	1400	1600
	<i>Erica fastigiata</i> L.	LES	rare							
	<i>Erica lateralis</i> Willd.	LES	rare							
	<i>Erica longifolia</i> Bauer	MES	rare							
	<i>Erica monsoniana</i> L.f.	MES	rare							
	<i>Erica plukenetti</i> L.	LES	occasional							
	<i>Erica sessiliflora</i> L.f.	LES	rare							
	<i>Erica setacea</i> Andrews	DES	rare							
	<i>Erica taxifolia</i> Bauer	LES	rare							
	<i>Erica vestita</i> Thunb.	LES	rare							
	<i>Erica</i> sp.	DES	frequent							
<b>EUPHORBIACEAE</b>										
	<i>Adenocline pauciflora</i> Turcz.	AH	rare							
	<i>Clutia alaternoides</i> L.	LES	rare							
	<i>Clutia laxa</i> Eckl. ex Sond.	LES	rare							
	<i>Clutia polifolia</i> Jacq.	LES	rare							
	<i>Clutia polygonoides</i> L.	DES	rare							
	<i>Euphorbia burmannii</i> E.Mey. ex Boiss.	LSS	frequent							
<b>FABACEAE</b>										
	<i>Aspalathus alpestris</i> (Benth.) R.Dahlgren	LES	rare							
	<i>Aspalathus biflora</i> E.Mey.	LES	occasional							
	<i>Aspalathus cordata</i> (L.) R.Dahlgren	LES	rare							
	<i>Aspalathus fusca</i> Thunb.	LES	rare							
	<i>Aspalathus hirta</i> E.Mey.	LES	rare							
	<i>Aspalathus juniperina</i> Thunb.	LES	occasional							
	<i>Aspalathus leucophylla</i> R.Dahlgren	LES	rare							
	<i>Aspalathus linearis</i> (Burm.f.) R.Dahlgren	LES	rare							
	<i>Aspalathus pachyloba</i> Benth. subsp. <i>macroclada</i> R.Dahlgren	LES	abundant							
	<i>Aspalathus spicata</i> Thunb.	DES	occasional							
	<i>Aspalathus tridentata</i> L.	LES	rare							
	<i>Aspalathus</i> sp.	LES	rare							
	<i>Indigofera porrecta</i> Eckl. & Zeyh.	LES	rare							
	<i>Indigofera</i> sp.	LES	rare							



APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo	ecotone		fynbos			
				400	600	800	1000	1200	1400	1600
	<i>Podalyria</i> sp.	LES	rare							
	<i>Rafnia acuminata</i> (E.Mey.) G.J.Campbell & B.-E. van Wyk	DES	rare							
GENTIANACEAE										
	<i>Sebaea exacoides</i> (L.) Schinz	AH	rare							
GERANIACEAE										
	<i>Geranium incanum</i> Burm.f.	PH	rare							
	<i>Pelargonium alchemilloides</i> (L.) L'Hér.	DES	rare							
	<i>Pelargonium caucalifolium</i> Jacq. subsp <i>convulvulifolium</i>	LES	rare							
	<i>Pelargonium elegans</i> (Andrews) Willd.	DES	rare							
	<i>Pelargonium hermanniifolium</i> (P.J.Bergius) Jacq.	LES	rare							
	<i>Pelargonium incarnatum</i> (L'Hér.) Moench	DES	rare							
	<i>Pelargonium longifolium</i> (Burm.f.) Jacq.	GEO	rare							
	<i>Pelargonium ovale</i> (Burm.f.) L'Hér.	DES	frequent							
	<i>Pelargonium rapaceum</i> (L.) L'Hér	GEO	rare							
	<i>Pelargonium</i> sp.	DES	rare							
HAEMODORACEAE										
	<i>Dilatrix ixiioides</i> Lam.	GEO	rare							
	<i>Wachendorfia</i> sp.	GEO	rare							
HYACINTHACEAE										
	<i>Ornithogalum dubium</i> Houtt.	GEO	rare							
IRIDACEAE										
	<i>Aristea africana</i> (L.) Hoffmanns	PH	rare							
	<i>Aristea juncifolia</i> Baker	PH	rare							
	<i>Aristea racemosa</i> Baker	PH	rare							
	<i>Geissorhiza confusa</i> Goldblatt	GEO	rare							
	<i>Gladiolus debilis</i> Sims	GEO	rare							
	<i>Gladiolus</i> sp.	GEO	rare							
	<i>Ixia longituba</i> N.E.Br. var <i>bellendenii</i> (R.C.Foster) M.P.de Vos	GEO	rare							
	<i>Tritoniopsis lata</i> (L.Bolus) G.J.Lewis	GEO	rare							

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo	ecotone		fynbos			
				400	600	800	1000	1200	1400	1600
LAURACEAE										
	<i>Cassytha ciliolata</i> Nees	HV	occasional		■					
LINACEAE										
	<i>Linum acuticarpum</i> C.M.Rogers	PH	rare		■					
LOBELIACEAE										
	<i>Cyphia volubilis</i> (Burm.f) Willd.	HV	rare				■			
	<i>Lobelia capillifolia</i> (C.Presl) A.DC.	LES	rare		■					
	<i>Lobelia coronopifolia</i> L.	PH	rare		■	■	■	■	■	
	<i>Lobelia jasionoides</i> (A.DC.) E.Wimm.	PH	rare		■	■	■	■	■	■
	<i>Lobelia pinifolia</i> L.	DES	occasional					■		
	<i>Lobelia</i> sp.	DES	rare				■			
MESEMBRYANTHEMACEAE										
	<i>Antimima hamatilis</i> (L.Bolus) H.E.K.Hartmann	DSS	rare	■	■					
	<i>Drosantheum flammeum</i> L.Bolus	DSS	rare			■	■			
	<i>Drosantheum speciosum</i> (Haw.) Schwantes	LSS	frequent	■	■	■				
	<i>Drosantheum</i> sp.	LSS	rare	■	■					
	<i>Erepsia gracilis</i> (Haw.) L.Bolus	LSS	occasional				■	■	■	
	<i>Lampranthus</i> sp.	LSS	rare				■	■	■	
	<i>Phyllobolus splendens</i> (L.) Gerbaulet subsp <i>splendens</i>	LSS	rare	■	■					
	<i>Ruschia caroli</i> (L.Bolus) Schwantes	DSS	occasional	■	■					
	<i>Ruschia lineolata</i> (Haw.) Schwantes	DSS	frequent	■	■					
	<i>Ruschia</i> sp.	LSS	occasional			■	■			
MONTINIACEAE										
	<i>Montinia caryophyllacea</i> Thunb.	MES	frequent	■	■	■				
ORCHIDACEAE										
	<i>Satyrium odorum</i> Sond.	GEO	rare				■			

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient								
				karoo		ecotone		fynbos				
				400	600	800	1000	1200	1400	1600		
OROBANCHACEAE												
	<i>Harveya bolusii</i> Kuntze	PH	rare	█	█	█						
OXALIDACEAE												
	<i>Oxalis depressa</i> Eckl. & Zeyh.	GEO	rare					█				
	<i>Oxalis engleriana</i> Schltr.	GEO	rare				█					
	<i>Oxalis pes-caprae</i> L.	GEO	rare	█	█	█						
	<i>Oxalis</i> sp.	GEO	rare			█						
	<i>Oxalis</i> sp.	GEO	occasional	█	█	█						
POACEAE												
	<i>Aristida diffusa</i> Trin.	GRA	frequent				█	█	█			
	<i>Bromus hordeaceus</i> L. subsp <i>molliformis</i> (J.Lloyd) Maire & Weiller	GRA	rare	█	█	█						
	<i>Cymbopogon pospischilii</i> (K.Schum.) C.E. Hubb.	GRA	rare			█						
	<i>Ehrharta capensis</i> Thunb.	GRA	occasional	█	█	█	█	█				
	<i>Ehrharta delicatula</i> (Nees) Stapf	GRA	occasional	█	█	█						
	<i>Ehrharta ottonis</i> Kunth ex Nees	GRA	rare						█			
	<i>Ehrharta ramose</i> (Thunb.) Thunb.	GRA	frequent								█	█
	<i>Ehrharta rehmannii</i> Stapf subsp <i>rehmannii</i>	GRA	rare						█			
	<i>Ehrharta rupestris</i> Nees ex Trin.	GRA	rare					█				
	<i>Ehrharta thunbergii</i> Gibbs Russ.	GRA	rare				█	█				
	<i>Merxmuellera arundinacea</i> (P.J.Bergius) Conert	GRA	rare	█	█	█						
	<i>Merxmuellera stricta</i> (Schrud.) Conert	GRA	rare			█						
	<i>Pentameris macrocalycina</i> (Steud.) Schweick.	GRA	occasional							█	█	█
	<i>Pentaschistis colorata</i> (Steud.) Stapf	GRA	rare							█		
	<i>Pentaschistis curvifolia</i> (Schrud.) Stapf	GRA	occasional								█	█
	<i>Pentaschistis eriostoma</i> (Nees) Stapf	GRA	frequent				█	█				
	<i>Pseudopentameris macrantha</i> (Schrud.) Conert	GRA	rare					█				
	<i>Schismus barbatus</i> (Loefl. ex L.) Thell.	GRA	frequent	█	█	█						
	<i>Stipagrostis zeyheri</i> (Nees) De Winter	GRA	rare								█	
	<i>Tribolium hispidium</i> (Thunb.) Desv.	GRA	rare				█	█				
POLYGALACEAE												
	<i>Muraltia heisteria</i> (L.) DC.	LES	occasional				█	█				

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient								
				karoo		ecotone		fynbos				
				400	600	800	1000	1200	1400	1600		
	<i>Muraltia muraltoides</i> (Eckl. & Zeyh.) Levyns	DES	rare	■								
	<i>Polygala fruticosa</i> P.J.Bergius	LES	frequent		■							
	<i>Polygala scabra</i> L.	LES	rare	■								
PROTEACEAE												
	<i>Leucadendron lauroleum</i> (Lam.) Fourc.	MES	occasional					■	■	■	■	
	<i>Leucadendron nervosum</i> E.Phillips & Hutch	MES	rare					■	■	■	■	
	<i>Leucadendron salignum</i> P.J.Bergius	LES	frequent			■	■	■	■	■	■	
	<i>Leucospermum calligerum</i> (Salisb. ex Knight) Rourke	LES	rare			■	■	■	■	■	■	
	<i>Paranomus dispersus</i> Levyns	LES	rare			■	■	■	■	■	■	
	<i>Protea amplexicaulis</i> (Salisb.) R.Br.	LES	rare					■	■	■	■	
	<i>Protea humiflora</i> Andrews	LES	abundant					■	■	■	■	
	<i>Protea laurifolia</i> Thunb.	MES	rare					■	■	■	■	
	<i>Protea lorifolia</i> (Salisb. ex Knight) Fourc.	LES	occasional					■	■	■	■	
	<i>Protea magnifica</i> Link	LES	occasional					■	■	■	■	
	<i>Protea neriifolia</i> R.Br.	MES	rare					■	■	■	■	
	<i>Protea repens</i> (L.) L.	MES	abundant					■	■	■	■	
	<i>Serruria gremialis</i> Rourke	DES	occasional					■	■	■	■	
PTERIDACEAE												
	<i>Cheilanthes contracta</i> (Kuntze) Mett. ex Kuhn	PH	rare					■				
RESTIONACEAE												
	<i>Askidiosperma paniculata</i> (Rottb.) Desv.	GRA	occasional									■
	<i>Cannomois nitida</i> (Mast.) Pillans	GRA	occasional						■	■	■	■
	<i>Cannomois scirpoides</i> (Kunth) Mast.	GRA	occasional					■	■	■	■	■
	<i>Ceratocaryum argenteum</i> Kunth	GRA	rare					■	■	■	■	■
	<i>Elegia filacea</i> Mast.	GRA	frequent									■
	<i>Elegia grandis</i> (Nees) Kunth	GRA	rare									■
	<i>Elegia racemosa</i> (Poir.) Pers.	GRA	abundant									■
	<i>Elegia stokoei</i> Pillans	GRA	frequent					■	■	■	■	■
	<i>Hypodiscus albo-aristatus</i> (Nees) Mast.	GRA	occasional									■
	<i>Hypodiscus argenteus</i> (Thunb.) Mast.	GRA	frequent									■
	<i>Hypodiscus aristatus</i> (Thunb.) C.Krauss	GRA	frequent									■

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient																
				karoo		ecotone		fynbos												
				400	600	800	1000	1200	1400	1600										
	<i>Hypodiscus laevigatus</i> (Kunth) H.P.Linder	GRA	occasional																	
	<i>Hypodiscus squamosus</i> Esterh.	GRA	frequent																	
	<i>Hypodiscus striatus</i> (Kunth) Mast.	GRA	occasional																	
	<i>Ischyrolepis capensis</i> (L.) H.P.Linder	GRA	frequent																	
	<i>Ischyrolepis curviramis</i> (Kunth) H.P.Linder	GRA	frequent																	
	<i>Ischyrolepis gaudichaudiana</i> (Kunth) H.P.Linder	GRA	rare																	
	<i>Ischyrolepis sieberi</i> (Kunth) H.P.Linder	GRA	frequent																	
	<i>Restio bolusii</i> Pillans	GRA	occasional																	
	<i>Restio filiformis</i> Poir.	GRA	frequent																	
	<i>Restio triticeus</i> Rottb.	GRA	frequent																	
	<i>Thamnochortus fruticosus</i> P.J.Bergius	GRA	rare																	
	<i>Thamnochortus lucens</i> (Poir.) H.P.Linder	GRA	rare																	
	<i>Willdenowia teres</i> Thunb.	GRA	rare																	
	<i>Willdenowia</i> sp.	GRA	rare																	
RHAMNACEAE																				
	<i>Phylica vulgaris</i> Pillans var <i>major</i> Pillans	DES	rare																	
	<i>Phylica</i> sp.	LES	rare																	
	<i>Phylica</i> sp.	LES	occasional																	
ROSACEAE																				
	<i>Cliffortia crenata</i> L.f.	MES	frequent																	
	<i>Cliffortia juniperina</i> L.f.	LES	rare																	
	<i>Cliffortia pungens</i> C.Presl	LES	frequent																	
	<i>Cliffortia ruscifolia</i> L.	LES	rare																	
	<i>Cliffortia sericea</i> Eckl. & Zeyh.	LES	rare																	
	<i>Cliffortia</i> sp.	LES	rare																	
RUBIACEAE																				
	<i>Anthospermum aethiopicum</i> L.	LES	rare																	
	<i>Anthospermum galioides</i> Rchb.f.	DES	rare																	
	<i>Anthospermum</i> sp.	DES	rare																	
	<i>Galium tomentosum</i> Thunb.	LES	frequent																	

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo		ecotone		fynbos		
				400	600	800	1000	1200	1400	1600
<b>RUTACEAE</b>										
	<i>Adenandra uniflora</i> (L.) Willd.	LES	rare				■	■		
	<i>Adenandra villosa</i> (P.J.Bergius) Licht. ex Roem. & Schult.	LES	rare						■	
	<i>Agathosma glandulosa</i> (Thunb.) Sond	LES	occasional		■	■	■	■		
	<i>Agathosma serphyllacea</i> Licht. ex Roem. & Schult.	LES	rare				■	■		
	<i>Agathosma stipitata</i> Pillans	LES	rare				■			
	<i>Diosma</i> sp.	DES	rare						■	
<b>SANTALACEAE</b>										
	<i>Thesium carinatum</i> A.DC.	DS,P	occasional				■	■	■	■
	<i>Thesium commutatum</i> Sond.	DS,P	rare			■		■	■	■
	<i>Thesium patulum</i> A.W.Hill	PH,P	rare	■	■	■				
	<i>Thesium spicatum</i> L.	DS,P	rare				■			
	<i>Thesium strictum</i> P.J.Bergius	LS,P	rare		■					
	<i>Thesium</i> sp.	LS,P	occasional			■	■	■		
<b>SAPINDACEAE</b>										
	<i>Dodonea viscosa</i> Jacq.	MES	occasional	■	■	■				
<b>SCROPHULARIACEAE</b>										
	<i>Microdon dubius</i> (L.) Hilliard	LES	rare				■	■		
	<i>Pseudoselago serrata</i> (P.J.Bergius) Hilliard	LES	rare						■	
	<i>Selago parvibractea</i> Hilliard	LES	occasional			■				
	<i>Sutera caerulea</i> (L.f.) Hiern	AH	rare	■	■	■				
	<i>Sutera uncinata</i> (Desr.) Hilliard	LES	rare	■	■	■				
<b>STERCULIACEAE</b>										
	<i>Hermannia angularis</i> Jacq.	LES	rare			■	■	■		
	<i>Hermannia aspera</i> J.C.Wendl.	LES	rare			■	■	■		
	<i>Hermania rudis</i> N.E.Br.	LES	frequent			■	■	■		
<b>THYMELEACEAE</b>										
	<i>Lachnaea pudens</i> Beyers	LES	rare				■			

APPENDIX II continued

Family	Species and author	Growth form	Abundance	Altitudinal range on gradient						
				karoo		ecotone		fynbos		
				400	600	800	1000	1200	1400	1600
	<i>Passerina obtusifolia</i> Thoday	LES	occasional	■		■				
	<i>Struthiola myrsinites</i> Lam.	LES	rare					■		
VISCACEAE										
	<i>Viscum</i> sp.	S,P	rare	■						
ZYGOPHYLLACEAE										
	<i>Zygophyllum fulvum</i> L.	LES	rare	■		■		■		

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